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## Twenty-first European Conference on Visual Perception Oxford, England 24–28 August 1998

### Abstracts

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## MONDAY

### THE PERCEPTION LECTURE

◆ **With colour in mind**

A Cowey (Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford OX1 3UD, UK; fax: +44 1865 310 447; e-mail: alan.cowey@psy.ox.ac.uk)

Focal brain damage can selectively impair colour naming, the use of colour words, short-term memory for colours, and perhaps colour constancy. The focus of the effective lesions, as revealed by structural magnetic resonance imaging (MRI), can now be correlated with extrastriate visual areas as revealed by functional MRI. However, by far the most striking disorder of colour processing caused by brain damage is cerebral achromatopsia, in which total loss of the perceptual experience of hue follows destruction of ventro-medial cortex, centred on the collateral sulcus and involving the rostral lingual and caudal fusiform gyri. Recent functional neuroimaging experiments and behavioural experiments in monkeys indicate that cerebral achromatopsia follows destruction of an area called V4 and V8 in the human brain and possibly analogous areas called TEO and TE in monkeys. The simplest explanation for cerebral achromatopsia is that the lesion destroys all extrastriate representation of the colour opponent, P, pathways, and that the puzzling features of cerebral achromatopsia, such as the subject's ability to detect chromatic boundaries despite not perceiving the hues that create them, reflect the sensitivity to contours of the intact broad-band and colour-blind M pathway. But recent studies of spectral sensitivity, detection of coloured targets in random luminance masking, discrimination of the apparent direction of chromatic gratings, saccadic eye movements to coloured targets, and unimpaired motion slowing with isoluminant chromatic gratings all suggest that in cerebral achromatopsia signals generated by wavelength differences are still processed cortically. It is the experience of hue itself that has been lost. Does this make cerebral achromatopsia like 'colour blindsight', as recently proposed? Almost certainly not, because the achromatopsic subject is always aware of what he is discriminating. The puzzle is why it is never coloured.

## TUESDAY

### ORAL PRESENTATIONS

#### MOTION MECHANISMS I

◆ **Motion processing: from elementary signals to global organisation**

O Braddick (Department of Psychology, University College London, Gower Street, London WC1E 6BT, UK; fax: +44 171 380 7576; e-mail: ucjtsol@ucl.ac.uk)

Twenty years ago, the main focus of visual motion research was on the nature and limits of the elementary motion-detecting mechanism(s). Newer work has been concerned with processes which integrate elementary motion signals for a variety of perceptual and visuomotor purposes. Evidence from primates, human neuropsychology, and functional imaging points to the role of extrastriate areas in this integrative processing. I discuss a number of aspects of integrative motion processing, including: (i) the detection of coherent global motion in the face of noise; (ii) the parsing of velocity distributions in space, to yield moving objects and surfaces, including transparency; (iii) interactions between local motions and between global motions in different directions; (iv) global motion processing as a signature of the dorsal cortical stream.

◆ **Computing motion in the presence of static pattern**

A Johnston, P W McOwan, C P Benton (Department of Psychology, University College London, Gower Street, London WC1E 6BT, UK; fax: +44 171 436 4276; e-mail: a.johnston@ucl.ac.uk)

In natural scenes we are often faced with the problem of computing motion when moving and static patterns are additively combined, as when viewing a scene through a smeared car window. In general, in these instances of motion transparency, the perception of motion is little affected by the presence of static pattern. However, most models of motion perception are seriously compromised by the addition of static pattern. Subtraction between neurons tuned to opposite directions of motion, as in the opponent-energy stage of the motion-energy model, should alleviate the effects of superimposed static pattern but the contrast normalisation stage of this model is sensitive to static pattern and thus the final computation can be compromised. Gradient methods typically deliver the component of motion in the direction of the image gradient which may well be dominated by the static pattern rather than the image motion. The inclusion of a band-pass or high-pass temporal filter prior to motion analysis—another possible strategy—would reduce sensitivity to slow movement. An approach to motion computation based on calculating the change

in image luminance within an image region and the flow of luminance over the boundary of the region in a specified temporal interval is described and generalised to deal with more complex patterns. This method is found to be robust to the addition of static pattern.

◆ **Spatiotemporal effects and individual differences in motion induction**

A Gorea, L Fyda (Laboratoire de Psychologie Expérimentale, Université René Descartes et CNRS, 28 rue Serpente, F 75006 Paris, France; fax: +33 1 40 51 70 85; e-mail: gorea@ext.jussieu.fr)

Motion induction was assessed as a function of (i) the temporal delay between test and inducers and (ii) the position of the latter relative to the directional axis of the test, ie displaced along or orthogonal to it. Temporal delay (SOA) effects should reveal the temporal course of the excitatory/inhibitory processes underlying motion induction. Dependence on the spatial relationship referred to would bear on the (an)isotropy of the underlying motion receptive field (MRF).

Observers had to specify the direction of a central quasi-counterphase horizontal grating whose ambiguous direction could be biased by manipulating the contrast balance between its two opposite-direction components while keeping their geometrical mean at 25%. This balance was monitored by an adaptive procedure set to converge on the 50% up/down responses. Two or four non-ambiguously drifting flankers (80% contrast) extended the test pattern vertically (parallel flankers), horizontally (collinear flankers), or both (parallel + collinear). Test and flankers were matched in spatial frequency (1 cycle deg<sup>-1</sup>), speed (2 or 10 deg s<sup>-1</sup>), size (1 or 4 deg), and duration (500 ms). SOA was varied between -666 ms and +500 ms.

Surprisingly, observers split up into two groups showing either motion contrast, or motion assimilation under most of the experimental conditions. Motion contrast decayed more rapidly for positive than for negative SOAs implying weaker backward than forward inhibition from the surround. Collinear and parallel configurations yielded equivalent effects, suggesting an isotropic MRF; and about twice weaker than their combination, supporting the notion of a linear MRF. Motion contrast increased with speed but, curiously, did not change into assimilation for 1 deg stimulus sizes. 'Motion assimilation observers' behaved much less consistently suggesting the involvement of fluctuating response strategies. Motion induction might not be a purely visual phenomenon.

◆ **Areas within and beyond the visual cortex differentially activated by coherent visual motion and dynamic noise**

J M D O'Brien, O J Braddick, T Hartley, J Atkinson, J Wattam-Bell, R Turner\* (Visual Development Unit, Department of Psychology, University College London, Gower Street, London WC1E 6BT, UK; † Wellcome Department of Cognitive Neurology, Institute of Neurology, University College London, 12 Queen Square, London WC1N 3BG, UK; fax: +44 171 380 7576; e-mail: justin.o'brien@ucl.ac.uk)

Detection of coherent motion vs noise is increasingly being used as a way of investigating global motion processing. To localise the brain mechanisms involved in this performance, fMRI techniques were used to compare brain activation during viewing of coherently moving random dots with that during viewing spatially similar dynamic noise. Rates of reversal of coherent motion and coherent-motion velocities (5 vs 20 deg s<sup>-1</sup>) were also compared. Differences in local activation between conditions were analysed by statistical parametric mapping.

Greater activation by coherent motion compared to noise was found in areas thought to be human V5 and V3/V3A, but not in V1. In addition, there were foci of activation outside classically visual areas: deep in the superior temporal sulcus; deep in the intraparietal sulcus; and in the region of corpus callosum/cingulate cortex. Thus, coherent-motion information, presumably transmitted through the dorsal visual pathway, has distinctive effects over a wide range of brain structures. The rate of motion reversal showed only weak effects in motion-sensitive areas.

In two out of three subjects, V1 was better activated by noise than by coherent motion, possibly reflecting activation of neurons with a wider range of motion selectivities. This was at a more anterior location in the comparison with the faster velocity, suggesting that 20 deg s<sup>-1</sup> motion is beyond the velocity range of V1 representation of central visual field [Supported by MRC Grant G79 08 507 and the Wellcome Trust.]

◆ **What is noise for the motion system: a fMRI study**

M O Scase, M A Horsfield†, D J Wilcock§, W S S Karwatowski# (Department of Human Communication, De Montfort University, Leicester LE1 7SU, UK; † Department of Medical Physics, Leicester University, Leicester LE1 5WW, UK; § Department of Radiology, Leicester University, Leicester LE1 5WW, UK; # Department of Ophthalmology, Leicester Royal Infirmary, Leicester LE1 5WW, UK; fax: +44 116 257 7708; e-mail: mscase@dmu.ac.uk)

Random-dot kinematograms are popular stimuli in psychophysical research as a performance measure of visual motion sensitivity. Investigators have, however, defined in two main ways how

'random' dots should move: dots might be moved in a random direction with a random displacement—'random position noise', or in a random direction with a fixed displacement—'random walk noise'. Motion coherence thresholds measured with these noise types are similar (Scase et al, 1996 *Vision Research* **36** 2579–2586) although the stimuli appear different.

We assessed whether these noise types excited different brain regions revealed by functional magnetic resonance imaging (fMRI). Stimuli consisted of blocks where subjects viewed a blank screen for 16 s ('off' condition) followed by 16 s of moving random dots ('on' condition). Separate experimental runs were performed for random position noise and random walk noise. The display subtended 11.3 deg by 8.9 deg; dot density was 8 dots deg<sup>-2</sup> and dot displacement for random walk noise equivalent to 6.6 deg s<sup>-1</sup>. Haemodynamic brain changes were measured by fMRI techniques on five subjects. Activation differences were analysed by times-series regression modelling. Random position noise and random walk noise both activated occipital cortex. Direct comparison of the two noise types with stimuli where the off condition was random position noise and the on condition was random walk noise revealed greater extrastriate activation with random walk noise (probably corresponding to human V5). We conclude that although motion-coherence thresholds measured with these two noise types are similar, different brain areas are being activated.

#### HIGHER-ORDER MOTION

##### ◆ First-order, second-order, and third-order motion systems

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This focussed review of computational theories of the psychophysics of human motion-direction discrimination begins in the 1980s with the introduction of Fourier, Reichardt, and motion-energy models by Watson and Ahumada, van Santen and Sperling, Adelson and Bergen, and others for what is now regarded as first-order motion.

Exceptions to first-order motion theories were noted by Braddick, Cavanagh, Derrington, Koenderink, and many others. Chubb and Sperling (1988) used drift-balanced stimuli to derive a formal theory to differentiate Fourier from non-Fourier motion phenomena (now called first-order and second-order motion). Lu and Sperling (1995) proposed a functional architecture of motion perception that further incorporated a third-order motion system.

All three motion systems receive an input that is a function of  $x$ ,  $y$ ,  $t$ , and all utilise a similar motion-energy algorithm. The inputs are: for first-order, point-contrast (the deviation of point luminance from mean luminance); for second-order, local feature density (the output of circularly symmetric 'texture grabbers'); for third-order, local salience (whether  $x$ ,  $y$ ,  $t$  is figure or ground).

Besides the type of stimuli processed, characteristics that differentiate the systems are: temporal cutoff frequency (first and second 10–12 Hz, third, 3–5 Hz), eye of origin (first and second are monocular, third is indifferent to alternation of stimuli between eyes); and the selective effects of brain lesions, gain-control, motion adaptation, attention (influences only third order), and which nonmotion tasks interfere with motion perception.

A phase independence paradigm in which superimposed same-direction motion stimuli cancel each other when they are processed in the same motion system is used to establish system independence. Finally, successful resolutions of some challenges to the three-systems theory are considered as well as its relation to the subsequent presentations.

##### ◆ Direction-specific modification of first-order-motion-evoked optokinetic eye movement by second-order motion

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A previous study (Harris and Smith, 1992 *Visual Neuroscience* **9** 565) has suggested that second-order motion is ineffective at driving optokinetic nystagmus (OKN) when presented alone. We recently reported (Harris and Smith, 1997, ARVO) that second-order motion can nonetheless attenuate the optokinetic response to simultaneously presented first-order motion moving in the opposite direction. Is this influence limited to attenuation or can OKN also be facilitated by second-order motion?

Dynamic random noise was used as a carrier for first-order and second-order drifting gratings (13.4 deg s<sup>-1</sup>; 0.25 cycle deg<sup>-1</sup>; 64 deg × 48 deg screen viewed at 28.5 cm). Second-order motion of a grating was defined by modulation of the flicker frequency of noise pixels of constant contrast (50%). Simultaneously a first-order, luminance-defined grating (13.4 deg s<sup>-1</sup>; variable contrast from 4%–50%) was moved in either the opposite, same, or orthogonal direction. Eye movements were

recorded by video-oculography from seven subjects as they tried to maintain their gaze straight ahead. The gain (eye velocity/stimulus velocity) of first-order-motion-evoked OKN increased with contrast, as expected. The presence of flicker-defined second-order motion in the opposite direction attenuated this OKN to close to zero below a first-order contrast of 25% although it had little effect at higher contrasts. When first-order and second-order motion were in the same direction, there was an enhancement of the OKN response in the same range of first-order contrasts. Orthogonal movement had no consistent effect. We conclude that although second-order motion is ineffective at evoking OKN it can modify the optokinetic response to simultaneously presented first-order motion.

◆ **Shape from linear but not nonlinear motion**

R F Hess, L Ziegler (McGill Vision Research, Department of Ophthalmology, McGill University, 687 Pine Avenue West, H4-14, Montréal, Québec H3A 1A1, Canada; fax: +1 514 843 1691; e-mail: rhess@bradman.vision.mcgill.ca)

Both motion and stereopsis are subserved by linear as well as nonlinear (second-order) mechanisms. We have recently argued that while nonlinear mechanisms can signal both signed and unsigned local depth, they nonetheless make no contribution to shape-from-depth processing [Ziegler and Hess, 1997 *Investigative Ophthalmology & Visual Science* 38(4) S906]. Is the same true for shape-from-motion?

We used a 2AFC paradigm where each trial consisted only of the motion (linear or nonlinear) of a random array of micropatterns. The screen location of each micropattern was as if from a point on a fixed surface, shaped as a sinusoid in depth. Two frames simulated viewer motion left and right. Observers had to detect monocularly orientation of the shape, either left or right oblique. Local linear motion was obtained by the displacement of Gaussian blobs. Nonlinear motion was achieved by either displacing only the contrast envelope of Gabor micropatterns or by also alternating their carrier frequency ( $\times 4$ ) between frames. Judgments were made over a wide range of simulated corrugation depths.

Shape perception was effortless (100% correct) between the well-defined limits of  $D_{\min}$  and  $D_{\max}$  when defined by linear motion. It was impossible, however, when defined by either type of local nonlinear motion: performance levels were at chance across the entire range of depths. Surface shape, defined either by disparity or by motion, is luminance-based, that is not supported by the nonlinear processing stream.

◆ **Dichoptically cancelled pattern-motion is visible**

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A monocularly viewed figure composed of slashes (/) against a ground composed of back-slashes (\) can be *dichoptically cancelled* by simultaneously presenting a complementary figure composed of back-slashes against a ground composed of slashes to the other eye. In brief displays both figure and ground appear as Xs, yet the figure can be located [Kolb and Braun, 1995 *Nature (London)* 377 336–338; Morgan, Mason, and Solomon, 1997 *Nature (London)* 385 401–402]. Here we report that monocularly viewed motion of a pattern defined by slashes and back-slashes is visible even when dichoptically cancelled by a pattern of back-slashes and slashes in the other eye. Thus the visual system can extract motion information between stages of oriented filtering and binocular combination.

◆ **On the combination of local motion signals in motion-defined gratings**

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Gratings that are defined by motion are powerful tools for investigating how local motion signals are combined in the human visual system, similar to luminance-defined gratings in the study of spatial vision. To produce such gratings, local motion signals are usually generated by the continuous displacement of randomly distributed dark and bright dots occurring with equal probability, which leads to a broad spatial-frequency spectrum. We performed experiments with sparse dot patterns, in which the lifetime of each dot, ie the duration of each individual trajectory contributing to the motion-defined pattern, as well as the spatial-frequency content of the local motion signals, can be controlled.

In our experiments, sets of randomly distributed dots moved in a vertical direction. The speed of each dot was determined by a cosine function producing motion-defined sinusoidal gratings, which could have a variable spatial-frequency orientation and direction of motion. The dots moved along continuous trajectories throughout the complete sequence, or were replaced

after four frames ('limited lifetime'). The subjects had to decide in a 2AFC paradigm whether they saw horizontal or vertical gratings (orientation task), or whether a vertical grating was moving to the right or to the left (direction discrimination). Our initial experiments indicate that performance is decreased by reducing the number of frames, as well as by limiting dot lifetime. When the dot density is increased, discrimination performance improves, without a clear shift of spatial-frequency tuning. These results suggest that the integration of motion information along the trajectory of an individual dot, as well as between dots, in space and in time, determines the visibility of motion-defined gratings.

#### EYE MOVEMENTS AND MECHANISMS

##### ◆ Comparison of pupil responses in man and monkey

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Pupil responses to increments/decrements in light flux and to equivalent illusory stimuli perceived to be brighter or dimmer than the surrounding background have been measured and compared in six human subjects and two rhesus monkeys. The illusory stimuli (O'Brian – Cornsweet illusory patterns) were generated by using boundary luminance gradients that do not cause an overall increment/decrement in light flux. Differences between increments and decrements and the effect of flash contrast and duration have also been investigated. For each stimulus condition we have averaged 36 traces. The stimuli were uniform discs of 6-deg radius presented centred on the fovea or peripheral annuli of mean radius 7 deg of equal light flux change.

The averaged pupil responses were then scaled for equal response amplitude and compared for differences in response latency. The results show that for the level of light adaptation employed, pupil response latencies remain independent of pupil constriction amplitude for all contrasts and flash durations investigated. Similar responses were obtained for the rhesus monkeys, but the corresponding pupil onset response latencies were found to be some 80 to 100 ms shorter and the recovery from constriction was more rapid than equivalent human responses. Comparison of pupil responses obtained for foveal and peripheral stimuli equated for light flux change show identical response latencies and amplitudes. Pupil light-reflex responses were also absent when illusory bright or dark discs were employed. The results suggest that when large, achromatic, uniform flashes are employed, the principal parameter that drives the pupil light-reflex response is the light-flux change.

##### ◆ Spatial localisation of double flashes during smooth-pursuit eye movement II: Action-oriented response

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Observers pursued a dot moving from left to right at  $5.6 \text{ deg s}^{-1}$  while an LED first produced a brief red flash and 400 ms later produced a second green flash. On separate trials observers were asked to position their right index finger to the perceived location of either the first or the second flash. Consistent with their perception (see part I), observers pointed to distinct locations for the two flashes. Intriguingly, observers placed their finger on the same side of the LED, but at a considerably greater distance from the LED for the first flash than for the second.

Since observers responded after the second flash, the elapsed time between the first flash and the response was greater than that between the second flash and the response. To test whether the elapsed time between the flash and response was critical, observers were presented with only one flash and were asked to respond with their finger pointing either immediately upon seeing the flash, or to wait till an audible click (50, 100, 200, or 400 ms after the flash) was presented. As predicted, the later the click occurred, the larger was the separation between the actual location of the flash and the finger position.

Recently, Nijhawan et al (1998 *Cognitive Neuroscience Society Abstracts*) reported that when an LED attached to the observer's invisible finger is flashed once, while the observer pursues a moving dot, the flash appears shifted in the direction of pursuit relative to proprioceptive finger position. We claim that this method produces a displacement of the flash that is an absolute minimum as it is due to neural delays in the processing of the flash. Thus, these displacement effects depend not only on the time that elapses before the flash is visible but also afterwards.

- ◆ **A hybrid system for scene analysis with saccadic eye movements: learning of feature relations**  
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We propose a model for a higher-level cognitive stage of scene analysis with saccadic eye movements. This model is embedded in a research project, in which a complete sensorimotor system for saccadic eye movements is investigated. The suggested model is derived from a combination of a knowledge-based approach with a preprocessing stage which is based on the behaviour of linear and nonlinear neurons in the visual cortex.

In contrast to the common view in 'computational vision', the knowledge representation is determined not only by afferent image features, but also by the motor action, ie by the eye movements. The elementary unit of representation corresponds to a single eye movement, and is defined by the presaccadic image feature, the postsaccadic feature, and its relative position to the former one measured on a qualitative scale. Each individual eye movement thus provides a certain degree of evidence for the present scene.

The resulting scene-analysis system is able to learn links between eye movements and scenes, builds up knowledge about already analysed scenes, and calculates in each step the eye movement which has to be made in order to reach a maximum of information about the scene. The information gain is calculated with a parallel strategy which is suitable for adaptive reasoning. The output of the system is a fixation sequence and a hypothesis about the scene. The results of our system are compared with results of psychophysical experiments on saccadic eye movements.

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- ◆ **Gaze accuracy, under natural conditions, declines as the clarity of vision improves**  
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We explored the domain first visited by Epelboim et al (1995 *Vision Research* 35 3401–3422; 1997 *Vision Research* 37 2597–2607) in which gaze was measured under natural conditions with the Maryland Revolving Field Monitor. Its goal was to determine how the clarity of vision affects manipulations requiring considerable visuomotor skill.

The gaze of an unrestrained subject, RMS (one of the authors), who at 70+ years of age no longer accommodates to nearby objects, was recorded with exceptional accuracy as he tapped 4 LEDs with a 1.5 cm long by 2 mm diameter rod cemented to a thimble worn on his index finger. This tapping task was hard. Its difficulty was varied by tapping: (a) with uncorrected vision, leaving vision fused, but blurred; (b) with contact lenses, permitting clear vision very near the eyes (10–20 cm), or relatively far, but within arms' reach (25–50 cm). The 'near' contacts made RMS a myope. He brought his eyes very near the targets as he tapped. The 'far' targets afforded clear vision within arms' reach. Mean cyclopean gaze accuracy was 3 deg without optical correction, 4 deg with 'far', and 6 deg with 'near' contacts. Correcting vision facilitated performance: dwell times before taps fell from 2.25 to 1.9 s.

Seeing better makes hard-tapping easier but gaze *less* accurate. So, gaze-accuracy is adjusted to match task demands, no better. These sensible, but unexpected, findings are under study in a second presbyope and in a young myope wearing contacts preventing clear vision beyond 20 cm.

- ◆ **Influence of occlusion and depth cues in saccadic localisation**  
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The perceptual system can infer the layout and shape of surfaces in 3-D from cues in the monocular image. Does the oculomotor system have access to a representation of these perceptually inferred surfaces?

In a series of experiments we studied the effect of occlusion and perspective cues on the saccadic localisation of simple shapes. Targets were triangles, quadrilaterals, and simple curvilinear shapes. Subjects tried to saccade to the perceptually inferred shape behind an occluder. Saccades directed to a full, unoccluded triangle landed near the centre of gravity. Saccades directed to the inferred triangle behind the occluder landed near the centre of the visible fragment, even though perceptually it appeared as a full triangle behind occluders. Contour completion cues were more effective: saccades to curvilinear blob fragments separated by occluders landed near the centre of the completed blob. Landing positions for quadrilaterals were biased to the centre of

gravity of the surface inferred in depth. We conclude that the saccadic system is sensitive to some but not all cues that recover surface structure. The visual representations that guide saccades may be more sophisticated than often assumed, but not identical to perceptual representation.

#### CONTRAST DETECTION AND ADAPTATION

##### ◆ **Template learning model predicts effects of fixed versus random noise in visual signal detection**

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In two-interval forced-choice detection, using the same (Twin) noise sample in both intervals, but changing it on each trial, elevates thresholds compared to always using the same (Fixed) noise sample (Beard and Ahumada, 1997 *Optical Society of America Annual Meeting, Technical Digest Series 11*). Our image discrimination models (Ahumada and Beard, 1997 *Journal of the Optical Society of America A* **14** 2471–2476) do not predict this difference. Watson et al (1997 *SPIE Proceedings* **3016** 1–11) refer to this difference as ‘entropy’ masking, relating it to the degree to which the mask is unknown. We present a template learning model similar to that used for auditory signal recognition (Jakowatz et al, 1961, in *Information Theory* Ed. C Cherry). On each trial, the observer correlates templates with the signals to determine the response and updates the templates with the signals. In addition to internal sensory noise, the model includes memory/decision noise (McIlhagga and Pääkkönen, 1997 *Perception* **26** Supplement, 3). The model predicts the difference between Fixed and Twin noise conditions and the additional threshold elevation that results from using a new random sample for every stimulus.

##### ◆ **Contrast detection and positional coding of collinear lines**

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Various psychophysical studies have shown that the contrast detection of line targets is facilitated by spatially separated, collinear, suprathreshold inducing lines or edges. This particular case of detection facilitation is now referred to as ‘spatial facilitation’ (Yu and Levi, 1997 *Vision Research* **37** 3117–3127; Wehrhahn and Dresch, 1998 *Vision Research* **38** 423–428). It is still unclear whether the visual mechanisms underlying spatial facilitation with collinear stimuli are connected to those underlying the visual coding of the relative spatial position of the target line with regard to the inducing line.

We approached this question in psychophysical experiments with human observers measuring (i) the effect of the lateral separation of a line target and two collinear inducing lines on spatial facilitation, and (ii) the positional threshold at which a lateral displacement (to the left or to the right) of one of two inducing lines is detected. The length of the line stimuli, their spatial separation, and the exposure duration (30 ms) were identical in the two tasks.

The results show that spatial facilitation disappears at a lateral separation between target and inducers that corresponds exactly to the spatial position where a lateral displacement between the two inducing lines is detected. The finding suggests that spatially induced detection facilitation and positional acuity have common underlying mechanisms. The extent to which these mechanisms may involve long-range interactions between cortical detectors is discussed.

##### ◆ **The effect of photon noise on increment detection thresholds**

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The theory that increment thresholds in vision are elevated by the randomness of photons generated by the adaptation field (‘photon noise’) was advanced by Krauskopf and Reeves (1980 *Vision Research* **20** 193–196) and by Reeves, Wu, and Schirillo (1998 *Vision Research* **38** 691–702). This theory, which is supported indirectly by studies of retinal-ganglion-cell discharge variability in cats (Troy and Robson, 1969 *Visual Neuroscience* **9** 535–553), was elaborated in the present study to include photon noise from the test. Noise from the 200 ms, 1.3 deg test was minimal in the standard increment detection task (control), but was appreciable in a grating perception task. Field noise was varied by varying field intensity from 0 to 4 log td. Thresholds were measured on the steady adapting field and 0.2 s after the start of dark adaptation. We conclude that (i) visual gain is inverse with the square-root of field intensity, (ii) thresholds are otherwise limited by noise from the field and the test, and (iii) the drop in threshold at the start of dark adaptation can be explained by the abolition of photon noise from the field, without having to assume any recovery in visual gain during this short period at all.

◆ **Contrast adaptation and visual search for colour**

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Contrast adaptation strongly affects colour perception by reducing sensitivity to the ambient stimulus, yet the functional consequences of these sensitivity changes are poorly understood.

We examined the role of contrast adaptation in a naturalistic 'foraging' task designed to mimic the problem of finding a fruit among foliage. A circular 0.5-deg target was presented against a dense background of ellipses. The luminances and chromaticities of the ellipses were chosen from a single colour–luminance axis (eg bright red to dark green), or were drawn from empirical colour distributions measured for natural outdoor scenes (which typically show a strong bias along specific colour–luminance axes). The targets included a wide range of contrasts and colour–luminance directions. Reaction times were measured for detecting the location of the target, which was presented at random positions to the left or right. Adaptation effects were assessed by comparing search times before and/or after subjects viewed successive random samples of the background distribution or a distribution that varied along a colour–luminance axis orthogonal to the background distribution. Search times varied from high values for targets within the distribution (where they are detected by a serial search for form) to asymptotically low values for targets far removed from the distribution (where targets pop out). For targets yielding intermediate reaction times, adaptation to the appropriate (background) axis facilitates search, while adaptation to the inappropriate (orthogonal) background impedes search. Contrast adaptation may therefore function to increase the salience of novel stimuli by partially discounting the ambient background.

◆ **Differences in perceived contrast in patterns with identical Fourier amplitude spectra**

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It has been proposed that perceived contrast is dependent upon the output of bandpass-filtering operations. If this model is correct then two patterns with identical Fourier amplitude spectra should have the same perceived contrast. We tested whether this was the case by using noise patterns consisting of luminance levels that were not symmetrically distributed around mean luminance ( $I_0$ ). Such patterns can have identical expected amplitude spectra but may differ widely in their luminance distributions. Our top-biased noise patterns contained luminance levels of  $I_0 + 2x$  and  $I_0 - x$  (where  $x$  is positive). The probability of each luminance level occurring was adjusted so that the mean luminance was  $I_0$ . For our bottom-biased patterns, the sign of  $x$  was reversed. Subjects matched the contrast of two patches of noise, a standard noise patch and a test noise patch. The standard patch consisted of either top-biased or bottom-biased noise and had a root mean square contrast ( $C_{RMS}$ ) of 0.6, 0.5, or 0.4. The test patch contained unbiased binary noise (evenly distributed around mean luminance). For the test patch, matching  $C_{RMS}$  was determined by an adaptive method of constants procedure. The two patches were presented adjacent to one another. Each patch was 5.89 deg × 5.89 deg square, noise check size was 2.76 min of arc, and  $I_0$  was 37.4 cd m<sup>-2</sup>. Our results showed that the bottom-biased noise appeared to have a higher contrast than the top-biased noise. These data may be successfully modelled by proposing a nonlinearity prior to bandpass linear filtering.

**FACE PERCEPTION**

◆ **From perception to recognition of faces: the missing link**

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In this talk I briefly describe the evolution over the past twenty years of a theoretical framework for understanding human face recognition. I argue that for the majority of this period our understanding of the cognitive processes of face recognition was in advance of our understanding of face perception. Recently there has been a rapid increase in understanding of perceptual processing of faces, and the similarities and differences between perception of faces and other visual objects. However, the link between accounts of face perception and those of face recognition is still relatively weak. Recent modelling work by Mike Burton, Peter Hancock, and myself (Burton, Bruce, and Hancock "From pixels to people: a model of familiar face recognition" *Cognitive Science* in press) has explored the marriage of a principal components analysis 'front end' for representing face patterns with an interactive activation and competition 'back end', with promising results. However, there remain many unsolved problems, including the intriguing and forensically important one of the difference between the perception and representation of unfamiliar and familiar faces.

◆ **Configural encoding of facial expression**

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Composite facial expressions were prepared by aligning the top half of one expression (eg anger) with the bottom half of another (eg happiness) posed by the same model. As a control condition noncomposite images were used; these were identical to the composites except that the top and bottom segments were misaligned horizontally. When asked to identify the expression shown in the top (or bottom) segments of these images, subjects' response times (RTs) were significantly slower for the composite condition. This result parallels the composite effect for facial identity shown by Young, Hellawell, and Hay (1987 *Perception* 16 747–759), and is consistent with the idea that facial expressions are processed configurally (or holistically). In experiment 2, we showed that the same composite effect is found when the two face halves are different models posing different expressions, but not when if they are different models posing the same expression. In experiment 3 subjects were presented with composite faces in which expression, identity, or both were incongruent across the two face halves. When the subjects were asked to identify the person shown in the bottom half of these images, their RTs were significantly slower when the incongruent attribute was identity. However, when the subjects were instructed to identify the expression shown in the same half, their RTs were significantly slower when expression was incongruent across the two halves. Furthermore, there was no further cost in RTs if the unattended attribute (eg expression in the identity task) was also incongruent across both halves. These results suggest that configural information relevant to facial-identity and facial-expression encoding is perceptually different.

◆ **Near-bilateral symmetry impedes symmetry discrimination**

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Bilateral symmetry is a salient object property. Will perceived bilateral symmetry impede our ability to discriminate shapes that are slightly asymmetric? Faces are naturally suitable to address this question, since they are asymmetric in varying degrees but largely symmetric in frontal views. We used 3-D scans of real faces to construct natural-looking synthetic faces with varying degrees of asymmetry. Two images of a synthetic frontal-view face were displayed side by side. The subjects decided which one was more symmetric.

Discrimination sensitivity increased with the average degree of asymmetry of the two faces, when their difference was kept constant ( $p < 0.0001$ ,  $n = 16$ ). This suggests that perceived symmetry impedes symmetry discrimination when asymmetry is introduced by interpolating between an asymmetric natural face and the bilaterally symmetric face of the same person (as opposed to adding uncorrelated random dots to a symmetric dot pattern). This result held for both upright and inverted faces, suggesting that it is not due to a familiarity effect. Nor is the result due to any artifact of the scale of asymmetry in the interpolation dimension. This is because the asymmetry distortion we used produces a linear displacement of feature points in 3-D space; and in the image space, the Euclidean distance of pixel values between the left and right halves of a face was found to decrease with the increasing degree of asymmetry of the test faces. We conclude that symmetry perception impedes symmetry discrimination.

◆ **Principal component analysis of expression sequences**

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Facial expressions may be considered as time series in the space of the image, with the image describing a trajectory as the face moves from neutral to fully expressing. This trajectory lies in a low-dimensional subspace of the image, and may be characterised with data reduction techniques, such as the principal components analysis (PCA). In this work, PCA is performed on a set of images of a number of subjects producing different facial expressions. Such an analysis ignores the temporal information in the sequence, considering the image population to be an unordered set. However, temporal information is implicit in the statistics of the set, as neighbouring frames are likely to be highly correlated.

In this experiment, PCA was performed separately on image sequences for each subject. The time sequence of the image, as coded in PC space, shows a characteristic trajectory. The first

component appears to mix a neutral face with varying amounts of a fully expressing face. The second component contributes solely to the transition from neutral to expressing, correcting for inaccuracies which would result from a simple linear interpolation between a neutral and an expressing face. This result is shown to be robust across subjects, ie different faces appear to undergo similar transformations in expression sequences.

◆ **When Dr Jekyll turns into Mr Hyde: Categorising and perceiving faces in scale space**

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Face categorisation presents an interesting example of object expertise. Unlike expertise with other object classes which only affect limited numbers of people, faces transmit a wealth of social signals that we must all understand fast and accurately to achieve competent social interactions with our peers.

We examined the perceptual underpinnings of face categorisations. In particular, we investigated how various face categorisations (gender, expressive or not, which expression, and identity) use spatial-scale information. Stimuli were counterbalanced face hybrids which combined either a man or a woman with a particular expression at a coarse spatial scale with a face of the opposite gender with a different expression at a fine spatial scale.

Experiment 1 was designed to test whether the scale bias that arose in the process of resolving a first categorisation (expressive or not vs which expression) transferred to a second, initially unbiased categorisation (gender). In experiment 2 we applied such transfer of a bias to the situation in which subjects initially learned the identity of faces—arguably the most prominent categorisation—before resolving another categorisation (gender, expressive or not, and which expression). The outcome revealed that the scale bias of identity transferred to all the other tasks, overriding the spontaneous biases that occur when faces are unknown. Thus, a succession of categorisations induces a perceptual set which changes the scale perception and categorisation of subsequent stimuli. Such spatial-scale set effect has important implications for classical issues, ranging from feedback loops in early vision to the early vs late models of selective attention.

## NATURAL IMAGES

◆ **Seeing and studying natural images**

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For several decades, vision researchers have attempted to dissect the visual system (both psychophysically and neurophysiologically) with stylised and precisely controlled stimuli such as lines, edges, and gratings. It is now appropriate to use the wealth of information gained with such stimuli to understand why the visual system is organised in the way that it is, and how its neuronal or channel constituents contribute to the task of seeing in the real world. It is a tenet of much research nowadays that the visual system must have evolved or have adapted neonatally to optimise its ability to code the spatiotemporal or chromatic information found in the real world rather than in the laboratory.

The simplest empirical approach to studying the vision of natural images is to measure how well neurons in experimental animals respond to them, asking whether these responses are consistent with the neuron's responses to lines and gratings, and whether the responses have any interesting statistical form that might suggest why evolution has favoured the spatiotemporal response properties of this type of neuron. Another approach is to characterise the higher-order statistics of natural images computationally, asking whether the known response properties of single neurons or channels suit them to extracting the characteristic statistical features of natural images. Lastly, psychophysical experiments can be performed with complex visual stimuli whose statistics are changed to be more or less natural, asking whether the overall behaviour of the visual system really is best for stimuli with natural statistics.

◆ **Adaptation effects at suprathreshold contrasts: spatial sensitivity and image statistics**

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To examine the effects of contrast adaptation on the spatial sensitivity of the visual system I used adapting patterns which vary in their spatial structure. Natural scenes have a characteristic structure, described by a power spectrum which falls as  $1/f^2$  such that contrast energy is approximately constant at different scales. Cortical coding of contrast appears to be matched to this property of the environment, ensuring a scale-invariant response to image contrast. Accordingly,

it is expected that the effects of adaptation to the images we typically encounter will be similar across spatial scale.

Observers adapted to broadband noise patterns whose spectra were similar to, or much steeper or flatter than, those typically reported for natural scenes. After adaptation, they matched the contrast of a grating in their unadapted field to an identical grating in their adapted field. Matches were made for six frequencies (0.5 to 16 cycles  $\text{deg}^{-1}$ ) at three suprathreshold contrasts. Adaptation effects vary with the spectral slope of the adapting stimuli. Decreases in perceived contrast are greatest at high frequencies after adapting to flat spectrum noise; this bias is reversed when the adapting spectrum is much steeper than  $1/f$ . By comparison, the effects are more evenly distributed across frequency after adaptation to  $1/f$  noise patterns. These results support the proposal that contrast coding is matched to the spatial structure of natural scenes. They are discussed in light of recent reports that contrast adaptation may be an additional mechanism which equalises the visual response to contrast across spatial scale.

◆ **Inferential reliability of contour-grouping cues in natural images**

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Numerous studies have attempted to measure the relative strength of visual grouping cues. However, little is known about the statistical utility of these various cues for natural images. In this study, we empirically derive posterior probability functions for cues to contour grouping in natural images, and then use these functions to compute the inferential reliability of each of these cues in terms of ROC curves. We consider three cues: proximity, good continuation, and brightness similarity.

To estimate the statistics of the image contours perceived by humans in natural images, we employ a new image editing tool called ICE (Interactive Contour Editing—Elder and Goldberg, 1998, CVPR). This tool allows observers to rapidly trace the contours they perceive in a given image. ICE then automatically represents these contours as a sequence of local curve tangents with properties of position, orientation, brightness, and contrast. The statistics of these human-selected contours are used to compute likelihood functions for each cue, given two successive tangents on a curve. These functions are found to be highly kurtotic. Random selection of curve tangent pairs allows computation of the likelihood functions given two tangents which should *not* be grouped. Prior terms are also computed from the human data. A signal estimation analysis reveals that, for contour grouping, proximity is by far the most powerful cue, followed by good continuation and brightness similarity (polarity reversal occurring with probability  $p = 0.18$ ). These three cues are roughly independent, and combine effectively to provide more powerful evidence for contour grouping than any single cue used in isolation.

◆ **Higher-order redundancies of natural scenes and their relation to biological vision**

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A number of recent studies have emphasised the importance of investigating the statistical properties of our natural environment in order to obtain a better understanding of neural information processing and behavioural control. In order to quantify the redundancies in natural images, most approaches have made use only of first-order and second-order statistics, where the latter evaluate the correlations between pairs of pixels (autocorrelation functions). It can be shown, however, that second-order statistics are completely blind to locally oriented image features, and are therefore inappropriate for explaining the emergence of oriented receptive fields, which are a common property of the cells in the primary visual cortex.

In order to overcome these limitations inherent in the second-order approach, we have investigated the bispectra and trispectra of natural images. Our statistical analysis reveals strong dependences between frequency components that are aligned to each other with respect to orientation. We argue that this higher-order redundancy can provide an explanation for the advantages of linear orientation-selective filter decompositions over isotropic schemes. However, a full exploitation of these higher-order dependences requires nonlinear processing, for which we propose i2-D-operators, which are selective to intrinsically two-dimensional (i2-D) image features. These operators respond only to curved image features such as corners and junctions and show a close resemblance to end-stopped or hypercomplex cells. Based on the Volterra–Wiener series expansion of nonlinear systems we have developed a generic class of such i2-D-selective operators.

We argue that these operators can be seen to decorrelate the statistics of natural images in a higher-order sense, thus providing an efficient representation of visual information with reduced dependences between the individual units.

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◆ **Luminance and contrast adaptation to time series of natural intensities**

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Natural time series of intensities have power spectra behaving approximately as  $1/f$  ( $f$  = temporal frequency), and average rms contrast for 1-s segments of 0.45 (van Hateren, 1997 *Vision Research* 37 3407–3416). We compared adaptation to 1 min of a natural time series with adaptation to the series raised to various powers (0–2), providing a wide range of rms contrasts. Average luminance was kept constant. As a test stimulus we used a small circular patch (20 min of arc), superimposed on the spatially homogeneous adaptation stimulus (6 deg). The test was presented during 1 s, at various moments in the time series. Test intensity during the presentation period was a fixed fraction  $c_v$  of the adaptation intensity. We measured the detection threshold by presenting a range of fractions,  $c_v$ , to each of which the observer responded by assigning one of five visibility ratings.

Threshold  $c_v$  for the natural time series ( $0.084 \pm 0.004$ ) is only slightly higher than for a constant luminance level ( $0.069 \pm 0.002$ ). Thresholds increased approximately linearly with stimulus contrast. In order to test whether this threshold elevation is caused by the increase in contrast or in slow luminance variations we tested adaptation stimuli with specific properties: a bipolar pulse series and a 10-ms-segment-shuffled time series, which have negligible slow luminance variations, and a low-pass-filtered time series, which has diminished contrast but still contains large luminance steps. Thresholds were found to depend solely on stimulus contrast; luminance adaptation is not a limiting factor for this experiment. Threshold increase with contrast appears to be consistent with contrast sensitivity of the parvocellular pathway.

### CROSS-MODAL INTERACTIONS

◆ **Alignment of auditory and visual space perception**

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A primary function of auditory localisation is to direct the gaze toward the source of sound. Accurate performance requires that the coordinates of auditory and visual space be in close alignment. This alignment was investigated by using a method of laser pointing toward acoustic targets combined with various tasks of visual fixation. Subjects, fixating either a target LED or a laser spot projected on a screen in a dark, anechoic room, directed a laser beam toward the sound (1–3 kHz bandpass-filtered noise; 70 dB SPL, 10 s) which was produced by one of nine loudspeakers, located behind an acoustically transparent screen, in different positions between 22 deg to the left and right.

The eccentricity of acoustic targets was generally overestimated (up to 10.4 deg) with only a slight influence of gaze direction. However, when the sound source was straight ahead, eccentric gaze had a substantial influence in that laser pointings deviated (by up to 5.6 deg) from sound direction toward the side to which the gaze was directed. The results suggest interactive effects of four distinct factors: (i) overestimation of sound eccentricity, (ii) effect of eye position on auditory localisation, (iii) effect of retinal eccentricity on visual localisation, (iv) extraretinal effect of eye position on visual localisation. The psychophysical findings correspond to neurophysiological data on brain maps of auditory space that are in approximate, but not perfect, spatial alignment with visual maps (eg Jay and Sparks, 1987 *Journal of Neurophysiology* 57 35–55).

◆ **Size discrimination of seen and grasped objects and the effect of presentation time**

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We investigated visuo–motor integration in grasping by studying haptic, visual, and cross-modal size discrimination. Our main interest concerned the effect of presentation time on discrimination performance and the differences between intramodal and cross-modal thresholds.

The experiments were conducted in a virtual environment in which two force-feedback devices (PHANTOM™) provided haptic information to the thumb and the index finger. Stereoscopically rendered objects were used for the visual presentation. In a two-interval forced-choice

paradigm subjects had to determine which interval contained the larger object (we used cubes in all cases). Depending on condition, subjects either saw or felt each cube for a specified time. Feeling a cube required subjects to perform a two-finger grasp. The intramodal tasks were repeated with an appropriate mask between the two presentations; in these runs haptic masking consisted of randomly disturbing the finger span by the force-feedback devices. Intramodal thresholds ( $\pm 4\%$  visual–visual;  $\pm 7\%$  haptic–haptic) were significantly smaller than cross-modal thresholds ( $\pm 13\%$  visual–haptic;  $\pm 14\%$  haptic–visual). Gradually decreasing the presentation time in the intramodal conditions to less than 50 ms increased the thresholds monotonically, but significantly less so for the visual–visual condition (from  $\pm 4\%$  to  $\pm 6\%$ ) than for the haptic–haptic condition (from  $\pm 7\%$  to  $\pm 20\%$ ). We found no significant effect of masking on these thresholds.

Visuo–motor adaptation studies have shown that the coordinate transformation from vision to touch exhibits a considerable amount of plasticity. We hypothesise that the continuous recalibration of this transformation during the experiment constitutes the reason for the inflated cross-modal thresholds. Furthermore, we conclude that acquiring precise size information is much slower in the haptic modality than it is in vision.

◆ **The consistency of letter–colour pairings in three cases of synaesthesia**

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“Grey, powdery like tailor’s chalk, but a bit more dusty” (subject LF, describing the letter V).

Synaesthesia is the term used to describe percepts in one modality induced by stimuli in another modality, for instance the perception of a colour when hearing a sound. The occurrence of synaesthetic experience is well documented [Cytowic, 1989 *Synesthesia* (Berlin: Springer)] but to date, attempts to quantify the experience do not rule out a language-based mapping; for example, Baron-Cohen et al (1987 *Perception* 16 761–767) asked subjects to give the names of colours associated with words.

Motivated by this issue, we conducted a non-linguistic experiment to investigate the precision of observers in identifying colour-space coordinates associated with textual stimuli. Three self-nominated synaesthetes took part in the study, presented in each case with a stimulus set consisting of typed letters of the alphabet and numerical digits, and a response set of colour chips. Colour chips were matched to stimuli by the subjects, who then returned and repeated the process a week later. In this way we were able to (a) gain a quantifiable measure of synaesthetic response and (b) establish its consistency.

The results show a remarkably consistent pattern of pairings for each subject [mean test/retest distance in Munsell colour space: 5.19 (LF); 2.13 (CC); 3.85 (LB)].

We also present evidence from one subject (LF) showing consistency not only in elicited hue but in an associated texture perception, extending the approach taken here to the more complex phenomenology of synaesthesia.

◆ **Does attention affect crossmodal visuotactile temporal order judgments?**

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Participants were presented with pairs of stimuli, one either side of fixation, and were required to make unspeeded (left vs right) temporal order judgments (TOJs) about which stimulus was perceived first. Four equiprobable stimulus combinations were used in the first experiment (VV—visual stimuli on left and right; VT—visual on left and tactile on right; TT; and TV) and participants were instructed to divide their attention equally between vision and touch. On cross-modal trials, the onset of the visual stimulus had to occur approximately 50 ms before that of the tactile stimulus in order for the two to be perceived as simultaneous. In experiment 2 all VV trials were replaced by TT trials (ie 50% TT, 25% VT, and 25% TV trials) and participants were instructed to attend to touch. Visual stimuli now had to occur more than 100 ms before the tactile stimuli for perceptual simultaneity to be achieved. In experiment 3 (50% VV, 25% VT, and 25% TV trials) participants were instructed to attend to vision, and perceptual simultaneity now coincided with objective simultaneity. By contrast, performance for intramodal VV and TT pairs was unaffected by our attentional manipulations. These results suggest that attending to a modality does not improve temporal resolution within that modality per se, but instead simply speeds up the processing of all stimuli in the modality relative to stimulus processing in other modalities.

◆ **Mapping visual images into musical space**

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A musical score is a graph that displays the relative distribution of musical notes as a function of time. Extending this simple observation we have developed a system that translates 'visual images' into distinctive musical forms, enabling normal blindfolded (and blind) subjects to auditorily discriminate different visual displays: (i) forms and contours, (ii) simple figure ground, (iii) regular textures, (iv) letters of the alphabet, (v) simple words and phrases, etc. displayed on a monitor and transformed into corresponding patterns of sound. Using this approach we have transformed some well-known visual illusions (Müller-Lyer and Ponzo illusions) into corresponding musical patterns without loss (of the auditory equivalent) of the visual illusory effect. In addition, subjects are also able to discriminate and identify different visual dynamic forms from their characteristic 'musical signatures', eg a walking man, a galloping horse, the flapping wings of a bird in flight, etc. Apart from its potential use as a sensory aid to the blind, the research promises to have profound implications for our understanding of perception and the nature of mind.

**READING**

◆ **Elicited sequential presentation vs RSVP and CCTV in low vision reading**

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People with severe low vision typically can read only with large letter sizes achievable on computer screens, or on closed-circuit television video magnifier reading aids (CCTVs). Even with magnified text, reading rates are usually substantially slower than those of normally sighted readers. A computer text presentation mode that has shown promise in enhancing low-vision reading performance is rapid serial visual presentation (RSVP). At ARVO 1998, we reported a variant of RSVP called elicited sequential presentation (ESP) that produces faster reading rates than RSVP for low vision. With ESP, the reader elicits presentation of single words via a button press, allowing him/her to control presentation rate on a word by word basis.

In the present study, we compared maximum reading speeds using the three methods in twelve subjects with low vision who were customary CCTV users but previously unexposed to RSVP and ESP. Text was 5th grade level, and presented with the same font (TrueType Arial) in all conditions at the subject's preferred font size or magnification. Reading speed for RSVP was determined by increasing or decreasing speed in coarse (20%) or fine (10%) steps until errors were made, while for ESP and CCTV, subjects were instructed simply to read as fast as possible without error. While ESP and CCTV yielded essentially the same speeds (78–79 words min<sup>-1</sup>, geometric averages), reading was on average 31%–32% faster with them than with RSVP. Since all subjects were highly practiced on CCTV reading, these results probably underestimate the true benefit of ESP.

◆ **A neural-network virtual-reality mobility aid for the severely visually impaired**

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Many people who are registered as blind nevertheless retain some residual vision and are said to have 'low vision'. Conditions resulting in such low vision include cataracts, diabetic retinopathy, age-related maculopathy, and retinal detachment. In recent years principles from computer vision have been increasingly applied to the requirements of the low-vision subject. A variety of conventional image-processing techniques have been used to enhance the visual appearance of a scene, and devices from the field of virtual reality such as head-mounted displays have been investigated as an aid to low vision. However, a fundamental limitation with conventional image-processing techniques is that they are applied to an entire image with no knowledge of scene content, resulting in unwanted emphasis of noise and unimportant detail.

Our aim is to produce a portable system comprising a processing unit with head-mounted camera and display which will allow a person with low vision to be self-sufficient and mobile in a typical urban environment. Our approach differs from previous research in that it uses a neural-network object classifier to allow images to be enhanced in a way which considers the

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identity of objects in the scene. Primarily, our system transforms an original image into a classified image in which the types of objects in the scene are identified by an object outline filled with a particular high saturation colour according to the object type, chosen by the user. By classification our system allows the user to identify important objects in a scene simply by their colour, requiring no perception of shape or high spatial frequencies, and minimal contrast sensitivity. The resultant images are very simple and uncluttered and we expect that users would adapt quickly to the system. Results obtained to date suggest that the system is capable of providing registered-blind users with useful visual information. We are now working on improving the speed and classification accuracy of the system, and investigating the applicability of our techniques to specific conditions.

◆ **Jagged letters are more easily recognised than smooth ones in the peripheral visual field**

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Diagonal and curved letters presented on a computer screen (CRT), are jagged while the same letters printed on paper are smooth. We asked whether jagged and smooth letters (of the same font and size) are perceived in the same way, especially in the peripheral visual field.

Pairs of letters, either smooth or jagged, were presented to the subjects tachistoscopically with slide projectors. One letter of each pair was at the centre of gaze and the other in the periphery along the horizontal line. In successive presentations the peripheral letters were at different eccentricities. In this way we made plots of correct recognition as a function of eccentricity of the peripheral letters, separately for smooth and jagged letters. Seven adult subjects (good readers) were tested.

At eccentricities larger than 7.5 deg (to the right and left sides), the jagged letters were recognised better than the smooth ones. All differences were statistically significant (except in 12.5 deg to the left). Additional experiments ruled out accommodation as an explanation. Similarly aliasing was ruled out. We suggest that the difference in perceiving smooth or jagged letters is in the different perceptual strategies used for the letter types. The strategies differ mainly in the spatial distribution of clarity. The strategy in the wider field resembles that of binocular rivalry, while that in the narrow field resembles that of ordinary reading.

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◆ **The optimal letter spacing for reading scales with letter size**

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We measured the effects of letter spacing and size on reading rates. We varied letter spacing from 2 to 100 letters per 12 inch line. By varying viewing distance, we varied letter size from 0.25 to 9 deg. The two typefaces used were upper and lower case Bookman (a standard serif font) and Kuenstler (a script font used in wedding invitations). We found that the optimal letter spacing for fast reading rates was proportional to the width of a letter 'M'—slightly greater than the standard spacing of Kuenstler font and slightly less than the standard of Bookman. This optimal letter spacing scaled with size for both fonts (log-log slope of 0.97). We suggest that reading rates are constrained by visual filters that are tuned to spatial frequency, based on letter width.

**WEDNESDAY****ORAL PRESENTATIONS****RELATING PHYSIOLOGY TO PERCEPTION (McDONNELL–PEW SYMPOSIUM)**

- ◆ **Common spatial reference frames for reach and eye movements in posterior parietal cortex**  
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Recent experiments from our laboratory have demonstrated that the lateral intraparietal area (LIP) is preferentially active when monkeys are planning eye movements, while a second area (posterior and medial to LIP) is preferentially active during the planning of reaching movements. We have previously shown that in LIP visual and auditory targets for saccades are represented in eye-centred coordinates modulated by eye- and head-position signals. We have now found that, in the adjacent reach region, reaching movements made to remembered locations in the dark are also coded predominantly in eye coordinates. This is true whether the animal is reaching to locations specified by auditory or visual stimuli. In addition, the retinotopic fields of these cells are gain-modulated by eye and limb position. The shared common reference frame for these two areas might be useful for programming reaching movements under visual guidance and for hand–eye coordination. The dominance of eye coordinates, even for reaches to auditory targets, may represent the fact that vision is a higher-resolution system in primates, and thus auditory targets for movements may be associated with visual stimuli. Finally, previous studies from our laboratory and other laboratories have suggested that the gain-modulation mechanism can represent eye-, head-, body-, and limb-centred reference frames simultaneously in the same population of neurons. Thus, these two cortical areas appear to use the same distributed format for representing space in which eye-centred receptive fields are modulated by body-position signals.

- ◆ **Neocortical areas underlying visual short-term memory: Evidence from fMRI**  
M W Greenlee, I Reinvang¶, S Magnussen¶, F M Kraemer, J Hennig (Departments of Neurology and Radiology, University of Freiburg, Breisacherstrasse 64, D 79106 Freiburg, Germany; ¶ Department of Psychology, University of Oslo, Blindern, Oslo, Norway; fax: +49 761 270 5310; e-mail: greenlee@ruf.uni-freiburg.de; WWW: <http://www.ukl.uni-freiburg.de/neurozen/nlo/greenlee/frame.htm>)

Gradient-echo echo-planar imaging (EPI) was used to investigate BOLD contrast effects in visual cortex and associated areas in temporal, parietal, and prefrontal cortex evoked during a short-term visual memory task. Imaging was performed with a 1.5 T whole-body Siemens Magnetom (Vision) equipped with a gradient system having  $25 \text{ mT m}^{-1}$  amplitude and 0.3 ms rise time. Fourteen 6-mm planes, positioned oblique to the axial plane, were imaged every 4 s by using T2\*-weighted sequence (TR = 1.76 ms, TE = 84 ms,  $\alpha = 90^\circ$ , FOV  $256 \times 256 \text{ mm}^2$ ,  $128 \times 128$  voxels). Standard and test stimuli (vertical orientation) were interleaved with distractors (horizontal stimuli). The task was to judge the relative spatial-frequency difference ( $\pm 20\%$ ) between the standard and the test. The visual stimuli were created on a VSG graphics board and shown in back-projection with an LCD-projector. Twelve subjects with normal, or corrected-to-normal, visual acuity participated. In the simple response condition, BOLD contrast effects were evident in voxel clusters located in striate and extrastriate cortex, as well as in frontal structures typically active in attention-demanding tasks. During the active detection task, additional clusters were evident in infero-temporal posterior parietal cortex, the anterior cingulate, as well as the ventral and dorsolateral prefrontal cortex. We conclude that several areas show significant BOLD contrast when a subject judges the spatial frequency of stimuli presented among distractors.

- ◆ **Neuronal correlates of amblyopia in the visual cortex of macaques with experimental strabismus and anisometropia**  
J A Movshon, D C Kiper, L P O'Keefe, J R Cavanaugh, L Kiorpes (Center for Neural Science, New York University, 4 Washington Place, Room 809, New York, NY 10003, USA; fax: +1 212 995 4183; e-mail: movshon@nyu.edu; WWW: <http://www.cns.nyu.edu>)
- Amblyopia is a developmental disorder of pattern vision. Macaques often develop amblyopia after surgical creation of esotropic strabismus in the first weeks of life, or after wearing  $-10\text{D}$  contact lenses in one eye to create anisometropia during the first months of life.

We studied the response properties of neurons in the visual cortex of six macaques, three anisometropic and three strabismic; we verified their amblyopia by extensive psychophysical testing—spatial contrast sensitivity was lower in the treated eye than in the untreated eye, with some variation in the depth of amblyopia from animal to animal.

In all monkeys, cortical binocularity was sharply reduced. In anisometropes, the amblyopic eye influenced a relatively small proportion of cortical neurons; in strabismics, the two eyes' influence was more nearly equal. In more severe amblyopes (of either type), cells had poorer spatial resolution and they preferred lower spatial frequencies when tested through the amblyopic eye than when tested through the fellow eye. Qualitatively, these abnormalities in visual cortex neurons are related to the depth of amblyopia. Quantitative analysis suggests, however, that these abnormalities alone do not explain the full range of visual deficits in amblyopia. Further studies in extrastriate cortical areas may uncover other changes that explain these deficits.

◆ **The DOG dogma and the equivalent contrasts of natural scenes**

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Visual responses depend on stimulus contrast and not simply on the absolute levels of retinal illumination. We have calculated the contrasts in 135 calibrated images of natural scenes using contrast operators that closely mirror the receptive-field organisation of typical mammalian retinal ganglion cells and of neurons in the lateral geniculate nucleus (LGN). Here we show that the conventional Difference-of-Gaussians (DOG) receptive-field model is an inadequate contrast operator unless it is modified to include the nonlinear effects of light-adaptation. Using such modified contrast operators, we found that the distribution of contrasts in natural scenes has a pronounced peak at zero contrast and that it tails off roughly exponentially with increasing positive and negative contrasts. Thus, the majority of contrasts that these neurons are likely to encounter in real world scenes are low, whereas high contrasts are very infrequent. We tested this prediction by recording the activity of single LGN units in paralysed, opiate-anaesthetised macaque monkeys, presented with images of natural scenes. Response distributions to these images confirm that the most frequent response level is, indeed, zero extra spikes  $s^{-1}$  above the spontaneous level. We have also determined how the responses of these neurons depend on the contrasts of spatially optimal concentric spots of light. This allowed us to express their responses to natural images in terms of the equivalent contrasts of the spatially optimal spot stimuli. We found that an equivalent contrast of 50% is sufficient to account for 80%–90% of the responses to images of natural scenes.

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◆ **Evoked magnetic fields to optic flow stimuli are largest for expansion**

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Magnetoencephalography (MEG) was used to investigate the hypothesis that complex motion is processed by specialised mechanisms in human vision. Stimuli contained 241 random dots with either expansion, rotation, noise, or translation, viewed through a 9.3 deg diameter aperture. In three conditions stimulus dots travelled linearly through 20% of their distances from the origin, and in two translation conditions moved laterally at either: (i) the same speed as the fastest dots in the other patterns or (ii) half that speed. Noise stimuli were the same as expansion/rotation except that dot directions were randomised. In all conditions, stimulus dots were displayed for 3 min, and transformed cyclically: 317 ms in an initial set of directions; 883 ms stationary; 317 ms in the reverse directions; 883 ms stationary. Magnetic responses were recorded with a 19-channel SQUID neuromagnetometer placed over the posterior left hemisphere. Evoked responses were obtained for all stimulus conditions with a latency of approximately 90 ms at the initial peak, though there were marked differences in their amplitudes. The responses to expansion were nearly twice the size of those to the contemporaneously recorded responses to contraction, implying neural mechanisms specialised for expansion. The weakest responses were to translation, noise and rotation producing intermediate responses. Magnetic source localisation was not inconsistent with MT/MST origin. The preferential activation seen for expansion may reflect high ecological validity of this stimulus and be reflected in greater cell numbers (Tanaka et al, 1989 *Journal of Neurophysiology* 62 642–656) and consequently larger evoked fields.

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**VISION IN A NATURAL ENVIRONMENT (McDONNELL–PEW SYMPOSIUM)**
**◆ Vision in a natural environment**

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It has been twenty years since David Marr produced his ground-breaking framework of vision as a hierarchical combination of distinct modules, each performing its own computation on retinal input. This modular theory is a computational simplification that treats the goal of vision as the extraction of visual cues. Researchers have been addressing how each of the modules could possibly operate in isolation. To this end we have had many ingenious inventions such as the random-dot stereogram, intricate plaid patterns, and colourful Mondrians. However, the simplifications afforded by such thinking are often offset by the difficulties they introduce. First, the world does not consist of plaid patterns—it's more complex than that. Second, isolation of visual information almost inevitably leads to ambiguity in the reconstruction of the real world. The ill-posedness of vision with isolated cues can be resolved by the combination of cues: disparity, shading, texture, motion, etc. Using statistical methods such the Bayesian framework allows for the maximisation of the information derived from various sources. But, it seems still not to be enough. Perhaps a better way of thinking about seeing can be reformulated: vision does not start at the retina. Vision starts when a particular task has to be performed. The role of vision is not one of reconstruction of the real-world in the brain but one of serving the needs of a mobile active being that functions in the real-world. The talks presented in this session perhaps give a flavour of how it has been in Vision and also perhaps a flavour of how it will be in the future.

**◆ A simple Bayesian model predicts a complex set of motion phenomena**

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To estimate the motion of an object, the visual system must combine multiple local measurements, each of which carries some degree of ambiguity. The ambiguity may arise from several sources, including the aperture problem, noise, etc. We present a model of motion perception whereby measurements from different regions are combined according to a Bayesian estimator. The estimator is one of the simplest reasonable estimators one can devise. The estimated motion maximises the posterior probability assuming a prior favouring slow and smooth velocities. We find that the estimator predicts a remarkable range of phenomena including: the bias toward vector average with plaids of low contrast, short duration, or narrow angle; the non-rigid appearance of rotating ellipses; and the strong influence of feature-like points. The model does not require specific mechanisms such as intersection of constraints, vector averaging, feature tracking, or second-order motion. It does not specify the machinery that should be used. It simply takes the raw pixel data as input and delivers the best motion estimate as output.

We argue that a range of complex phenomenology can be explained by assuming that the visual system is employing a simple and reasonable computational strategy.

**◆ Combining retinal images to form a spatial reference frame. I: theory**

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There are currently no detailed suggestions about how retinotopic information might be used to build up a representation of the location of objects that could survive both head and eye movements. One candidate is a 3-D, world-based reference frame but it is not known how or where this might be computed in the brain.

We present an alternative hypothesis in which only the relative positions (ie relative visual directions) of points are recorded. These angles can be used to triangulate the entire viewing sphere or optic array. Gaze direction with respect to the head is not used. Relative positions are independent of eye rotation and, for triples of distant points, also independent of eye translation. The set of distant points thus forms a stable reference frame onto which the rest of retinotopic information can be mapped.

We show how this type of representation can be generated from retinal motion and disparity across a series of fixations. In the traditional analysis, gaze-holding eye movements (in which active counter-rotation of the eye compensates for head movement) complicate the reconstruction of 3-D geometry. For the representation proposed here, gaze-holding eye movements are positively advantageous: changes in position of features relative to the fixated object are automatically computed even at the earliest stages in the visual system. We also argue that, although full 3-D

reconstruction is not possible, the information stored may be sufficient to generate saccades, control posture, judge the relative distance of widely separated points, and navigate to remembered locations.

[Supported by the MRC.]

◆ **Using a 'virtual illusion' to put parallax in its place**

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Visual illusions and ambiguous figures have provided researchers with important insights into how the human visual system interprets its visual environment. The advent of computers capable of producing compelling virtual scenes has enabled researchers to use complex environments whilst retaining the controllability and repeatability of traditional experimental designs. Having control of the environment permits certain rules which apply in the real world to be broken, creating new types of visual illusions.

In this experiment, we moved an object in a room in antiphase with the simulated motion of the observer, ie we manipulated motion-parallax information for this object relative to all others. Under monocular viewing, observers perceived the object not as moving, but as closer and smaller than before. Thus, the perceived depth, size, and location of an object can be controlled via the motion-parallax cue. We also tested stereo viewing and found that, if the object remained within the useful stereo range, the object's real position was re-established and it was correctly perceived as moving. The results indicate that motion parallax is an important cue for deciding the distance of an object from the observer, overriding other cues such as prior experience (a chair is usually on the floor and not toy-sized). However, it is not sufficient to counteract these cues in conjunction with correct stereo information. We discuss these results and go on to consider how virtual reality opens the door to a new generation of virtual visual illusions, tailored to investigate specific perceptual tasks.

◆ **Depth, lightness, and transparency: An anchoring rule for perceived transmittance**

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We performed a series of experiments to understand how and when the visual system decomposes textures into a multi-layered representation of surfaces in depth. Observers viewed a family of 1-D and 2-D textures through simulated apertures. Binocular disparity was used to cause the texture to appear in front of the aperture boundaries. Using a method of adjustment, observers judged the apparent lightness and perceived depth of regions within the texture. Dramatic shifts in both the perceived depth and lightness of the two layers were observed when the contrast polarity of the background/texture border reversed. When the background was darker than the texture, the texture appeared as a distant light layer visible through dark 'clouds'; when the background was lighter, the texture appeared as a distant dark layer visible through light clouds. These regions of highest and lowest luminance (respectively) appeared to reverse in depth when the contrast polarity of the background/texture border was reversed, without any concomitant changes in binocular disparity. A new theoretical framework is introduced to explain the coupled changes in depth, lightness, and transmittance of these new illusions. This framework asserts that the visual system employs an anchoring rule that treats the highest-contrast image regions as unattenuated surface patches, and all lower values of contrast are assigned proportionally lower transmittance values. It is argued that this general principle can explain all versions of stereoscopic transparency reported to date, and provide a principled reason for the coupled computations of lightness, depth, and opacity.

## STEREO MECHANISMS

◆ **The variability of neuronal firing in cortical area V1 of awake, behaving monkeys**

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The variable firing of cortical neurons limits the reliability of the signals they provide about visual stimuli. Studies from V1 in anaesthetised cats and monkeys suggest that the variance of firing rate is proportional to the mean over a wide range. Although neurons may differ in the ratio of variance to mean firing ( $V/M$  ratio), these differences could be due to anaesthesia or other unidentified factors. Results more relevant for perception are obtained when the activity of neurons is recorded during the performance of a psychophysical task.

Data were obtained from foveal and parafoveal V1 in awake monkeys, in which the receptive fields were stimulated binocularly with either dynamic random-dot patterns or moving sinusoidal gratings, whose stimulus parameters were adjusted to provide a wide range of firing rates. The animals were required to fixate and carry out psychophysical discriminations of stereo depth on the targets in the receptive fields, thus ensuring the animal's attention to the visual stimuli. Substantial differences in the  $V/M$  ratio were found among the sample of V1 neurons: regression of variance against mean showed that slopes for individual neurons varied from near zero to ten.

Although external factors (stimulus and eye-movement related) undoubtedly contribute to the variability of neuronal firing, the wide range of  $V/M$  ratios suggests that there are genuinely significant differences from one neuron to the next. We conclude that it would be unsafe to use a single value for  $V/M$  ratio for modelling the whole population of V1 neurons.

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◆ **Nonius alignment can be used to measure vergence**

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Dichoptic vertical lines (nonius), presented at a different depth plane from the plane of current vergence fixation, must be given a horizontal displacement for apparent alignment. This angular displacement is equal to the disparity between the nonius plane and the fixation plane, hence its use as a vergence estimate. Our aim was to validate this subjective estimate against a simultaneous objective binocular eye-movement measurement.

Three observers responded to brief (160 ms) nonius following a 230 ms small random-dot stimulus of  $-60$  to  $+60$  min of arc disparity. Vergence was estimated subjectively and objectively, as a function of disparity. Two dual-Purkinje trackers provided a binocular eye-movement record. Nonius displacement was varied by a staircase procedure. Response frequencies in the nonius alignment task were fitted with a cumulative normal, across 40 trials at each disparity, to obtain a subjective vergence estimate. Recorded vergence change during the stimulus interval was averaged over the same 40 trials to obtain an analogous objective estimate.

Subjective vergence strongly resembled objective vergence. Both estimates had the same slope as a function of disparity and were significantly correlated. A  $t$ -test showed no differences between their means, even for one observer with considerable fixation error. If a nonius target is presented simultaneously with a binocular object, binocular 'capture' may influence apparent visual direction and hence alignment (Erkelens and van Ee, 1997 *Vision Research* 37 1735–1745; Shimono et al, 1998 *Vision Research* 38 591–600). However, our results show that alignment of nonius flashed subsequently to a stimulus provides a reliable measure of vergence.

◆ **Vergence eye movements explain some aspects of contextual modulation in primate V1**

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Zipser et al (1996 *Journal of Neuroscience* 16 7376) recently showed that the responses of neurons in V1 of the awake monkey can be modulated by the binocular disparity of stimuli far outside the receptive field. We re-examined this phenomenon using static random-dot stereograms in two monkeys trained to fixate binocularly. The central region (2 deg) covering the receptive field had zero disparity, while the disparity of the surround (10 deg) varied between trials. Confirming Zipser et al's results, we found that (i) the initial transient response of the neurons was not influenced by the surround disparity; (ii) 50–100 ms into the response, average firing rates were higher when the surround region was presented with an uncrossed disparity.

Because these experiments used static texture patterns, eye movements could have a strong influence on neuronal firing. Substantial increases in neuronal firing were induced by small fixational eye movements, but these movements were not systematically related to the surround disparity.

However, surround disparities did induce vergence eye movements at short latencies (60 ms) even though the fixation marker had zero disparity. The enhanced neuronal responses appear to represent visual responses to movement of the stimulus across the retina caused by the vergence movements. Zipser et al found that changes in stimulus size reduced the magnitude of contextual modulation. The same changes systematically reduce the magnitude of the vergence responses. We conclude that the contextual modulation by disparity observed in V1 reflects changes in the stimulus *within* the receptive field induced by eye movements.

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◆ **The role of spatial scale in stereoscopic segmentation**

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Stereopsis is useful for perceptually breaking up dense scenes such as foliage into different depth layers. We have considered the importance of spatial scale in this process, using a novel stimulus which we term a 'dual-surface' disparity-grating. This is constructed by combining two sinusoidal disparity-gratings in opposite spatial phase. Each surface is composed of randomly positioned Gabor micropatterns, and the micropattern content of the two surfaces can be the same or different. Under appropriate conditions the two surfaces appear to weave in and out of each other giving rise to a strong sensation of depth transparency. We measured the threshold amplitude of disparity modulation for identifying the orientation (left or right oblique) of a 0.4 cycle deg<sup>-1</sup>, 1200 micropattern dual-surface grating, as a function of the difference in micropattern luminance spatial frequency between the two surfaces. When the micropatterns on the two surfaces were identical, thresholds were high (eg between 10 and 40 min of arc depending on micropattern). However, with as little as 1 octave difference in luminance spatial frequency, thresholds fell sharply to near-asymptotic levels (eg 1–2 min of arc). Along with this improvement in thresholds, the appearance of the dual-surface grating changed from irregular depth to vivid transparency. In the light of these results, the functional role of spatial scale in facilitating stereo-segmentation in natural scenes is discussed.

◆ **Interactions between chromatic and achromatic stereopsis mechanisms**

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It is well known that chromatic information can assist in solving the stereo correspondence problem. Recent studies have suggested that there are two independent first-order stereopsis mechanisms, one sensitive to chromatic contrast and the other sensitive to luminance contrast (Simmons and Kingdom, 1997 *Vision Research* 37 1271–1280). Could the effect of chromatic information on stereo correspondence be subserved by interactions between these mechanisms?

To address this question, disparity thresholds (1/stereoacuity) were measured with 0.5 cycle deg<sup>-1</sup> Gabor patches. The stimuli possessed different relative amounts of chromatic and luminance contrast which could be correlated or anticorrelated between the eyes. Stereoscopic performance with these compound stimuli was compared with that with purely isoluminant and isochromatic stimuli at different contrasts and interocular contrast ratios.

It was found that anticorrelated chromatic contrast severely disrupted stereopsis with achromatic stimuli and that anticorrelated luminance contrast severely disrupted stereopsis with chromatic stimuli. Less dramatic, but still significant, was the improvement in stereoacuity obtained when using correlated colour and luminance contrast. The comparison data obtained also allowed these effects to be calibrated in terms of changes in interocular contrast ratios and/or binocular contrasts. These data are consistent with there being positive and negative interactions between chromatic and achromatic mechanisms that take place after the initial encoding of disparity, but before the extraction of stereoscopic depth.

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**CLINICAL ASPECTS OF PERCEPTION**

◆ **Visual efficiency in amblyopic macaque monkeys**

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Amblyopes have reduced contrast sensitivity as well as acuity. This reduction in contrast sensitivity could arise early in the visual system (peripherally) or centrally. We have now studied the limits on contrast sensitivity in amblyopes, using the visual masking paradigm of Pelli to measure the way in which visual noise affects contrast detection. We measured the effect of dynamic spatio-temporal masking noise on contrast detection in strabismic or anisometropic *Macaca nemestrina*. The monkeys were trained to detect the presence of a grating target in varying levels of background noise, by a two-alternative forced-choice procedure. We measured contrast threshold at low and moderate spatial frequencies over a range of noise contrasts from 0 to 50%. The subjects ranged in age from 6 months to 8 years at the time of test.

The effectiveness of noise in elevating contrast threshold is given by the equivalent input noise (Neq), the noise contrast that doubles squared threshold, and the asymptotic threshold signal-to-noise ratio (Rsn) in high-contrast noise. Interocular comparisons revealed that elevated contrast thresholds in the amblyopic eyes were not consistently related to elevation in Neq, but were more often associated with increases in Rsn. Thus Rsn was elevated—often substantially—in amblyopic eyes, while Neq was typically more similar in the two eyes. Since Neq is held to represent the efficiency of peripheral encoding, while Rsn represents other factors, our results are consistent with the hypothesis that contrast sensitivity in amblyopia is dependent on central factors.

◆ **Adaptation to visual motion and self-motion in the absence of VI**

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We investigated whether a patient (G) with unilateral damage to the primary visual cortex adapts to visual motion presented in his blind hemifield. We also considered whether nonvisual signals associated with active self-motion, such as those that occur during locomotion, may influence differently visual adaptation and aftereffects than visual signals alone. While G is blind to the stimulus in the normal sense, he can nevertheless report the presence and direction of a motion stimulus in his blind hemifield despite the unilateral absence of a functioning VI (Barbur et al, 1980 *Brain* 103 905–928; Barbur, 1994 *Ophthalmic and Physiological Optics* 14 436). This residual visual capacity has been attributed to motion-sensitive extrastriate areas (Barbur et al, 1993 *Brain* 116 1293–1302), and the degree of awareness to subcortical and cortical activation (Sahraie et al, 1997 *Proceedings of the National Academy of Sciences of the USA* 94 9406–9411). Our preliminary tests on the visual motion aftereffect (MAE) include the finding that while G is completely unaware of any MAE after stimulation restricted to the blind hemifield, concurrent stimulation with optic-flow stimuli of opposing direction and balanced to both his blind and sighted hemifields virtually eliminates the MAE in the sighted hemifield, as it does in normal subjects. With additional experiments on the role of self-motion signals we conclude that VI is not required for adaptation that would normally lead to motion and self-motion aftereffects [eg Pelah and Barlow, 1996 *Nature (London)* 381 283].

◆ **Measuring the unseen aftereffect of an unseen stimulus in blindsight**

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A change in the colour of a stimulus with no change in either photopic or scotopic contrast causes a highly reproducible transient pupillary constriction. Interestingly, a small but reliable pupil constriction also can be observed to both red and green afterimages at stimulus offset. In this study we made use of the fact that long wavelength (red) stimuli elicit pupil colour responses in the 'blind' hemifield of a subject (G) with damaged primary visual cortex. Isoluminant green or blue stimuli produce little or no response. Good correlations for the same stimuli have also been found between pupillary responses in the blind hemifield, discrimination performance in 2AFC psychophysical tasks, and results of fMRI activation (Barbur et al, *Vision Research* in press). In the present study there was, as expected, a reliable pupillary constriction to the onset of a saturated red stimulus, but little or no constriction to a green stimulus in G's blind hemifield. Unexpectedly, a highly reliable pupillary constriction was observed at the green stimulus offset, when a normal subject would see the red afterimage. No significant response was observed to a red stimulus offset when a normal subject would see a green afterimage. Throughout the study, G reported being completely unaware of the green stimulus or of the red afterimage. Thus, one can detect and measure the unseen aftereffect of an unseen stimulus in the absence of VI.

◆ **Different cortical involvement in strabismic and anisometropic amblyopia, investigated with fMRI**

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We investigated the cortical involvement in the amblyopic deficit in individual strabismic and anisometropic subjects, using functional magnetic resonance imaging (fMRI). Eight patients with unilateral amblyopia (four strabismic, four anisometropic) and four normal observers were investigated psychophysically and with an fMRI protocol at 1.5 T with a gradient-echo EPI sequence.

Psychophysically, the subjects, contrast sensitivity functions, and psychometric curves were assessed monocularly and binocularly. Brain activity was assessed monocularly with horizontal and vertical gratings of four spatial frequencies (0.5, 4.0, 8.0, and 16 cycles  $\text{deg}^{-1}$ ). To obtain a complete and reliable separation of the two monocular images, the subjects wore custom-made red–green goggles; the gratings were viewed via red or green filters with spectral transmittances identical to those of the goggles. Functional images were superimposed onto anatomic reference scans. Data analysis was performed with Brain Voyager 2.5 [Goebel et al, 1998 *EJN* 10(5)].

Functional brain activity through the non-amblyopic eyes was seen for all spatial frequencies in areas V1, V2, V3, VP, and V5. In the strabismic but not in the anisometropic subjects, area V1 showed a slightly reduced response during amblyopic eye stimulation as compared to dominant eye stimulation. In all amblyopic subjects, the fMRJ correlate of the psychophysically addressed amblyopic deficit became progressively more pronounced with increasing hierarchical cortical levels, confirming previous PET studies [Imamura et al, 1997 *Investigative Ophthalmology & Visual Science* 308(4) S105].

◆ **Pattern and motion detection in blindsight**

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Blindsight is the ability of some patients with occipital lobe brain damage to discriminate unseen stimuli in the clinically blind regions of their visual fields when forced-choice procedures are used. To some people, this implies that a lesion in striate cortex produces a sharp dissociation between visual performance and visual awareness, but others have argued from signal detection theory that it is indistinguishable from the behaviour of normal subjects near the lower limit of conscious vision where such dissociation could arise from the use of different response criteria during clinical and forced-choice tests.

We tested the latter possibility by measuring the sensitivity of a blindsighted, hemianopic subject independently of response bias during yes–no and forced-choice detection of static and moving targets. We found that his sensitivity to static targets was greater in the forced-choice than the 2AFC task, whereas his sensitivity to moving targets in both tasks was identical. Difference in response bias could therefore account entirely for dissociations between yes–no and forced-choice detection of moving stimuli, but not of static stimuli, which could explain why patients with blindsight are apparently more often aware of moving stimuli than of static stimuli. The results imply that pattern detection and motion detection in blindsight may depend on different sets of neural mechanisms during yes–no and forced-choice tests.

**ATTENTION**

◆ **Attention: a peaceful haven for studies of conscious information processing**

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Over the past twenty years, research on attention has skyrocketed, increasing by 400% relative to other categories of cognitive publications. Why? I claim that it has been a cover for, and the sole fundable niche of, increasingly sophisticated work on conscious information processing. Attention originally targeted limited-capacity, selection processes. Visual-search paradigms contributed the notion that attention was required to bind features together. Dual-task studies completed the sweeping acquisition of all conscious processes by adding the notion of attentional load. Two tasks interfered if they both competed for attentional, central resources. But, selection and binding for what? And what is this central resource? The common, normally well-camouflaged answer is, of course, conscious information processing. We have recovered from behaviourism sufficiently to accept that there are internal mental states. Concrete computer examples helped. But conscious mental states seem harder to embrace—no computer examples can be of use here. So why bother? Just the word consciousness conjures up thoughts of loss of scientific credibility, two thousand years of re-entrant, philosophical debates, hucksterism, emeritus status, or worse. These are powerful sociological forces, but curiosity about conscious states has not been stemmed; instead much of it has been diverted into research labelled ‘attention’. The usefulness of this covert haven has now passed. I suggest a new division of the central pie, limiting attention to resource scheduling for the routines (individuation, translation, tracking, animation, means–ends analysis, etc) called on by the information channel it supervises—conscious information processing.

◆ **Do attentional effects differ across visual fields?**

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It has been reported that attentional resolution is greater in the lower than in the upper visual field [He, Cavanagh, and Intriligator, 1996 *Nature (London)* 383 334–337]. Because stimulus complexity and distractor heterogeneity varied across tasks in the He et al's study, we decided to further evaluate their hypothesis. We explored whether observers' performance in several detection tasks, considered to impose different attentional demands, varied as a function of the visual field in which the target appeared. Observers performed several feature-search (eg. detect a vertical target amid tilted distractors) and conjunction-search (eg. detect a red vertical target amid blue vertical and red tilted distractors) tasks. Performance was assessed by measuring speed and accuracy for targets appearing in the four quadrants of the visual field.

A significant and consistent pattern emerged for both types of search: detection was slower and less accurate in the left-lower quadrant of the visual field. However, this pattern emerged for both feature and conjunction searches, and the degree of the asymmetry did not interact with the presumed attentional demand of the task. In a second study we explicitly manipulated covert attention by peripherally cueing target location in: (a) feature-search and conjunction-search tasks, and (b) acuity tasks specifically designed to index spatial resolution (eg Landolt square). When a field asymmetry emerged it did so for both cued and neutral trials. Consistent with our previous results, the attentional effect did not differ consistently across visual fields.

◆ **Detecting scene changes: an overview and a framework for recent findings**

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Detecting even large changes in pictures of natural scenes can be very difficult if the changes are accompanied by brief transients in the visual field, for example when the changes occur at the same time as a brief flicker of the image, or if small 'mudsplashes' are spattered over the picture at the moment of the change. Similar results have also been obtained in studies where picture changes are synchronised with observers' blinks or eye movements, or when, in film viewing, they occur at the time of a film cut. In some studies, eye-movement measures show that the observer can often be looking directly at the change location and still not see it.

The findings are overviewed and related to those obtained in a new, more tractable paradigm, in which similar effects are observed with 'scenes' of alphabetic characters of different size, font, and colour.

The results are interpreted in relation to findings in visual search showing that the representation of a visual region dis-aggregates after attention leaves that region. It seems that even though observers have the impression of seeing a very rich visual environment, the only information that is available to awareness is the information that is part of the current 'centre of interest'. The results favour the theory (O'Regan, 1992 *Canadian Journal of Psychology* 46) according to which there is no picture-like internal representation of the visual field. The outside world acts as its own representation—it is an 'outside memory'.

◆ **Mismatch negativity in the visual modality**

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Auditory mismatch negativity (MMN) is a preattentive response to a discriminable change in a repeating sound. Recorded when the subject's attention is diverted from the stimulation, it takes the form of a negative augmentation of the N2 component, N2a (Näätänen, Gaillard, and Mäntylä, 1978 *Acta Psychologica* 42 313–329; Näätänen, 1995 *Ear and Hearing* 16 6–18). The present study was designed to establish whether a similar physiological correlate of preattentive processing exists in the visual modality.

Visual evoked potentials were recorded in twelve subjects (eight females, four males) from 16 electrodes (F7, Fz, F8, C3, Cz, C4, T3, T4, Pz, O1, Oz, O2) with respect to mastoids in common references and also the horizontal and vertical EOG. Traces from the 10–20 electrodes were subsequently re-referenced to Fz. Subjects fixated a blue square in the centre of a VDU screen and responded with a button press whenever the square changed to red (which it did for 200 ms at random intervals, mean 11.3 s). Periodically white bars appeared simultaneously above

and below the square, ie outside the area to which the subject was attending (SOA 612–642 ms, duration 200 ms). The bars were single or split (probability 16 : 1). Responses to the split (deviant) stimuli were significantly more negative than those to the solid (standard) stimuli from the beginning of N160 (N2) onward in recordings from posterior electrodes. The effect resembles auditory MMN in its polarity, in its distribution over the stimulated sensory cortex, and as a response to deviation in the properties of an unattended, repeated stimulus. Further work is in progress to determine whether the effect is indeed independent of attention as intended.

◆ **The role of the parietal cortex in visual attention and learning**

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Using single-pulse transcranial magnetic stimulation (TMS) we have shown that a region of the right parietal cortex is important for normal performance on difficult visual-search tasks irrespective of the location of the target in the visual field. The right parietal cortex involvement appears to be restricted to tasks with which the subject is unfamiliar and needs to perform in a serial manner. Training subjects until the task is easy (eg performed in parallel) negates the effects of TMS. Here we show, in agreement with neuropsychological findings, that the left parietal cortex is also important for some visual-search tasks but only when the target lies in the right visual field. We also show that, as one becomes trained on search tasks, the role of the parietal cortex changes at an early stage of learning (ie while subjects still find the task difficult) rather than after learning has occurred.

**COLOUR MECHANISMS I**

◆ **Colour mechanisms: from retina to cortex**

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Over the last twenty years, our understanding of colour vision has advanced significantly. In this talk I review some of the important developments during that time.

◆ **Measures of lightness constancy as an index of the perceptual fidelity of computer graphics**

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How close do 3-D computer-graphics systems come to representing real visual scenes? Often, graphics representations appear to lack the fine detail which is a common feature of the visual environment. In addition, the luminance and dynamic range of a VDU display are typically lower than those of natural scenes. Does this matter?

Existing measures of the fidelity of photorealistic graphics take account of the Fourier content of the image, but this may not reveal specific errors in the portrayal of lighting and shadows; furthermore, it could be argued that one needs a measure which involves assessment of performance on a specific visual task—performance on that task in the real scene is compared with performance in the graphics scene to give an index of fidelity. Perception of the lightness of patches varying in reflectance may be a suitable candidate for the choice of visual task. It is simple to perform, and it is known that lightness constancy depends on the successful perception of the lighting and the 3-D structure of a scene.

We have compared lightness perception in a real scene with similar perception in a particle-traced graphics representation. Fifteen subjects were required to match the reflectance of various gray patches to a reference set. For simple scenes, there was a high degree of correlation between the real and graphics results, suggesting that the graphics scenes were perceptually equivalent to the real scene. For scenes of greater complexity, this correlation may be lowered, suggesting imperfections in the graphics procedure.

◆ **Colour thresholds for elongated targets**

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Predicting the visibility of differently shaped targets in colour displays relies upon understanding the manner in which form and colour are processed.

In this study we evaluated the colour discriminability along two chromatic directions and a luminance direction for objects of several length-to-width ratios, primarily below 2 deg visual angle. In the case of luminance contrast, elongated targets should be more detectable than

compact ones of equal area, if the visual threshold is set by orientation-selective cells. If orientation and colour are processed separately, elongation of chromatic targets should not enhance their detectability. Fourteen observers were presented square or horizontal rectangular objects in the centre of a mid-level white surround on a CRT display. The aspect ratios were varied from 1:1 to 16:1 for four equal-area series. The target objects ranged in size from 0.125 deg by 0.125 deg to 4 deg by 0.25 deg. Just noticeable difference settings were made along the cardinal colour directions, red/green, chartreuse/violet, and achromatic.

Incremental thresholds for the achromatic luminance direction did show improved discrimination (approximately 30% lower thresholds) for longer narrower targets for the two largest area series. Decremental targets, however, clearly showed the opposite trend: an elongation cost, not a benefit. The discrimination thresholds for the two isoluminant colour directions (red/green and chartreuse/violet) showed no effect for any of the four areas tested. Thus, neither isoluminant nor achromatic thresholds consistently show the elongation benefit expected for orientation-selective processing; incremental achromatic targets do show it, but decremental ones do not.

◆ **The temperature effect on long-wavelength sensitivity is not significantly different in rods and cones**

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Stiles (see Lewis, 1955 *Journal of Physiology* 130 45–52) suggested that the energy needed to activate a visual pigment molecule could be supplied partly by the energy of the photon and partly by thermal energy. As molecular thermal energy is typically one order of magnitude less than the energy of 'visible' photons, a temperature effect on activation probability is expected to be apparent only for low-energy photons. The prediction is that the fall-off of spectral sensitivity in the far red should be less steep at higher temperatures. De Vries (1948 *Experientia* 4 357–358), raising his body temperature with hot baths, obtained psychophysical results in agreement with this. Stiles's theory also implies that the energy barrier for activation is lower the more red-sensitive is the pigment, eg lower in L-cones than in rods. In agreement with this, apparent rates of 'spontaneous' (purely thermal) isomerisations, estimated from response variability and receptor noise, are higher by a factor of  $10^4$  in L-cones compared with rods (Donner, 1992 *Vision Research* 32 853–866).

Accepting this, we might expect the effect of temperature on the steepness of the long-wavelength limb of the sensitivity spectrum to be smaller in L-cones than in rods. We recorded spectra of 501 nm rods and 562 nm cones in the frog retina at temperatures of ~5 and 25 °C over a wavelength range from 397 to 752 nm. There was a clear and reproducible temperature effect on the long-wavelength slope of both cone and rod spectra. For example, sensitivity at 752 nm relative to peak was more than two-fold higher in 'warm' than in 'cold' retinas. Contrary to the hypothesis, however, the temperature effect did not differ significantly between cones and rods.

Our results suggest that the temperature effect on the long-wavelength limb of the spectral sensitivity curve and the noise-derived rates of thermal events in photoreceptors do not reflect the same molecular properties. One possibility is that purely thermal isomerisations originate in a small sub-population of visual pigment molecules [Barlow et al, 1993 *Nature (London)* 366 64–66], while the long-wavelength slope is determined by the main pool of visual pigment.

◆ **Ratios of L and M cones in the normal retina**

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We estimated the ratio of long-wave-sensitive (L) to middle-wave-sensitive (M) cones in ten observers diagnosed as normal trichromats by their Rayleigh match, increment spectral sensitivity thresholds on white backgrounds, and flicker detection on chromatic backgrounds. The L/M cone ratio estimates were obtained from: (i) optical reflectance spectra of the fovea, measured with a Utrecht Retinal Densitometer; (ii) heterochromatic flicker photometric (HFP) functions, measured with a 2 deg diameter, 25 Hz (390 to 690 nm in 5 nm intervals) target, flickering in counterphase with a 560 nm standard, and superimposed on a 18 deg diameter white background; (iii) flicker nulls

for different ratios of L to M cone modulation contrast, measured at 15 Hz; (iv) sensitivity ratios for L and M cone isolating stimuli, measured at 20 Hz; and (v) flicker electroretinography (ERG), measured at different ratios of L to M cone contrast at a frequency of 30 Hz and recorded with a DTL fibre electrode.

In general, the L/M cone ratios estimated by these five procedures, which tap into processes at different levels of the retina, correlate highly. Two of the procedures—optical reflectance of the fovea and HFP—yield ratios, which range from  $-3.3$  (for a normal male) to  $-0.3$  (for a heterozygotic carrier for congenital X-linked protanopia). Given that optical reflectance of the fovea corresponds to the photopigment level, it seems likely that these estimates actually correspond closely to cone numerosity. However, the estimates provided by other procedures, such as flicker ERG, appear to be exaggerated by factors such as relative synaptic efficiency or weighting.

## COLOUR MECHANISMS II

### ◆ The structure of colour space near the neutral point

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Our goal has been to develop a nonlinear remapping of colour space that predicts perceived colour differences in simple centre-surround displays (or to prove that none exists).

Perceived colour differences near the neutral point are known to be nonlinearly related to separation in LMS space. The difference scaling methods we employ permit accurate quantitative estimation of the nonlinear distortion needed to account for perceived colour differences along any line in colour space. At the recent ARVO meeting, we reported measurements of perceived colour differences along lines in LMS space that passed through the neutral background point and parallel lines that did not. Our results were consistent with a non-isotropic, 'fish-eye' magnification of apparent colour differences near the neutral point. The magnification was symmetric in the L-M directions but asymmetric in the luminance direction. Estimated differences along the parallel line *not* passing through the neutral point were, in contrast, *linear* with separation in LMS for all subjects.

We present a model of perceived colour difference based on these data and discuss the implications of these results for later stages of colour processing as well as their possible functional significance.

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### ◆ Effects of macular pigmentation on blue-green chromatic visual evoked potentials

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A Moreland anomaloscope, modified for motion photometry, was used to assess the retinal distribution of macular pigment. Subjects set minimum motion for circular foveal and annular extrafoveal, bichromatic gratings ( $0.3 \text{ cycle deg}^{-1}$ ,  $\sim 14 \text{ Hz}$ ) composed of narrow-band wavelengths 460 nm (macular pigment absorbance peak) and 580 nm (zero pigment absorbance). The retinal absorbance profile of macular pigment was deduced from changes in the minimum motion settings with eccentricity. Chromatic grating stimuli ( $2 \text{ cycles deg}^{-1}$ ), subtending different field sizes, were generated on a colour monitor, with the use of blue and green phosphors with peaks at 455 nm and 540 nm, respectively. These were used to elicit chromatic visual evoked potentials (VEPs) from the same subjects. Colour specificity was verified by comparing chromatic onset VEPs (reflecting sustained activity) with chromatic reversal VEPs (reflecting mainly transient activity). We also used Fourier analysis whereby colour-specific responses are dominated by the fundamental and achromatic-transient VEPs by the second harmonic. The results demonstrate that blue-green onset VEPs elicited from a heavily pigmented subject contain achromatic-transient components when circular gratings greater than 4 deg are employed. Such effects are reduced when annular fields are used with isoluminance set for the annulus. VEPs elicited from subjects with less macular pigmentation contain smaller intrusions. We conclude that achromatic-transient components, produced by large blue-green gratings provide an objective index of subject-specific macular pigmentation.

- ◆ **Similar functions of hue/saturation constancy for Munsell and monitor-displayed colours**  
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Colour constancy can be evaluated on the  $u'/v'$  chromaticity plane by either confounding (by using one-dimensional Brunswik ratio, BR), or separating hue and saturation constancy (two-dimensional BR). Constancy was studied by sequential colour matching with a restricted ( $\sim 5$  s) period of adaptation to a variable illuminant (1997 *Acta Psychologica* 97 25). Colour appearance of a test stimulus, viewed under a variable illuminant (near A:  $u'/v' = 0.256/0.53$ ; greenish:  $u'/v' = 0.16/0.5$ ; bluish:  $u'/v' = 0.141/0.414$ ), was matched by a standard under illuminant C. The neutral background was about 40% darker (value 5) than the chips (value 7, chroma 4). Two types of colour stimuli were used: (i) 40 real Munsell chips, (ii) simulated equivalent colour patches presented on a Barco monitor. Under comparable viewing conditions, 1-D BRs were found to be similar functions of hue for both stimuli: slightly higher for categorical hues, but lower for hues along the illuminant changes. 2-D (vector) analysis shows that the minimal hue and maximal saturation shifts occurred along the axes of illuminant changes, but maximal hue shifts and minimal saturation shifts occurred for colours approximately orthogonal to the axis of the illuminants. An analysis of transformations which model constancy, shows both expansion along eigenvectors of the operator, and rotation. One of the eigenvectors of the operator was located close to the illuminant axis. For the bluish illuminant, however, this operator has only one real eigenvector; two other vectors are complex—the resulting operator could be described by both expansion and rotation.

- ◆ **Evidence for rectified unipolar submechanisms in the cone-opponent and luminance postreceptoral pathways**

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There is evidence that three types of postreceptoral mechanism determine detection threshold: a red-green differencing by L and M cones, a blue-yellow differencing by S with (L + M) cones, and a luminance mechanism summing by L and M cones. We used a method of noise masking to determine whether each of these is split into two separate submechanisms representing the two poles of their response (eg 'red' vs 'green'). Test stimuli were Gaussian-enveloped bars (spread = 0.5 deg for luminance, 2 deg for colour). The noise was low-pass filtered (4 cycles  $\text{deg}^{-1}$  cut-off), binary, and half-wave rectified. A sandwich (forward and backward) noise-masking procedure was used. All stimuli were represented in a 3-D cone contrast space.

Measurements of threshold vs noise-masking functions revealed distinct asymmetries of masking within all postreceptoral mechanisms. L + M (red) stimuli are strongly masked by L - M (red) noise, but are not masked by M - L (green) noise. This asymmetry also occurs for M - L stimuli, which are masked by M - L noise but not L - M noise. A similar asymmetry is found within the blue-yellow mechanism and the luminance mechanism, for which little cross masking occurs between cone increments and decrements.

We conclude that separable on and off submechanisms in the postreceptoral pathways mediate detection of red, green, blue, yellow, black, and white stimuli.

- ◆ **Intrinsic dimensionality of surface-colour representations under artificial illuminants**  
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The response distributions of the three colour-opponent visual pathways appear closely related to the first three principal components of natural surface reflectances, but since the intrinsic dimensionality of surface-reflectance variations in our natural visual environment is almost certainly greater than 3, a visual system that encodes chromatic information in a three-dimensional space underdetermines the colorimetric properties of natural surfaces. The dimensionality of the surface-colour representation could in theory be increased by comparing the different colour signals produced by viewing the same surface under different illuminants: the feasibility of such an approach is largely an empirical issue, as it requires that the projections of the different colour signals onto the three cone classes be sufficiently uncorrelated.

A computational study was designed to investigate whether the human visual system could use the diverse illumination conditions of the indoor environment to increase the dimensionality of surface-colour representations. The spectral irradiance distributions of several artificial illuminants, the principal components of the spectral reflectances of a collection of natural and man-made objects, and the CIE standard observers were combined to form a linear system of equations. By determining the conditions under which this system could be solved and the increase in dimensionality that would result, we found it possible to characterise a (non-trivial) class of surfaces whose reflectance properties could be determined more accurately if viewed under more than one artificial illuminant.

### LEARNING AND MEMORY

#### ◆ **Learning to live with conflict: Can we improve on a pair of tasks that require opposing perceptual judgments?**

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Improvement on early perceptual tasks is often stimulus-specific, suggesting an early cortical site of learning. We consider two alternative hypotheses: the 'earliest-modification' and the 'output-level modification' assumptions, which postulate, respectively, that learning occurs within the earliest representation which is selective for the trained stimuli, or at cortical levels receiving outputs from this level. Subjects performed a pop-out task using light-bar distractor elements of one orientation, and a target element rotated by 30° or 90°. The additional conflicting stimulus set had swapped target and distractor orientations. We examined learning through initial training, subsequent learning with swapped orientations, and a final re-test with the original stimuli. According to the earliest-modification hypothesis, if the task depends only on orientation discrimination, improvement should transfer across swapping. On the other hand, if performance depends on greater target than distractor salience, improving one should hinder the other. Any learning process that increases target salience relative to that of distractors for one set should decrease salience for the other, if the same cortical detection mechanism is used in both cases. We found learning does not transfer across orientation swapping. However, after swapping, a similar performance level is reached as with original orientations. Learning neither facilitates nor substantially interferes with performance with altered stimuli. The two can coexist. Coexistence of similar asymptotes for conflicting stimulus sets refutes the earliest-modification hypothesis, supporting output-level modification. We conclude that secondary cortical processing levels use outputs from the earliest orientation representation to compute higher-order structures, promoting and improving successful task performance.

#### ◆ **Visual-working-memory characteristics in monkeys with bilateral parietal cortex lesions**

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The characteristics of visual working memory were tested in a delayed-discrimination task on two groups of rhesus monkeys. The parietal cortex area 7 was removed bilaterally in animals of one group. The remaining animals served as unoperated controls. The monkeys were trained to discriminate stimuli with different shape, size, colour, orientation, as well as complicated two-dimensional scenes with various spatial relationships between components of the scene during development of a delayed (0–32 s) instrumental reflex. The results show that the duration of information storage markedly decreases (by a factor of 3–4) and motor reaction time increases in the monkeys after the bilateral lesions of parietal cortex area 7 for delayed discrimination of visual stimuli connected with spatial-relationship features. When the monkeys were required to discriminate colour or black-and-white geometrical figures of different shapes, the duration of information storage significantly decreased (by a factor of 2–3) and these changes were accompanied by a reliable increase of motor reaction time. These results suggest that area 7 is involved in the mechanisms of visuospatial information processing as well as in working memory which may be caused by the synchronisation processes which bind neurons distributed across different cortical areas in synchronised assembly activities.

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#### ◆ **Scanpath-based model of working memory in geometry**

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Eye movements and verbal protocols were recorded while subjects solved geometry problems posed with diagrams. Observed scanpaths were highly redundant: the subjects scanned diagram elements

(lines, angles, etc) repeatedly even when solving relatively simple problems. This redundancy, not evident in verbal protocols, suggested that memory for the diagram has limited persistence and must be refreshed frequently, by using visual information. This observation led to the formulation of a stochastic working memory model, which postulated that diagram elements stored in working memory drop out randomly and are immediately re-acquired by scanning relevant parts of the diagram. This model was used to estimate the capacity of working memory on the basis of the observed distribution of times between repeated scans of the same diagram elements. Estimates were close to the range of the 'magic' number  $7 \pm 2$ . Our method for estimating working memory capacity on the basis of eye movements is novel because it is used with a realistic, complex cognitive task. This contrasts with conventional memory-capacity estimates, which use simple, artificial tasks, such as the 'number recall' task. Applications of this approach to other visually guided tasks are discussed.

◆ **The effects of level of identification and prior experience on recognition thresholds for plane-disoriented pictures of familiar objects**

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In three experiments, we investigated the effects of plane rotation on the minimum presentation duration required to identify pictures of familiar objects. A briefly presented, immediately masked picture was subsequently identified with the use of an unsped picture – word verification task. Subjects selected from 126 written alternatives. The large number of alternatives ensured that visually similar response alternatives were available for all stimuli, such that a correct response required quite specific picture identification. The presentation duration of a given picture was increased incrementally until the object was correctly identified, or until the subject had had fourteen unsuccessful attempts to identify that view of the object, by which time the picture had been presented for 250 ms. Mirroring the results of speeded, unmasked picture-naming studies, plane disorientation systematically increased the minimum presentation duration required to identify a picture. The orientation effects attenuated with experience at identifying a particular stimulus, but not following general experience at the task. In addition, in contrast to recent claims, robust orientation effects were found for subordinate level items as well as for entry level items. The results bridge the findings from unsped verification and from speeded naming tasks, suggesting that the same orientation-sensitive processes are being tapped in both cases.

◆ **Neural plasticity as the basis of perceptual learning?**

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There is evidence that the visual system is not merely a hard-wired system, but shows, under certain conditions, neural plasticity [Kirkwood et al, 1996 *Nature (London)* 381 526–528]. We (Meinhardt and Mortensen, 1998 *Biological Cybernetics* in press) found in various experiments support for the notion of detection by matched filters of small spatial targets with unambiguous features. It can be shown that under suitable training conditions Hebb's rule implies that a neuron turns into a matched filter for the stimulus aspect covering its receptive field; that is, matched filters may develop for certain spatial-stimulus aspects.

In order to test this hypothesis, we carried out learning experiments combined with sensory threshold measurements in a pretest–posttest design. As sensory measures, we used line-spread functions (lines), extrapolated tuning functions (compound grating patterns), and extrapolated sensitivity functions (compound disk-patterns) obtained prior to and after the learning tasks. In the learning conditions we used Vernier tasks (lines), spatial-frequency discrimination (gratings), and an identification task (disks). The confusion matrices obtained from the identification task were analysed with correspondence analysis which allows the learning process to be represented by trajectories of the stimuli in a latent perceptual space whose dimensions correspond to the relevant stimulus aspects with respect to which the stimuli differ.

The data do not unambiguously allow us to explain the increase of performance in the learning tasks by the development of matched filters for the whole patterns, but may be interpreted in terms of detection by cell assemblies with individual neurons having adapted to stimulus aspects according to Hebb's rule.

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**THURSDAY**
**ORAL PRESENTATIONS****BINOCULAR STEREOPSIS**◆ **Recent developments in stereopsis**

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Classical work in stereoscopic depth perception had focused on geometric cues to horizontal disparity and the local properties of depth perception. One exception to this was Ogle's induced effect of vertical size differences, which generated non-local depth effects from vertical disparities. In this survey I cover the more recent progression of stereoscopic analysis through the channel structure of the underlying mechanisms, global interactions in random-dot stereograms, the increasing appreciation of vertical-disparity processing, and the role of 3-D attentional structures in the resulting depth percept. This has not been a linear progression, but a process of expanding knowledge on many fronts.

Channel structure is an issue of the tuning of the separable processing mechanisms that are identifiable psychophysically. Stereoscopic mechanisms are tuned with respect to retinal location, disparity, and spatial frequency, although our recent work suggests that the channels are limited to high spatial frequencies ( $>2.5$  cycles  $\text{deg}^{-1}$ ). Global interactions, which have been explored extensively since the development of random-dot stereograms by Julesz, take various forms from long-range inhibition to top-down influences for familiar surfaces. An extensive theory of vertical-disparity processing has been developed in the last two decades, revealing many counter-intuitive properties of depth scaling and slant perception. The interpolation process for the perceived depth surface has been explored through various conceptualisations, most concerning an attentional or adaptive reconstruction process of interpreting the most plausible 3-D shape.

This survey does not include studies of the extensive interactions between stereopsis and other compelling depth cues, but these have also shown signal advances in recent years. [Supported by NEI 7890.]

◆ **Stereoscopic slant reversals occur for horizontal disparity and overall disparity but not for vertical disparity**

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Stereoscopic slant around a vertical axis may appear reversed, especially for stimuli with strong perspective cues. Gillam (1993 *Perception* 22 1025–1036) attributed reversals to a new kind of induced effect in which the combination of zero perspective and positive horizontal disparity signals an eccentric surface, resulting in appropriate scaling of horizontal disparity. This theory predicts even stronger reversals when vertical disparity is added to the horizontal disparity in the same eye, since this will reinforce the eccentricity scaling of the surface. Previous researchers have not found slant in the reverse direction for this stimulus (an overall magnification of one eye's view) but they have not used stimuli with strong perspective information. Horizontal, vertical, and overall magnification were each imposed on one eye's view of large ( $>60$  deg) fields viewed with a NEC projection TV. Stimuli were digitised photographs of the back wall of a leaf room, or of a brick wall. Slant was monitored as it developed during a 60 s viewing period with the use of a palm board. Viewing distance was 2 m. Most subjects showed clear reversals of direction of slant which were, as predicted, more frequent for the brick wall than the leaves, and more frequent for overall magnification than for horizontal magnification, with few reversals for vertical magnification. These results indicate that both stereoscopic slant reversals and the induced effect result from a scaling of horizontal disparity for eccentricity. They do not support the view that it is a response to the deformation of the disparity field.

◆ **Predicting individual differences in cue integration in stereograms**

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In a dimly lit room we measured each observer's susceptibility to texture/outline cues compared with disparity cues in stereograms of parabolic ridges (Buckley and Frisby, 1993 *Vision Research* 33 919–934). The observer's task was to judge the amplitude of a series of ridges some of which

contained conflict between cues to amplitude and others where cues were in accord. There were marked individual differences in the cues that influenced an observer's percept in the cue-conflict stimuli. Some observers relied solely on the stereo cue, others on the texture/outline, while others relied on a combination of cues. We have tested a speculation of Frisby, Buckley, and Horsman (1995 *Perception* 24 181–198) who suggested that individual differences of this sort may be explained by an observer's resting state of accommodation in the dark (DA). Each observer's DA was measured with a Canon R1 Auto-refractor. Significant correlations were found between DA and susceptibility to texture/outline cues. Observers with high susceptibility to texture/outline cues had a DA more distant than the 57 cm screen distance. Those with DA at or close to the screen relied more on the stereo cue. The effectiveness of possible 'cures' for these individual differences is discussed. These results may help explain individual differences found when computer monitors are used for psychophysical experiments of binocular vision. They may also have important consequences for the design of virtual-reality displays.

◆ **Cyclovergence, extraretinal signals, and stereopsis**

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When a frontal surface is slanted about a horizontal axis, horizontal-shear disparities are altered, but vertical-shear disparities are barely affected. Opposed torsional eye movements (cyclovergence) create changes in horizontal and vertical shear. Howard, Rogers, and others have shown that changes in horizontal shear due to cyclovergence are not perceived as surface-slant changes because the induced vertical shear corrects the induced horizontal shear. This resistance to cyclovergence could also be accomplished by using extraretinal signals to correct induced horizontal shear. Does this means of correction exist?

Observers fixated a large cyclorotated pattern which produced cyclovergence (verified by nonius method). After 10 s, the pattern was replaced briefly by a stereoscopic surface with smooth vertical lines; vertical shear cannot be measured with this stimulus. Observers adjusted the surface slant (horizontal axis) until it appeared gaze normal. The experiment was repeated with random-dot stimuli (allowing vertical-shear estimation).

Slant settings were expressed as horizontal shear at the retina. With the vertical-line stimulus, settings varied systematically with cyclovergence. The change in proximal horizontal shear that was accepted as gaze normal was half the cyclovergence, so the gain of extraretinal correction is  $-0.5$ . With the random-dot stimulus, settings (expressed as retinal horizontal shear) varied with cyclovergence with a gain of  $-1$  because vertical shear was available.

Two means of correcting retinal disparities for cyclovergence exist. One compares horizontal-shear and vertical-shear disparities (shown previously); the other uses an extraretinal estimate of the eyes' cyclovergence.

◆ **Early vision in Oxford**

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The work of Robert Boyle (1627–1691) and Robert Hooke (1635–1703) on vision is well known. Boyle described colour contrast and a case of colour blindness, as well as commenting on aspects of binocular vision. Hooke adopted a theory of colour vision based on two components, and he made some of the first measurements of visual acuity. Less well known is the work of Jean Théophile Desaguliers (1683–1744) who gave lectures and demonstrations on many branches of natural philosophy in Oxford and London. In 1716 he reported a method of binocular combination that became widely employed in other studies of binocular vision, namely placing an aperture in such a position that two adjacent objects were in the optical axes of each eye. Under these circumstances red and green patches of silk did not mix after the manner of combining prismatic lights, but engaged in rivalry. Size perception was raised above the level of polemic by Desaguliers in 1736: when two candles of equal size were so perceived (even when one was twice the distance of the other), he substituted a smaller one of equal visual subtense for the far one, with no change in perceived size. Therefore it was apparent distance rather than physical distance that determined apparent size. Moreover, Desaguliers did not base his conclusions on his own observations but on those of "any unprejudic'd Person". He used this result to interpret the moon illusion. In addition, he speculated on the mechanisms of accommodation and binocular single vision.

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**SURFACE AND SHAPE PERCEPTION**
**◆ Surface and shape perception**

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The perception of shape is one of the most ancient topics in vision. Classically one distinguishes primarily two-dimensional shapes (in drawings, the 'visual field') and the shapes of three-dimensional, mainly rigid, objects (things in the 'visual world'). A relation between these two is the perception of three-dimensional shape from two-dimensional depictions (or renderings) which may be a uniquely human competence and has given rise to much scientific and philosophical debate. A relatively modern development (perhaps originating with Gibson, if one ignores pre-scientific contributions, and forcefully defended by Nakayama) is to put the emphasis on surfaces. This somewhat merges the 2-D/3-D approaches since many 'visual-field' phenomena as well as '3-D shape' aspects can be discussed in this setting. My recent interest has been largely in the perception of 3-D shape from 2-D renderings: Here all these approaches meet.

An aspect that has perhaps been somewhat neglected (but recently gaining much interest in computer vision) is that of 'metamerism': In probably all cases the interpretation of pictures is underconstrained by their structure. Typically infinitely many physically different scenes could have yielded the same photograph! Here the observer has to apply acquired prior knowledge and inherited good horse sense (the Gestalt apparatus), otherwise just willy nilly stick his neck out when forced to respond. Of course the retinal images are equally subject to these fundamental ambiguities.

I show examples of various ways to approach pictorial perception operationally. Typically observers agree quite well with each other in so far as the response depends causally on the data (image structure). Otherwise, we find various idiosyncrasies that tend to depend on details of the nature of the task.

**◆ Amodal completion in the absence of image tangent discontinuities**

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It has been widely believed since Helmholtz that tangent discontinuities in image contours, such as T or L junctions, will occur when one object occludes another. Here we describe a class of occlusion relationships where changes in 'border ownership' (Nakayama and Shimojo, 1992 *Science* **257** 1357–1363) and amodal completion take place in the absence of tangent discontinuities in the image. We propose that even subtle curvature discontinuities can be a signal to potential changes in border ownership, and are valid ecological cues for occlusion in certain scenes. In particular, second-order discontinuities (ie where the second derivative taken along the contour equals zero) may be interpreted as occlusion junctions in the displays presented here. A single image contour can be segmented at points of abrupt curvature change into portions owned by different surfaces. We suggest that, compared with a theory based exclusively on first-order contour discontinuities and reliability (Kellman and Shipley, 1991 *Cognitive Psychology* **23** 141–221), a theory based on surface and volume formation and the generic viewpoint assumption provides a more parsimonious explanation of these aspects of border ownership, amodal completion, and transparency perception in static monocular images. On this account, first-order and second-order image discontinuities provide context-dependent cues to occlusion that operate at a level of surface and volume representation. A final percept of surfaces and volumes and their spatial relationships is realised only after many such cues constrain one another globally. Image fragments can undergo amodal completion in the absence of either first-order tangent discontinuities or relatable contours. Several examples of this class of occlusion relationships are considered.

**◆ The 'patchwork engine': An interface between low and high levels of visual shape representation**

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A core model for mid-level vision is proposed. It involves the extraction of medial axes from boundary contours via a new method, defined in a purely Cartesian framework. The method intrinsically copes with noisy, jagged, and scaled shape outlines, and the completeness of boundary contour signals is not a prerequisite for this method to succeed. Local maxima in medial axes are isolated and grouped into meaningful ensembles. Maxima of medial axes are then used to reconstruct boundary contours as a set of silhouettes, called a 'patchwork' pattern, which corresponds

to possible image substructures. Results correspond favourably to various perceptual phenomena, including strong and weak illusory figures, and the model goes further in that it proposes a new framework for the segregation of Julesz-type textures, based on the comparison of neighbouring features in the output. The model takes various aspects of mid-level vision (eg as discussed by the Gestaltists, Marr and Ullman) into account and its interaction with lower and higher levels of vision is clearly conceptualised. It is thought to function as an interface between more realistic image representation (early vision) and more symbolic representation (higher-level vision).

◆ **The rectangularity constraint in linear perspective**

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Scenes depicted by linear perspective should appear deformed if they are not viewed from the correct viewpoint. This geometrical property of linear perspective is often forgotten because our visual experience of paintings, pictures, or movies does not reflect such deformations. There are two potential explanations for this phenomenon: either (i) linear perspective is not a fully metric depth cue so that we can tolerate deformed images (say up to an affine transformation), or (ii) linear perspective is subject to the 'relocation' of one's viewpoint to the correct location (the centre of projection); one powerful way to achieve this relocation is to assume that corners of objects are rectangular.

A psychophysical experiment was designed in the hope of deciding between these two explanations. Parallelepipeds were viewed monocularly and oriented such that their front edge was always vertical. The images were consistent with rectangular objects only if viewed from a location distinct from the actual viewpoint. Observers had to choose the face (left or right) that was the longest in 3-D. This task could be easily performed, which suggests that some metric information is available from linear perspective. However, even though the objects appeared rectangular, observers' judgments were significantly different from those predicted from the rectangularity constraint. The fit of observers' performance by a model based on the rectangularity constraint revealed an assumed viewing distance dramatically reduced as compared with the one used to generate the stimuli. In summary, the rectangularity constraint could not alone account for human performance.

◆ **'Lattice and stretch' cues: Articulating an approach to the recovery of structure in depth**

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The aim of this paper is to make explicit a natural strategy for perceiving form in depth. The strategy involves two stages. First, features are organised into sets governed by relationships which imply that conclusions about their depths are logically connected. The term 'lattice' is a graphic way of describing that kind of structure. Second, quantitative information is obtained about a few key points or relationships: and because of the relationships which define the lattice, setting those points or relationships has the effect of 'stretching' the structure as a whole in depth. Many of the cues to depth and slant discussed in psychology are naturally considered as a source of stretch parameters. However, their explanatory power depends heavily on there being a lattice which they can be used to stretch, and much less has been said about possible lattices. Computational vision offers many examples worth pursuing. The assumption that viewpoint is general is a powerful source of lattices. 'Blocks world' programs developed lattices based on that and the assumption that surfaces were plane wherever possible. Replacing assumptions about planarity with assumptions about parallels gives related results. Shading, texture, disparity, and flow with weak perspective can all define lattice-like results.

**ATTENTIONAL EFFECTS IN EARLY VISION**

◆ **Distraction of attention may control the slope of the psychometric function**

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The influential uncertainty theory attributes nonlinear contrast sensitivity near threshold to the inability of the observer to discriminate between the signal from stimulated locations and the noise from non-stimulated locations. The present study introduces an alternative distraction theory to describe the behaviour of an observer who knows exactly which location was stimulated but may miss the test stimulus because his/her attention was diverted by irrelevant (noise) signals. For any stimulus sample, the observer may tell whether it is relevant or irrelevant to the stimulus. The nonlinear effects predicted by distraction theory are similar to those predicted by uncertainty theory.

◆ **Effect of noise and attention on orientation discrimination**

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We measured the effect of attention on orientation discrimination in the presence of binary visual noise. Observers judged whether a briefly presented grating (target) embedded in a circular Gaussian envelope was tilted clockwise or counterclockwise. The target was presented together with several vertically oriented distractors. Separate psychometric functions were collected for different noise contrasts (from 0% to 100%) and number of distractors (from 0 to 5 distractors), both when the target was cued and uncued. With no distractors, cueing the stimulus had no effect on acuity at any noise level. Increasing the number of distractors decreased sensitivity in the uncued but not the cued condition. For both cued and uncued conditions, and for all numbers of distractors, adding noise decreased sensitivity, providing an estimate of internal or 'equivalent' noise. The estimate of equivalent noise did not vary with distractor number, or with cueing. For all noise levels, orientation thresholds increased with the square root of the set size. The results are consistent with a model that assumes the existence of a second-stage integrator which sums the noisy outputs of local mechanisms that analyse the orientation of the target and distractor stimuli. The integration decreases the average orientation, but also reduces noise (internal and external), accounting for the square-root relationship.

◆ **Attentional modulation of first-order and second-order motion components and their motion aftereffects**

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We have recently shown that the processing of one motion direction of a complex motion stimulus (transparent plaid) can be facilitated by directed selective attention, so that the ensuing component motion aftereffect (MAE) is lengthened in duration. In the present study, we investigated whether selective attention can influence the MAE if the complex stimulus consists of a first-order grating superimposed on a second-order grating. We used an adapting stimulus where the first-order luminance-defined component and the second-order contrast-defined component had a direction difference of 90° and were matched in motion salience. Contrast-reversing test gratings were either oriented like the attended component or perpendicular to it. We found that directed attention can very strongly increase the duration of the flicker MAE for both types of motion. The usual negative MAE is often followed by a vivid positive MAE in the opposite direction. Testing the nonattended component revealed a reduced negative MAE (as compared to a non-selective attention condition), and often only the positive MAE. We also measured the maximum time for which one component can be tracked attentionally and found that this can be done for extended periods, especially by experienced observers, and is comparable for both kinds of motion. These results have implications both for attention (different levels of motion processes can be probed in a top-down fashion) and for motion (facilitation of processing at one level can simultaneously give inhibition of processing at the other).

◆ **An attentional blink for visual motion perception**

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Subjects can identify with high accuracy a letter or digit presented briefly within a temporal sequence of other letters or digits. But, when they have to identify two letters in the sequence, their ability to identify the second is impaired if it occurs within 400–500 ms of the first. This has been called the attentional blink (AB).

We used moving random-dot patterns (RDPs) to test if an AB also exists in visual motion tasks. Subjects viewed a rapid serial visual presentation of RDPs. Discrimination of the second target was impaired when it appeared within ~500 ms of the first target. Just as previous studies with stationary stimuli, we find that the first distractor after each target is both necessary and sufficient to create an AB, and that the other distractors have little or no influence. These results suggest that the effect obtained in our motion studies is due to the same phenomenon as in the studies with letters and digits. We also found an AB when presenting a letter as the first target and a moving-dot pattern as the second target.

Our results demonstrate that allocation of attention (even to non-motion stimuli) can strongly modulate the subsequent processing of motion stimuli. Therefore, the AB is not limited to high-level cognitive tasks such as letter identification. Our results are in agreement with physiological studies in our laboratory which demonstrate strong attentional modulation of visual motion processing in early extrastriate visual cortex.

◆ **Alerting the motion system**

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In previous work, we found that a single dot moving in a consistent direction is easily detected amidst other dots in random motion. We also found that an extended trajectory (200 ms) presented at a random location in the motion noise was much more detectable than two independent 100 ms segments in noise. Our results suggest that a specific motion network selectively facilitates motion units lying along the projected path of the trajectory.

To test the specificity of this hypothetical motion network, we presented a 200 ms motion sequence at a randomly chosen location amidst random motion noise, within a 2 deg × 2 deg square centred on fixation. The subject judged which of two intervals contained the motion sequence in noise. Five different sequences were presented at random during a block of trials: (a) a 200 ms linear trajectory (normal sequence); (b) a 100 ms segment followed by a 100 ms segment moving in the opposite direction, so that the two segments pointed toward each other; (c) a 100 ms segment followed by a segment at 45° to the first; (d) a 100 ms segment followed by a segment at 45°, but offset slightly from the end of the first; (e) two 100 ms segments presented in reversed sequence (second segment located at start of first).

At all noise levels, the normal sequence (a) was the most easily detected, but surprisingly the four other sequences were more detectable than two 100 ms segments at independent locations. Apparently, the weak initial signal alerts the motion system to the location of potential features in motion, so that any subsequent motion signal in the vicinity is enhanced. This weak signal is sufficient to 'cue' the motion system to a possible object of interest.

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## ATTENTIONAL SEARCH

◆ **Limits to attentional selection for orientation**

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Attention is needed to detect change under 'flicker' conditions, where an original and a modified image are continually alternated, with a brief blank field separating them (Rensink et al, 1997 *Psychological Science* 8 368–373). To determine the efficiency of attentional selection, flicker displays were created from arrays of rectangles, with half the items black and the others white, and half the items horizontal and the others vertical. All combinations were equally likely. In half the trials, displays differed by a feature change in one of the rectangles; in the remainder, displays remained the same. Observers were asked to detect in each trial whether a change was occurring between the two alternating images.

The efficiency of selection for contrast polarity was determined by comparing search speed for unconstrained orientation change against that for orientation change where the target was always black. For display on-times of 80 ms and off-times of 120 ms, efficiency was close to 100%. The efficiency of selection for orientation was similarly determined by comparing search speed for unconstrained polarity change against that for polarity change where the target was always vertical. Here, however, a different pattern emerged: for on-times of 80 ms and off-times of 120 ms, efficiency was only 30%. This was not due to slower processing. For increasing display on-times to 320 ms caused efficiency to fall to zero. Instead, these results suggest that attentional selection for orientation is limited to only one object at a time.

◆ **Determining visual-search strategies with reaction-time models**

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Inferring visual-search strategies from reaction times has a long tradition. Recently, the classical serial/parallel dichotomy of strategies has been increasingly doubted. What search strategies are used between the two poles: 'pop-out' and 'strictly serial search'? And can they still be determined from reaction-time functions although the slope-analysing method has come to its limits?

In the present approach, reaction times were modelled as sums of the durations of successive search steps. Model parameters were task characteristics (similarity, number, and arrangement of target and distractors), and processing characteristics of the subject (eg attention dwell and shift durations). Based on current ideas about the nature and interaction of parallel and serial subprocesses in search tasks (eg guided search), several model variants were formulated and fitted numerically to empirical reaction times. From the parameter estimations, the search strategies were computed (sequence and duration of search steps in each task condition). The model fit and the plausibility of the estimated values and strategies were compared between the model variants.

The best fitting model (more than 98% explained variance) proposed that (i) more than one item can be processed in a single fixation, (ii) movement of attention is discrete and not continuous, and (iii) an explicit attention shift to the target is not always necessary before the answer. Here the estimated parameter values showed a good psychological validity (ie their relations to each other regarding the experimental conditions). Strategies were determined for a continuum of search efficiencies and agreed at the two poles 'pop-out' and 'strictly serial search' with the traditional classification by slope. All other model variants failed at least one of these criteria.

◆ **Visual search with radial frequency patterns**

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We recently introduced a new class of deformed circular stimuli called radial-frequency (RF) patterns, and have shown that human observers are exquisitely sensitive to these deviations from circularity. Here we report on the ability of observers to detect and discriminate RF patterns in a visual-search paradigm.

Three stimuli were used: circles, and RF patterns of 5 cycles and 12 cycles, in all possible target-distractor pairings. Radial-frequency amplitudes were about 8 times threshold. Patterns were bandpass in spatial frequency and had mean radii of 0.25 deg. Reaction times for target-present/target-absent decisions were measured for set sizes of 5, 10, 15, and 20 elements.

In pairings between circles and RF patterns, clear evidence of search asymmetry was found. Search times for RF targets were nearly flat: slopes of < 10 ms per item were found for target-present conditions. For circular targets in RF distractors, slopes of 40–60 ms per item were recorded. When RF targets were paired with RF distractors, results were intermediate to those described above, irrespective of whether the target was of high or low radial frequency.

These findings are discussed in the context of Treisman and Gormican's (1988 *Psychological Review* 95 15–48) findings with circles and ellipses, and in terms of our recent model of concentric units which we have argued may reside in visual cortical area V4 (Wilson et al, 1997 *Vision Research* 37 2325–2330).

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◆ **Rapid detection of shaded curved-surface targets: performance asymmetry and categorical processing**

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In a study of target detection with curved-line elements (Savage and Foster, 1995 *Perception* 24 Supplement, 123), it was shown that rapid visual processing of line curvature is categorical. Is rapid visual processing of surface curvature also categorical?

A target-detection experiment was performed in which displays comprising 9 white matte elements on a grey background were presented for 200 ms. A target element, differing in surface curvature from the uniform non-target elements, appeared with probability 0.5. Elements were rendered ellipsoids of height and width 1 deg visual angle, with two axes in the plane of the display and the third perpendicular to it. They appeared in a square region of side 22 deg visual angle and their depth was varied from 0 to 50% (non-targets) or from 0 to 66% (targets) of their height. They were shaded according to the Phong model with parallel illumination at 45° to the display in the horizontal plane.

A pronounced detection asymmetry was found: high-curvature targets among low-curvature non-targets were much more detectable than low-curvature targets among high-curvature non-targets. With low-curvature non-targets, detection of intermediate-curvature and high-curvature targets was very reliable and largely independent of non-target curvature. With high-curvature non-targets, only low-curvature non-targets were reliably detected. Thus there appear to be at least two perceptual categories for surface curvature, with more reliable discrimination between than within categories.

◆ **Probing attentional shifts in visual search**

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Parallel and serial search are assumed to differ in the attentional load that is required to detect and identify targets. The increase of mean reaction time with the number of displayed items in serial search is thought to reflect sequential shifts of focal attention among items, while parallel search characteristics are believed to reflect instantaneous target detection without attentional requirements.

We have tried to localise the momentary focus of attention in a search task, using the illusory line motion effect (Hikosaka et al, 1993 *Vision Research* 33 1219–1240). Subjects were asked to search for a vertical line in samples of up to 12 lines around the fixation point. While they performed this task, an additional test line was presented between the fixation point and one of the items. Subjects had to indicate, after their reaction to the search task, in which direction this line appeared to move. Movement away from an item was taken to indicate that attention was directed to that position. When test lines were presented after subjects had just finished their search, attention was located at the target position, and away from other items. This was the case both in serial and parallel search tasks. However, when test lines were presented at various delays before search completion, the observed variations of perceived line motion did not reflect sequential shifts of focal attention during search but targets and non-targets sometimes induced initially similar effects.

**SPATIAL VISION**

◆ **Detection and representation of variations in luminance and contrast: separate streams in spatial vision?**

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Spatial vision extracts both local luminance features and more global, texture boundaries from images. Our aim was to study both processes under comparable conditions, with the same psychophysical tasks. We used contrast-modulated (CM) gratings as a generic form of texture variation, and compared them with luminance-modulated (LM) gratings in a variety of tasks.

We measured 2AFC detection and discrimination of stationary LM and CM gratings in static 2-D white noise, to test whether separate channels are used for the analysis of LM and CM, and if so whether these channels are later integrated in perception. Sensitivity curves for LM and CM were similar low-pass functions of spatial frequency, and in both cases vertical and horizontal gratings could be discriminated at threshold. The key evidence for separate mechanisms comes from the finding that near-threshold LM gratings did not facilitate CM detection, nor vice-versa, even though each facilitates its own kind. The two channels also carry distinct perceptual labels, because near threshold LM and CM gratings can be recognised (discriminated from each other) about as well as they can be detected (discriminated from noise alone).

Orientation coding may be very similar for LM and CM, since orientation discrimination thresholds for LM and CM are about the same, and both exhibit the tilt aftereffect (TAE). Adapting to tilted LM gratings caused almost complete transfer of the TAE onto vertical CM gratings, and vice-versa, implying some form of pooling. This led us to expect an improvement of orientation discrimination when LM and CM were combined. No such improvement for LM+CM was found, even where doubling the signal strength for LM or CM alone showed clear gains in discriminability. This suggests that adaptation underlying the TAE is pooled across LM and CM channels, but orientation information is not integrated. Nevertheless, other forms of LM/CM integration (across space, or in perception of surface depth corrugation) remain quite likely and are discussed.

◆ **Sensitivity to amplitude modulation depends on carrier spatial frequency and orientation**

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It has been proposed that detection of contrast modulation involves two stages of linear filtering separated by a rectifying nonlinearity. We investigated the form of the notional first-stage filters in this scheme by measuring amplitude modulation (AM) thresholds for bandpass noise carriers whose contrast was modulated by a Gabor envelope. For isotropic carriers, AM thresholds show an inverse dependence on the spatial frequency of the carrier. For oriented carriers at low spatial

frequencies, AM thresholds vary in inverse proportion to the difference in orientation between carrier and envelope, performance being very poor when carrier and envelope are at the same orientation. This dependence on carrier orientation diminishes as the spatial frequency of oriented carriers is increased, approaching isotropic tuning at the highest frequencies tested. These results are due neither to spurious contrast structure in the carrier (AM thresholds are similar in the absence of such structure) nor to the presence of side-bands. Masking stimuli with unmodulated noise images reveals that first-stage filters are bandpass in both the orientation and the spatial frequency domain. We propose that the observed dependence of envelope detection on carrier orientation is the consequence of selective connectivity between oriented first-stage and second-stage filters, whose purpose is to dissociate the type of image structure that the first-order and second-order systems utilise.

◆ **Orientation, spatial frequency, and length tuning in Vernier acuity**

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In order to unmask the mechanisms underlying Vernier acuity, we measured the orientation, spatial frequency, and length tuning over a broad range of conditions using a simultaneous oblique masking paradigm. The test stimuli consisted of a pair of short vertical ribbons of horizontal cosine grating with a vertical Vernier offset between the ribbons. These stimuli have two important advantages for studying Vernier acuity: (i) they are localised in spatial frequency, and (ii) they are localised in their horizontal extent. The masks were superimposed sine-wave gratings which extended over the entire screen.

We found that the mechanisms underlying Vernier acuity are tuned to both orientation and spatial frequency. The peak of the bimodal orientation-tuning function varies systematically with the spatial frequency of the ribbon. The peak of the spatial-frequency-tuning function varies systematically with the ribbon length, but not with the size of the gap between the ribbons. A quantitative, template model is able to account for many features of the data, including: (i) the bimodal orientation-tuning function (despite a unilateral offset), (ii) the systematic variation in the peak of the orientation-tuning function with spatial frequency, (iii) the systematic effect of ribbon length on spatial-frequency tuning, and (iv) the effect of gap size. Our results are consistent with an ideal-observer model based on an adaptive localised template which can signal a Vernier offset with high precision.

◆ **Comparison over a distance**

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How do we compare two briefly presented stimuli that are separated by many degrees of visual angle? Little seems to be known about the precision of such judgments or about the underlying mechanisms.

We presented pairs of Gabor patches and required the subject to judge which was of higher spatial frequency. The centres of the two patches always lay on an imaginary circle of 5 deg radius and the separation between their centres could vary between 2 and 10 deg in different blocks. The centre of the arc joining the two stimuli was chosen randomly for each presentation. We ran simultaneously two randomly interleaved staircases to measure the discrimination thresholds for decrements and increments relative to a fixed reference frequency.

We found that Weber fractions were higher when the Gabor patches were separated by small distances, but then decreased and remained constant for the larger separations, ie the observer's performance was better for well-separated stimuli than for adjacent Gabor patches.

If spatial-frequency discrimination in our task depended only on local mechanisms of contrast or texture segregation, mediated by short lateral connections within striate or prestriate cortex, then one might expect the very opposite result. The elevation of threshold at short separations may arise because two adjacent Gabors in the parafovea excite common channels. But the primary interest is in the fine discrimination of stimuli separated by 10 deg: we believe that this implies a cortical level at which stimuli are represented by an abstract code, perhaps running on a central bus, rather than by the activity of single neurons with fixed meanings. Otherwise, the bulk of long connections would be too great.

◆ **Near-field visual acuity of Japanese jungle crows**

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Vision is one of the most important sensory systems in birds. Visual acuity has been studied in several species of birds, but no behavioural studies of visual acuity in crows have been reported so far. We tried to measure near-field visual acuity of three Japanese jungle crows (*Corvus leuallantii japonensis*) by means of operant conditioning. As stimuli, a grating pattern (positive) and a uniform gray (negative) were used. Subjects were trained to hold their heads in a fixed position to keep a constant observing distance. The position of the head was measured by a microsensor placed on the side panel of the cage. On each trial, a grating pattern and a uniform gray appeared on adjacent windows. When the subject pecked on the window with the grating pattern, he got food as a reward. If the correct response was more than 80%, a finer grating pattern was used in the next session. The threshold was measured by up-and-down method between sessions. The crows showed better visual acuity than pigeons (3.9–11.7 min of arc; luminance: 54.0 cd m<sup>-2</sup>) examined by the same procedure.

**IMAGE PROCESSING**

◆ **Estimating video quality with a vision model**

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The rapidly expanding market for digital video applications, including digital television, digital camcorders, digital movies on an optical disk, internet video, videophones, and various desktop video applications, has created an intense and urgent need for methods of automatically estimating the visual quality of digital video. In response to this demand, the International Telecommunications Union (ITU) has announced a competition for video quality metrics in order to move towards an international standard metric. We have developed a digital video quality metric (DVQ) based upon a model of early vision. I describe this metric, and show how it incorporates spatial, temporal, and chromatic contrast sensitivity, light adaptation, contrast masking, and error pooling, all within an extremely efficient computational design. Application of the metric to both classical psychophysical results and actual sequences of digital video of varying quality are shown. Design of such metrics is an interesting and powerful challenge for comprehensive models of early vision.

◆ **Oriented energy analysis of shape from texture**

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The projected appearance of the texture on a surface changes with surface shape. These changes are generally characterised as variations in size, density, or foreshortening of texture elements. We have characterised these as more general changes in oriented energy using a two-dimensional spatial-frequency analysis. Gratings, plaids, and noise were drawn onto planar surfaces which were then sinusoidally corrugated in depth. We computed the perspective and parallel projections of these surfaces. The projected image was divided into a grid of small Gaussian-windowed patches. 2-D fast Fourier transforms of each patch were taken. The energy spectrum of each patch was transformed into a tuning curve representing total energy within each of eight orientation ranges. Differences between these tuning curves across the image characterised changes in local oriented energy. We found that: (i) Perceptually nonplanar regions of the surface are characterised by systematic changes in oriented energy, whereas perceptually planar (or near-planar) regions of the surface show little or no change. (ii) The changes in nonplanar regions are solely due to variations in the texture that are orthogonal to the depth curvature of the surface: variations along the depth curvature contain little or no change in oriented energy. (iii) Changes in oriented energy are almost completely lost in parallel projections. We discuss heuristics for the inference of shape from texture based on the pattern of two-dimensional variations in local oriented energy.

◆ **What makes a good T junction?**

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T junctions are usually taken to signal occlusion, but some T junctions may be better indicators of occlusion than others. When a T junction results from occlusion, the visual system should categorise it as a spurious feature that is extrinsic to the contours composing the T. One important consequence of this is in motion interpretation, where extrinsic (and hence spurious) features have less influence. We made use of an example of this, the coherence of a pair of perpendicular crossbars, to assess the occlusiveness of different types of T junctions. We found that the bars

cohere when occlusion cues are present, and thus measure T-junction occlusiveness via the degree of coherence of the bars in the presence of a particular type of T junction.

We found that (i) T junctions whose heads are illusory contours are just as occlusive as luminance-defined T junctions; (ii) T junctions are more occlusive when the contour forming the head of the T is high contrast; (iii) occlusiveness also tends to be high when the contour forming the stem is low contrast (cf Shapley et al, 1995, ARVO); (iv) T-junction occlusiveness remains high despite the presence of a small but clearly visible gap between the stem and the head of the T; (v) there is a striking dependence of T-junction occlusiveness on angle: occlusiveness remains high when the angle between stem and head deviates from orthogonal by less than 40°, but then drops rapidly; (vi) the acute-angle effect can be strong enough to overcome the usual preference for slow speeds.

◆ **The effect of noise density on threshold for patterns with fixed area**

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Human sensitivity to contrast increases with area beyond the size of receptive fields in the early visual pathway. Since summation exceeds receptive-field size, the mechanism of integration must involve accumulation of, or some other lateral interaction between, signals within the early visual stream. Predictions of contrast sensitivity as a function of the input *quantity* therefore require a model of signal integration.

Observers were directed to detect spatial waveforms derived from white Gaussian noise. For a square stimulus aperture of dimensions 3.94 deg × 3.94 deg, and a stimulus made up of 128 × 128 pixels (dimensions 0.0307 deg × 0.0307 deg), the experimental variable was the noise average power. The magnitude of the noise was increased 'uniformly' across the stimulus by increasing the noise spatial density, defined as the proportion of stimulus pixels that differ in luminance from the stimulus mean, in logarithmic intervals between 0.78125% and 100%. The magnitude of these inputs is uniform in the stochastic sense, and this discounts possible effects of weighted accumulation by the visual system across the retinal plane.

Contrast threshold declined with the square root of the noise magnitude. However, a linear system driven by white noise acts as a variance estimator which would predict a linear relationship between the threshold performance of the observer and the density/average power of the waveform. Since data collected within this study demonstrate a *nonlinear* relationship, the observed data require an alternative explanation to the hypothesis of summation at threshold determined solely by quantal absorption of photons.

◆ **Membrane conductance changes in simple cells of cat visual cortex**

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The membrane conductance of simple cells in the primary visual cortex (V1) has been shown recently to grow substantially during visual stimulation. To determine the visual properties and possible synaptic origin of these conductance increases, we recorded the membrane potential of cat V1 simple cells while injecting steady currents and presenting visual stimuli of varying contrast and orientation. We analysed data from seven cells in which a range of currents elicited approximately linear membrane potential deflections. Membrane conductance grew by 20%–200% with stimulus contrast, and was maximal for stimuli with the preferred orientation. Conductance increases thus do not sharpen the orientation tuning of the cells, and do not provide a gain-control mechanism that depends on contrast alone. By modeling the neurons as simple passive cell bodies, we derived the excitatory and inhibitory synaptic conductances underlying the visual responses. The orientation tunings of excitation and inhibition were similar, consistent with recent evidence that orientation tuning is not sharpened by intracortical inhibition.

**COLOUR CONSTANCY**

◆ **Simultaneous colour constancy: How colour appearance and surface colour vary with the illuminant**

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In scenes with more than one light source subjects can set two types of colour matches across differently illuminated parts of the scene: appearance matches and surface matches. In two series

of experiments I investigated how each of the two types of matches varies with the illuminant, and whether the appearance and surface matches differ quantitatively or qualitatively.

Subjects saw CRT simulations of two identical Mondrians side-by-side: one Mondrian rendered under a standard illuminant, the other rendered under one of several test illuminants. They adjusted a matching field under the test illuminant so that it (a) had the same hue, saturation, and brightness (appearance match), or (b) looked as if it were cut from the same piece of paper (surface match) as a test surface under the standard illuminant. Matches were set for three different surface collections.

Consistent with earlier work, the surface matches showed a much higher level of illuminant adjustment than the appearance matches. Besides this difference in amount of adjustment, the appearance and surface matches showed two major similarities. First, both types of matches were well described by simple parametric models. In particular, a model based on the notion of von Kries adjustment provided a good, although not perfect, description of the data. Second, for both types of matches the illuminant adjustment was largely independent of the surface collection in the image. The two types of matches thus differed only quantitatively, there was no qualitative difference between them.

◆ **A reduced variance of receptor codes in chromatic scenes activates a 'discounting the illumination' mechanism**

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We argue that the perceptual categories 'surface colours' vs 'illumination colours' do not coincide with the corresponding physical categories. Rather, they are constituted by a set of biologically relevant features that are specific to physically contingent organism – environment relations. The experiments that we conducted within such an ethology-inspired perspective are based on two lines of argument. First, phenomenological observations (as well as physical considerations) on the relationship between illumination and object colour show that the gamut of colours tends to shrink with increasing deviation of the illumination from a white one. This gives rise to the conjecture that the visual system exploits something like the variance of receptor codes to assess the illumination. Second, there is strong empirical and theoretical evidence which suggests that centre-surround type stimuli can be regarded as 'minimal' stimuli for triggering those mechanisms of the visual system which provide basic constituents for the perceptual categories of 'illumination colour' and 'object colour' and their interplay.

In our experiments subjects made red – green equilibrium settings in centre – surround configurations with inhomogeneous surrounds. Surrounds consisted of a random structure of overlapping circles of a fixed diameter. These surrounds have been spatially modulated along the red – green axis only (isoluminance condition), along the luminance axis only (isochromatic condition), and along both axes, while keeping the space-average fixed. Our results indicate that a reduced chromatic variance in the surround increases the visual system's propensity to interpret the configuration as an illuminated scene and to activate a 'discounting the illumination' mechanism.

◆ **A fresh look at colour constancy: heuristic-based algorithms**

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In natural scenes, colours change when the illuminant spectrum changes. I suggest that the problem for the visual system to solve is not to bring about stable colour appearance under different illuminants by discounting them, but to recognise that objects are indeed being viewed under different illuminants and to discover what the illuminant properties are. For collections of flat matte surfaces under uniform illumination, object colour identification can be simplified considerably by the empirical result that sets of object chromaticities under one illuminant are approximately affine transformations of the chromaticities of the same objects under spectrally different illuminants. Affine assumptions also hold for many scenes consisting of rough, faceted, non-Lambertian surfaces. I have devised algorithms that use the affine nature of the correlation as a heuristic, and can identify objects with identical reflectance functions and surface roughness across scenes lit simultaneously or successively by two different illuminants. The correspondence problem can be solved even when surfaces are presented in different spatial arrangements under the two illuminants and when only a subset of the objects under one illuminant is present under the second. The relative chromaticities of the illuminants are estimated as part of the computation. Such algorithms can enable an observer to recognise the same objects under different illuminants despite there being a discernible shift in the colours of the objects.

◆ **Parallel processing of surface-reflectance change under illuminant change**

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The perceived relations between the colours of surfaces generally remain constant under changes in illuminant. This relational colour constancy is violated when the spectral reflectance of a surface is changed. Is such a change detected in parallel over the visual field, that is, independent of any other surfaces in the field whose reflectances remain unchanged?

In an experiment to test this question, observers were presented with computer simulations of one or more randomly positioned pairs of abutting, 1.2-deg square surfaces, each drawn randomly from the Munsell set. The array of pairs, presented on a black field, was limited to 6 deg × 6 deg at a viewing distance of 150 cm and was uniformly illuminated by randomly selected daylight. In each trial, the array was displayed undergoing either an abrupt illuminant change or the same abrupt change with just one randomly selected surface undergoing a simultaneous reflectance change. Total display duration was 2 s. Observers had to indicate in each trial whether a reflectance change occurred.

It was found that the detectability of the reflectance change decreased little as the number of pairs in the array increased from 1 to 8, and less rapidly than would be expected from serial sampling of surface locations. Fast parallel processes thus seem to underlie the detection of violations in relational colour constancy under illuminant changes.

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◆ **Remote adaptation in colour vision—experimental study**

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Our purpose was to establish the existence of remote colour adaptation and determine its origin in the visual pathway and its time frame. We refer to remote colour adaptation as the influence of remote (not-adjacent) chromatic stimuli on a centre chromatic stimulus.

We conduct a series of psychophysical experiments using stimuli projected on a CRT screen and by a high-intensity projector. We measure the amount of remote chromatic adaptation using a nulling paradigm similar to the one used by Krauskopf et al (1986 *Journal of the Optical Society of America A* 3 1752–1757). The remote area is modulated in time with frequencies of 0.5–3 Hz, while keeping the two colours complementary (to maintain a gray average). To study the origin of remote adaptation we use an eye-separation paradigm where the surrounding field and the centre field stimulate the right and left eye separately. We also vary the intensity and area of the remote field, to evaluate the spatial properties of the remote adaptation.

Experimental results show a positive nulling amplitude which indicates the existence of remote adaptation. The eye-separation paradigm suggests that the phenomenon originates from a precortical stage. The phenomenon is found to be fast (taking less than 250 ms). We suggest that this phenomenon plays a major role in colour constancy, and confront our results with a recently developed model for colour constancy (Spitzer and Rosenbluth, 1998, ARVO).

**NEURAL MODELLING**

◆ **Network model of colour representation in extrastriate cortex**

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Recent observations in monkey inferotemporal cortex indicate that most units there are colour-tuned to local patches in 1931 CIE colour space (Komatsu et al, 1992 *Journal of Neuroscience* 12 408–424). This suggests the possibility that high-level colour representations exist as a population code within what is essentially a hue-saturation space.

In this study, a 4-layer network was created and the back-propagation algorithm was used to examine how such a high-level colour representation might be implemented. The input (layer 1) consisted of the three cone types, and the output (layer 4) formed a population of units having overlapping, 2-D Gaussian receptive fields in CIE colour space. Layer 2 units were a set

of linear colour-opponent channels plus a luminance channel, and layer 3 units had properties which developed in the course of training the network to have the desired input/output relationship. The network was able to implement successfully the transform from cone responses to circular receptive fields in CIE space. The layer 3 units developed diverse properties that were difficult to classify, though they might be called 'complex colour-opponent units'. In the wavelength domain they differed from simple opponent units in having tuning curves that changed shape nonlinearly with stimulus intensity, and which could have one or two excitatory peaks. In the CIE domain, complex opponent units had a greater tendency than simple ones to respond vigorously to desaturated colours.

◆ **Ultra-rapid visual categorisation: large-scale simulations using SpikeNET**

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The ability both of monkeys and of humans to perform ultra-rapid visual categorisation of previously unseen natural scenes poses a number of problems for conventional views of visual processing. For example, we have argued that firing rate codes may not be fast enough to be compatible with the short latency of category-specific evoked potentials. An alternative scheme uses the analog-to-delay transformation characteristic of retinal ganglion cells to produce an asynchronous wave of spikes in which information can be encoded by the order in which cells fire.

To test the plausibility of this hypothesis we have performed large-scale simulations of the propagation of spikes through the visual system using SpikeNET, a neural network simulator. SpikeNET is suitable for simulating networks involving millions of neurons and hundreds of millions of connections and can be used to study a wide range of architectures. We have also been working on hardware implementations of SpikeNET capable of supporting near real-time performance. We have found that even relatively simple feed-forward architectures can perform complex visual processing tasks that include the localisation of faces in natural scenes. One of the most remarkable features of these simulations is that they can be made to work even under conditions where each neuron in the network is only allowed to emit a maximum of one action potential, thus effectively excluding any possibility of using a conventional firing rate code.

◆ **The 'two-stimulus-two-choice' paradigm for psychophysics: Range-frequency model and adaptation-level theory compared for the evaluation of stimulus frequency**

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Predictions by the range-frequency model and the adaptation-level theory were compared with respect to size judgments in an a verbal two-category experiment. Squares of different size were presented in nine different frequency distributions. After a two-stimulus-two-choice training, in which the subjects ( $N = 208$ ) learned to which of the two response categories a small or a large square belonged, a generalisation context-series test followed. The nine test series represented the nine different frequency distributions used (experimental evaluations concerned the arithmetic mean, the median, and the midpoint). Furthermore, to investigate which experimental design would be appropriate for this research paradigm, a study was carried out on the basis of both a between-subjects design and a within-subjects design.

The results largely confirmed the predictions provided by the adaptation-level theory (Thomas, 1993 *Psychological Review* 100 658–673) but not the range-frequency model (Parducci, 1983, in *Modern Issues in Perception* Ed. E A Geissler et al (Amsterdam: North-Holland) pp 262–282; Parducci, 1995 *Happiness, Pleasure, and Judgment: The Contextual Theory and Its Applications* (Mahwah, NJ: Lawrence Erlbaum Associates)). The between-subjects design resulted in larger context effects than the within-subjects design. The question is discussed why the predictions of the range-frequency model were not supported by the results of the research paradigm (stimulus generalisation) with respect to (i) the potential difference between verbal and nonverbal research paradigms, (ii) the potential difference between unimodal and bimodal frequency distributions, (iii) the specific influence of a two-category task as compared to a multi-category task, and (iv) the specific influence of memory on judgment processes.

◆ **The role of V4 concentric and radial units in form vision: a model**

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Primate area V4 is a key site in the form vision pathway, as it provides a major input to the highest areas of the ventral pathway in inferior temporal cortex. Furthermore, damage to macaque

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V4 results in extensive form vision deficits. Recent psychophysical evidence from our laboratory indicates that the human form vision system contains units that pool oriented responses from V1 so as to extract information about concentric, cross-shaped, and X-shaped configurations in the visual image. On the basis of comparisons with physiological data, we conjecture that these units reside in human V4.

We have developed a quantitative neural model of these V4 units and their interactions based upon sequential processing in V1 and V2. Concentric, cross-shaped, and X-shaped units have been simulated on several spatial scales. In addition, the model incorporates spatially localised 'winner-take-all' interactions within V4, and these provide an explanation for certain perceptual scintillations and a basis for attentional effects. V1 receptive field figure-ground effects can be predicted on the basis of V4 concentric unit feedback to V1. The model has been successfully applied to human faces and a range of natural and man-made objects.

◆ **Visual segmentation without classification: A proposed function for primary visual cortex**

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Stimuli outside classical receptive fields have been shown to influence significantly the activities of neurons in primary visual cortex. While there has been substantial experimental and theoretical interest in the phenomena and mechanisms of these contextual influences, computational insight into their roles in visual processing is limited.

It is proposed that contextual influences are used for visual segmentation. The cortex locates GLOBAL region boundaries by detecting the breakdown of homogeneity or translation invariance in the input, using LOCAL intracortical interactions mediated by horizontal connections. This is implemented in a biologically based model of V1, in which contextual influences highlight neural activities near input region boundaries. Being more salient, the boundaries can pop-out perceptually for segmentation, as demonstrated in texture segmentation and figure-ground segregation. Our proposal introduces a new framework for visual segmentation—segmentation without classification—namely, segmentation occurs without classification of features within a region or comparison of features between regions. This framework is simpler than traditional approaches, making it implementable through V1 mechanisms. However, it is powerful enough to handle segmentation problems that are tricky for traditional approaches. The model is suggested as performing pre-attentive segmentation; higher-level mechanisms are needed to refine its output. In addition, the model performs segmentation in exactly the same neural circuit that solves the dual problem of the enhancement of contours (and displays the usual phenomena of contextual influences such as iso-orientation suppression and its contrast dependence). Theoretical predictions are discussed to propose experimental tests of the theory.

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**FRIDAY**
**ORAL PRESENTATIONS****MOTION AND DEPTH PERCEPTION**

◆ **Estimating the direction of motion and time of arrival of an approaching object**

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We proposed that: (1) stereomotion and static depth perception are determined by different mechanisms; (2) binocular judgments of the direction of motion in depth of an approaching object are based on the relative activity of eight mechanisms tuned to the ratio between the left and right image velocities [1975 *Journal of Physiology (London)* **249** 387]. But this ratio is uninformative for motion within the vertical meridian. We now find that direction discrimination thresholds are the same for motion within vertical and horizontal meridians and, furthermore, are not greatly different for cyclopean and noncyclopean targets (Weber fractions for speed are identical) (1996 *Vision Research* **36** 3625). We concluded that both discriminations are cyclopean. Observers can discriminate direction [ie  $(d\phi/dt)/(d\delta/dt)$ ] while ignoring variations in both the frontoparallel-plane component of velocity  $(d\phi/dt)$  and the rate of change of disparity  $(d\delta/dt)$ , and discriminate  $d\delta/dt$  while ignoring variation in direction and distance moved. Observers can use  $(d\phi/dt)(d\theta/dt)$  to discriminate direction monocularly while ignoring variations in both  $d\phi/dt$  and rate of expansion  $d\theta/dt$  (1994 *Vision Research* **34** 163). Binocular estimates of absolute time to collision (TTC) based on the ratio  $1/[D(d\delta/dt)]$  show small (2.5%–10%) overestimations ( $I$  is interpupillary separation,  $D$  is object distance). When both monocular [ $\theta/(d\theta/dt)$ ] and binocular information is available, errors can fall to 1.3%—sufficiently low to explain the 2 ms accuracy of top sportsplayers (1998 *Vision Research* **38** 499–512; 1979 *Scientific American* **241**(1) 136–151). Monocular (but not binocular) estimates of TTC with small objects are unreliable. Similarly, monocular (but not binocular) estimates of TTC with slowly rotating nonspherical objects are unreliable.

◆ **Motion in depth can be elicited by dichoptically uncorrelated textures**

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Opposed motion of the stereoscopic half-images of an object evokes a compelling percept of motion in depth. This percept could arise from positional disparity or from interocular differences in motion signals. Correlated dynamic random-dot stereograms have been used to dissociate position and motion disparity. We have taken a different approach using uncorrelated random-dot displays. The stimulus consisted of two random-dot displays, one just above a central fixation point and a second just below the fixation point. One of these served as the test image and the other as the comparison image. The test image was typically binocularly uncorrelated; the comparison image was correlated. The half-images of both displays oscillated horizontally in counterphase. The boundaries of each image were stationary, so that there were no moving deletion–accretion boundaries. Subjects adjusted the oscillation of the comparison display until its perceived velocity matched that of the test display. The effects of variation of dot density, dot lifetime, stimulus velocity, and oscillation frequency were studied. All subjects perceived strong apparent motion in depth in the uncorrelated display. Motion in depth was often accompanied by the appearance of sideways motion. No consistent impression of depth was obtained if the motion was stopped. Thus, dynamic depth can be created by changing disparity in a display with zero mean instantaneous disparity. We propose that the impression of motion in depth arises because of the consistent sign of changing disparity between randomly paired dots.

◆ **Limits on depth scaling from motion/stereo interaction**

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Since the motion and disparity cues to depth scale differently with viewing distance, these two cues might interact to compute an estimate of the viewing distance. This estimate could be combined with other estimates (from vertical disparities, vergence, accommodation, or a default tendency). Econopoulou and Landy (1995, ARVO), following up on the work of Johnston, Cumming, and Landy (1994 *Vision Research* **34** 2259–2275), used a rotating, stereoscopically viewed cylinder, and found

that this interaction did occur and resulted in an improved viewing-distance estimate that was applied to an adjacent, stationary cylinder. Here, we examine whether this interaction affects shape judgments of a static object that is not at the same distance as the rotating object.

Two simulated, textured ellipsoids were presented in stereo on a computer screen with the use of LCD shutter glasses in complete darkness. Subjects set the width, height, and depth of each ellipsoid to match that of a tennis ball (*shape judgments*), and set the perceived distance of the right-hand ellipsoid to half that of the left-hand ellipsoid (*distance judgment*). The distance of the left-hand ellipsoid was determined at random on each trial (80–200 cm). The left-hand ellipsoid was either static (half the trials) or rotating back and forth around a horizontal axis.

As expected, rotating the left-hand ellipsoid influenced its set depth: rotating ellipsoids were set to be much more spherical. But, there was no influence of rotation of the left-hand ellipsoid on the set width, depth, or distance of the right-hand, static ellipsoid. Distance-halving judgments were poor. Two explanations of these results are: (i) Econopouly and Landy's subjects were using a strategy involving disparity matching between the two objects, or (ii) the improved viewing distance estimate can only be applied to nearby objects within a restricted range of relative disparities. [Supported by NIH grant EY08266.]

◆ **Shape-from-shading under diffuse lighting: does dark mean deep?**

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It is well known that when a smooth matte surface is illuminated by a point-light source such as the sun, the visual system may infer surface shape but only up to a twofold ambiguity. This ambiguity corresponds to a depth reversal. When the light source is diffuse, however, this ambiguity does not exist. The reason is that each convexity on the surface receives more illumination than its neighbouring concavity, and thus the convexity is brighter. Recently, it was shown that the visual system can use shading under diffuse lighting to infer qualitative shape (Langer and Bülthoff, 1997, ARVO) and that, for the class of surfaces tested, observers performed better under diffuse lighting than under point source lighting. The question arises, however, whether observers in that study were merely using a simple default model that 'dark means deep' under the diffuse condition, or whether they used a model more closely related to the actual physics of shading. Here we present results from a control experiment in which we asked observers to judge the relative depth of two nearby points. Performance was better at this task than a 'dark means deep' model would have predicted. This implies that the visual system uses a more accurate shape-from-shading model under diffuse lighting than was previously thought. A computational model of shape-from-shading under diffuse lighting offers some insights into how a visual system might achieve the improved performance under diffuse lighting.

◆ **Temporal and spatial characteristics of shape-from-shading**

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Shading within a circular aperture produces a compelling perception of depth, appearing as a spheroid 'bubble' or 'cavity' depending on the direction of the contrast gradient. Contrast sensitivity functions for the 3-D effect have been measured as a function of spatial and temporal frequency, phase, and aperture size, and compared with contrast sensitivity for detection of the corresponding 2-D pattern. Maximum 3-D effects occurred when 0.5 cycle of a sinusoidal grating appeared in the window in cosine phase at horizontal (top-lit) or oblique (top-left-lit) orientation, for all spatial frequencies. At low frequencies of temporal modulation, 'top-lit' spheroids appeared to alternate between concave and convex forms ('side-lit' spheroids are unstable even without temporal modulation). 3-D shape was not visible at the contrast detection threshold, but, for small apertures and low temporal frequencies, 3-D shape appeared at a low suprathreshold contrast, ie as soon as the circular contour of the aperture became visible. This was not the case for high temporal frequencies: the temporal sensitivity function for the 3-D percept was found to cut off at 5 Hz, compared with a high-frequency cut around 40 Hz for contrast detection. For 0.5 cycle displays, the temporal tuning of the 3-D effect was independent of spatial frequency/size except at 4 Hz, where more depth was seen at high spatial frequencies. There was a measurable tendency for displays of less than 0.5 cycle and low contrast displays to appear flatter. To conclude: detection of contrast and contour in an appropriate spatial configuration is not sufficient for the 3-D percept: temporal integration is also necessary.

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**PERCEPTION AND ACTION**
**◆ Perception in action: where are we going?**

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Gibson (1958 *British Journal of Psychology* **49** 182–194) proposed that visual perception needs to be considered in the context of the environment in which it takes place and the activities of the perceiver within that environment. Forty years on this perspective has stimulated several sub-areas of enquiry related to Gibson's exemplars of steering, aiming, and collision avoidance. Gibson's proposals on steering stimulated a body of research into the perception of heading [Warren and Hannon, 1988 *Nature (London)* **336** 162–163; van den Berg and Brenner, 1994 *Nature (London)* **371** 700–702; Banks et al. 1996 *Vision Research* **36** 431–443; Stone and Perrone, 1997 *Vision Research* **37** 573–590]. It is not clear, however, that research on heading perception generalises to active steering, but a common issue is the role of extraretinal information in heading and/or steering. Research into judging and controlling collisions has focused predominantly on the role of optic expansion (Wann, 1996 *Journal of Experimental Psychology: Human Perception and Performance* **22** 1031–1048) although there is strong evidence that binocular motion also supports such judgments (Gray and Regan, 1998 *Vision Research* **38** 499–512). We are still lacking an adequate account of how monocular (looming) and binocular inputs may be integrated in natural interceptive actions, but once again the potential role of extraretinal information, such as vergence, is under re-examination (Brenner et al. 1996 *Vision Research* **36** 699–706). This talk focuses on the two behaviours of locomotor control and anticipating collisions. We are still some distance from a comprehensive account of these everyday actions. Some consensus is emerging in recent work and an agenda for future research is taking shape.

**◆ Contributions of visual information and vestibular and somesthetic information in orientation discrimination**

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We examined the contributions of cues in the visible surround, such as the edges of the computer screen, and other sensory inputs in providing a reference for orientation discrimination. Subjects judged the orientations of Gabor patches under combinations of the following variables: extended dark field vs visible surround; subject sitting upright or lying flat to provide or reduce somesthetic and vestibular cues to principal orientations; near-principal or oblique orientations of the visual stimuli; low-spatial-frequency (2 cycles deg<sup>-1</sup>) or high-spatial-frequency (10 cycles deg<sup>-1</sup>) stimuli. Each block of trials commenced with a 20-s presentation of a high-spatial-frequency and a low-spatial-frequency reference at either 0°, 45°, 90°, or 135°. After a 10-s retention interval stimuli were presented from a low-spatial-frequency set of 11 orientations and a similar high-spatial-frequency set in randomly intermixed order. Subjects judged whether each stimulus was tilted clockwise or counterclockwise from the references. In a second experiment we used Gabor patches of low and high spatial frequency from sets of orientations with shifted midpoints, to examine sequential effects in accordance with the procedures of Lages and Treisman (1998 *Vision Research* **38** 557–572). The results show that reducing somesthetic and vestibular cues reduces accuracy in judging principal but not oblique orientations, and that the decision criterion is affected by preceding orientations dependent on spatial frequency.

**◆ The effects of head turn on the perception of gaze direction**

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We can perceive another person's gaze direction when the person is facing us. When the person's head is turned, however, gaze perception becomes inaccurate and is shifted in the direction opposite to head turn. This error has been attributed to the misjudgment of the gaze itself, but the errors in head-turn evaluation could stem from another source. Examining such a possibility was the main objective of this study. First, we measured the accuracy of gaze-direction estimation with several head-turn angles. Full-size colour photographs of faces with nine gaze directions (0°, 3°, 6°, 9°, and 12°; right and left) and five head-turn angles (0°, 15°, and 30°; clockwise and counterclockwise) were presented on a CRT and viewed at 57 cm. Results indicate that gaze perception is accurate from straight ahead, but that with a head turn a small but systematic error occurs in the direction opposite to head turn. Next, we had subjects evaluate head turns for similar stimuli by using a thumb-tack-like probe after Koenderink, and found that the head turn is

generally underestimated. The results suggest that the error in estimating gaze direction could be an effect of underestimation of head turn. We then examined this possibility by presenting synthesised images in which underestimation of head turns was compensated by adding more head turn while keeping the eyes the same. The error was dramatically decreased for these pictures. These results demonstrate that the error in gaze-direction perception is not caused by misjudgment of gaze itself, but results from an underestimation of head turn.

◆ **Eye movements during music reading: How far ahead do pianists look?**

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Playing the piano from a printed score requires the music to be fixated, deciphered, and processed in a sequential manner, and then reorganised for motor output. This is particularly difficult when sight-reading a dual-staved, previously unknown piece. To study this music-reading process, the eye movements of several pianists were recorded with a fully portable head-mounted eye tracker, which allows normal movement of the head and body. Subjects varied in skill from novice sight-reader to professional accompanist, so that different abilities could be compared. Pianists of all skill levels read dual-staved music via a zigzag pattern of eye movements, moving the gaze between the two staves. This means that the two sets of information are read independently, and must therefore be combined later on, higher up in the processing system. Additional results were acquired by obtaining a continuous eye-hand span (EHS). This is the separation between the position of the eye on the musical score and the point of performance—the 'lag' between eye and hand. The EHS was measured in time (the length of time between fixating a scored note and subsequently playing it—the 'time index') and in notes (the number of notes between hand position and simultaneous eye position—the 'note index'). These were found to show predictable differences with performance tempo and with the skill level of the subject. A faster tempo produced shorter time indexes in all pianists, but had no effect on the note index. Conversely, the mean note index was significantly affected by the performers skill, with novice pianists producing shorter note indexes than more skilled pianists.

◆ **Body sway induced by changing-disparity and changing-size cues**

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We measured body sway and the perceived magnitude of motion in depth while viewing a stimulus simulating a frontoparallel plane that is moving in depth by using changing-disparity and/or changing-size cues. The stimulus variable was the size of the changing area. Fourier transform was used to analyse the body-sway data. For the stimuli with changing disparity, the local peaks of the power spectrum were clearly observed at the frequencies of the image motion. This was not found for the stimuli with changing size.

Psychophysical results showed that the magnitude of perceived depth for the stimulus with changing disparity decreased as the size of the motion area increased, confirming previous results (eg Erkelens and Collewijn, 1985 *Vision Research* 25 583–588). In addition, changing size produced a strong sensation of motion in depth for the stimuli, irrespective of the size of the moving area. We also decomposed the disparity field simulating a plane moving in depth into two factors. The first factor was the differential perspective and the second factor was the disparity field manipulating vergence. For the stimuli with changing differential perspective, the local peaks of the power spectrum were observed at the frequencies of the image motion when the size of moving area was large. For the stimuli with changing-disparity field manipulating vergence, the local peaks of the power spectrum were not observed for the same condition of moving area.

These results indicate that changing-disparity cues are used for the control of body posture, but changing-size cues are not. Furthermore, differential perspective and the pattern manipulating vergence are processed differently for the control of body posture.

## MOTION MECHANISMS II

◆ **Perceived spatial position is altered by motion adaptation**

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Prolonged adaptation to motion in a particular direction can alter the perception of subsequently presented stimuli. Stationary stimuli can appear to move in the opposite direction whilst those moving in the same direction as the adapting stimulus can appear reduced in speed. Motion can be encoded in terms of spatiotemporal energy and thus we might expect to find changes in perceived timing and position from motion adaptation. The former has been previously reported (Bennett and Westheimer, 1985 *Vision Research* 25 565–569); here we report upon the latter.

Subjects adapted to a pattern of random lines (half dark, half light) in their upper visual field that moved horizontally at  $12.6 \text{ deg s}^{-1}$  or were stationary. They were then presented with two lines, one in the upper adapted portion of the field and one in the lower field, and made a judgment as to the offset of these lines (Vernier acuity). Both stationary and moving (in the same direction as the adaptation pattern) tests were tried. Adaptation to the moving stimuli caused a perceived shift in the point of subjective equality in the position-matching task that was consistent with the MAE or perceived slowing. This was true for physically stationary test stimuli and for the moving test stimuli. Thus the change in perceived motion caused by motion adaptation is also reflected in spatial as well as temporal judgments (see also Nishida and Johnston, this issue).

◆ **Influence of the motion aftereffect on position judgment**

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Illusory motion seen after motion adaptation (MAE) is accompanied by a change in spatial position (Takeuchi, unpublished; Snowden, 1998 *Perception* 27 Supplement, this issue). We examined how this positional shift changes over time, and how it interacts with real motion. After adaptation to a windmill (sinusoidal luminance modulation: 2 cycles/rotation, 4 deg in diameter) rotating at 6 Hz, a test windmill was presented with a given spatial phase. We measured the orientation shift seen in the test stimulus by a staircase procedure in which subjects had to compare the test stimulus (up to 2 s) with an adjacent comparison windmill (0.2 s). The test windmill appeared rotated in the MAE direction even when the comparison was presented at the onset of the test stimulus. The orientation shift increased as a function of the delay between the onset of the test and the presentation of the comparison (0–2 s). Varying the interval between adaptation offset and test onset (0.5–2 s) had no effect. The rate of change of orientation was much less than expected from the MAE speed measured by matching or nulling. When the MAE was nulled by a real motion [which by itself induced an apparent position shift (De Valois and De Valois, 1991 *Vision Research* 31 1619–1626)], the orientation shift almost disappeared. Normally, we think of the encoding of spatial position as independent of the extraction of motion information. However, these results demonstrate clear interactions between spatial analysis and motion processing.

◆ **The aftereffect of transparent motion: Integration or segregation is determined by the type of test pattern**

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After adaptation to bivectorial motion, the motion aftereffect (MAE) is generally unidirectional and opposite to the weighted vector sum of the adaptation directions. If the two motions differ substantially in speed, however, the type of test pattern largely determines the direction of the MAE. The MAE is about opposite to the fast component with a dynamic test pattern [dynamic visual noise (DVN)] and to the slow component with a static test pattern [static visual noise (SVN)].

In a series of new experiments we investigated the MAE of transparent motion using a new type of test pattern. This test pattern has static (SVN) as well as dynamic (DVN) characteristics. For these patterns, the SVN/DVN ratio (SDR) can be manipulated. This kind of test pattern reveals surprising results. After adaptation to transparent motion, the MAE is not unidirectional but transparent. One MAE direction is carried by the DVN and moves opposite to the fast adaptation component, whereas the SVN pattern carries the MAE opposite to the slow component. This effect is extremely robust. It occurs for SDRs varying from around 100 to around 0.1, for test-pattern contrasts as low as 0.04, and for a range of adaptation speeds. Moreover, the effect is perceived after adaptation to oppositely directed transparent motion, orthogonal transparent motion, and even when both components move in the same direction.

The results indicate that high-velocity and low-velocity specific channels are adapted separately. Their MAEs show up under different test conditions. The fact that we see transparent motion aftereffects when submitting them to our new test pattern makes it tempting to suggest that vector summation in the MAE is not a general rule, but occurs when only one of these channels is tapped by the test pattern.

- ◆ **The detection of motion in depth is not simply predicted from the average binocular signal**  
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The detectability of a single dot moving only in depth decreases as a function of increasing number of stationary distractors, whilst the detectability of a single dot moving laterally does not [Harris et al, 1997 *Investigative Ophthalmology & Visual Science* 38(4) S1167]. This would be predicted if the left-eye and right-eye signals were crudely summed or averaged, as the average binocular signal for motion in depth is zero. Here we test this 'crude average' hypothesis.

We measured percentage correct performance for the detection of a single dot moving along a range of 3-D trajectories as a function of increasing number of stationary distractors. The 'crude average' hypothesis would lead to the predictions that: (i) detection performance should improve as the distance moved laterally (the  $x$ -component) is increased; (ii) for any fixed  $x$ -component, detection performance should be the same irrespective of the distance moved in depth (the  $z$ -component). We report that: (i) as predicted, for a constant value of  $z$ , performance improves with increasing  $x$ ; (ii) however, for a constant value of  $x$ , performance also improves with increasing  $z$ . This is inconsistent with a mechanism based solely on a crude average or sum of the left-eye and right-eye signals.

The combined results indicate that performance improves with increasing distance moved in both the  $x$  and  $z$  directions. However, the two components do not have equal weighting for detectability, since the value of  $z$  required for a certain level of performance is considerably larger than the equivalent value of  $x$ .

- ◆ **Spatial integration of temporally modulated gratings**  
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For stationary sinusoidal gratings contrast sensitivity first increases with grating size and then saturates, indicating that the visual system is able to integrate spatial contrast information over a limited area only. The saturation of integration takes place at an approximately constant number of grating bars, indicating scale invariance of spatial integration. We studied whether the visual system can integrate spatial information when grating stimuli are moving, and if so whether the scale invariance of spatial integration holds for temporally modulated gratings.

We measured contrast sensitivity for cosine gratings as a function of area of 1 to 8 cycles at low (1 cycle deg<sup>-1</sup>) and high (6 cycles deg<sup>-1</sup>) spatial frequency and a range of temporal frequencies (0.5–16 Hz). As with stationary gratings, contrast sensitivity first increased as a function of grating area and then saturated at an approximately constant number of grating bars in all stimulus conditions. Thus, spatial integration seems to operate in a similar manner for stationary and moving gratings.

## TEMPORAL PROCESSES

- ◆ **Linear luminance processing in motion and flicker**  
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Is luminance processing logarithmic or linear? A grey spot looks darker on a light surround than on a dark surround. But a spot that flickers between black and white shows flicker-augmented contrast (FAC), looking almost white on a dark surround and almost black on a light surround.

*Reason:* The phase with the higher contrast is favoured disproportionately. Also, in cross-over motion a black spot interchanges luminances with a nearby white spot.

*Result:* On a light [dark] surround the black [white] spot appears to jump, so that apparent motion is assigned to the spot with the higher contrast. The null luminance for the surround, at which both simultaneous contrast and crossover motion seemed to disappear, was the arithmetic (not geometric) mean of the black and white, both for FAC and for motion.

*Conclusion:* In both motion and flicker, the visual system disproportionately favours spots with higher contrast, and luminance is processed linearly, not logarithmically.

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◆ **Chromatic and achromatic processing show different temporal characteristics: further evidence based on detection probabilities**

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There is evidence from several recent reaction-time studies that chromatic changes of colour stimuli are mediated by sustained-like mechanisms, while transient-like mechanisms are responsible for achromatic changes. These results suggest a number of hypotheses about the detectability of colour stimuli that vary over time. First, the probability of detecting a transition between two isoluminant stimuli a and b should increase with the length of the time interval following the change. Second, a short chromatic peak at the onset of stimulus b should not substantially improve detectability. Third, detecting pure luminance changes should be hard (easy) when the transition from one level to the other is smooth (abrupt). And fourth, stimulus duration should have no effect on the detectability of pure luminance changes.

These hypotheses were tested in a detection experiment that used uniform 1.3 deg × 1.3 deg square light patches as stimuli. In each trial, three stimuli were presented in successive time intervals of equal duration. One of the stimuli showed a (chromatic or achromatic, abrupt or gradual) change after 780 ms, and the subject had to indicate the position of that stimulus.

While independent of stimulus duration, the detectability of pure luminance changes is markedly reduced by smooth transitions. Short and medium stimulus durations facilitate the detection of chromatic changes, but performance decreases for longer durations. This is consistent with the idea of a slow detector mechanism adapting to the current level of activation. For chromatic changes with short initial peaks, however, the results deviate from the predicted pattern.

◆ **Pulse detection on flickering backgrounds: effects of test pulse polarity**

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In recent studies (Hood et al, 1997 *Vision Research* 37 1177–1191; Wu et al, 1997 *Journal of the Optical Society of America A* 14 2367–2378; Snippe et al, 1997 *Perception* 26 Supplement, 25) detection thresholds have been measured for brief luminance pulses presented on flickering backgrounds. Thresholds depend strongly on the timing of the test pulse in the background modulation cycle, even for high frequencies (30–40 Hz) of the background flicker. These rapid threshold variations have generally been interpreted as due to a luminance adaptation process that is sufficiently fast to follow these high-frequency modulations. However, if the measured threshold variations are indeed caused by a fast adaptation of sensitivity to the background luminance, one would expect that these variations are independent of the precise nature of the test pulse that is used to probe this sensitivity.

We tested this prediction by comparing detection thresholds for positive test pulses (a brief, spatially localised increment of the background luminance) with those for negative test pulses (a brief and local decrement of the background luminance). Both test signals were presented at various phases in the background modulation cycle. We find that at many modulation frequencies the phase-dependence of the detection thresholds is dramatically different for positive and negative test pulses. Hence threshold variations in this task cannot be simply interpreted as sensitivity changes of the visual system caused by the background modulation: interactions of the test pulse with the background modulation cause at least part of the observed threshold variations. We discuss the possible nature of these interactions.

◆ **Temporal integration and visual persistence with different kinds of objects**

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Form-part integration tasks were performed in which the subject was presented with square arrays of sixteen positions in two successive presentations with eight forms presented on the first presentation and seven on the second (or vice versa). The subject's task was to detect the missing position. Several types of forms were used: those defined by a (i) luminance difference, (ii) colour difference, (iii) relative-motion difference, (iv) depth difference of random noise, (v) texture difference, and (vi) instantaneous transition (transient) of random static noise. In all cases, performance was recorded as a function of stimulus onset asynchrony (SOA), and the SOA at which performance reached asymptotic levels was noted. The asymptotic SOAs were shortest for the luminance dots (about 100 ms) and longest for the transient-noise condition (about 220 ms). Furthermore, performance asymptoted at higher levels in the transient-noise condition. These results were fit with a variant of the Dixon and Di Lollo (1994 *Cognitive Psychology* 26 33–63) filter-correlation model. While there are several free parameters, the best fits seemed to require filter time constants that were several times longer in the transient-noise condition.

A second experiment was performed in which the luminance and transient-noise forms were mixed, the initial presentation being all of one type and the second presentation all of the other. The data fell in between the all-luminance and all-transient forms in terms of asymptotic SOA, but there was an asymmetry between the two. The luminance–transient condition yielded better performance, as evidenced by a slower performance decrement with increasing SOA and a higher asymptotic level. The finding of better performance in the luminance–transient condition was predicted (at least qualitatively) by the model, but the model did not predict the different asymptotic levels.

◆ **Visual synchrony affects grouping and segmentation**

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One of the most attractive schemes proposed to underly binding and segmentation of visual information in the nervous system is temporal synchrony. If synchrony plays a major role in binding, one would expect that grouping and segmentation are facilitated in visual displays that induce stimulus-dependent synchrony by temporal manipulations. We report two sets of experiments demonstrating that visual grouping is facilitated when elements of one percept (are presented simultaneously and) are temporally separated, on a scale below the integration time of the visual system, from elements of another percept (or background elements).

In the first set of experiments we tested grouping within a symmetric square lattice display, which is typically perceived as either rows or columns. It was found that the temporal structure in which lattice elements are presented, affected subjects' perception; subjects tended to group the elements as rows or columns depending on whether elements were presented together, according to a spatiotemporal design that favoured those configurations. In the second set of experiments we tested the effect of temporal structure on a task of target detection from background. It was found that target detection was improved when target elements are presented together and separately from background elements (with a time delay of 13 ms). Control experiments indicate that the effect is due to a global mechanism of grouping and not to a local mechanism of motion computation, and that grouping by temporal asynchrony interacts with spatial information (excluding a simple decision mechanism based on two independent sources of information).

**CONTRAST INTERACTIONS AND GAIN CONTROL**

◆ **Visual processing of contrast patterns speeds up at high contrasts—one mechanism or two?**

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The visual processing of contrast patterns is faster at high contrasts. In this talk I review the evidence that this effect is due to the involvement of one mechanism or two mechanisms.

◆ **Two processes underlie centre–surround contrast suppression?**

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Orientation-tuned contrast gain-control processes may mediate centre–surround contrast interactions. We extended previous work with simple modulations in centre and surround to include plaid modulation patterns in order to assess contributions of gain-control processes that pool over orientation. We measured apparent contrast of a centre disk embedded in a surround using three stimulus configurations and two phase relations ( $0^\circ$  or  $180^\circ$ ): (1) identical vertical sinusoidal gratings ( $1.5 \text{ cycles deg}^{-1}$ ) in centre (19% contrast) and surround (5%, 25%, 10% contrast); (2) same as (1) but with a horizontal masking grating superimposed on the surround; (3) same as (2), but with a horizontal grating added to the centre. Observers compared test centre to an identically modulated disk with no surround. Comparison disk contrast was varied in a 10-step, 2AFC method of constant stimuli. The point of subjective equality (PSE) was estimated from each resultant psychometric function, and its difference from the physical contrast taken as the measure of suppression or enhancement.

The results were as follows. Simple sinusoids,  $0^\circ$  phase: contrast was strongly suppressed at high contrasts; suppression became weaker at lower surround contrasts. Simple sinusoids,  $180^\circ$  phase: no suppression occurred at any surround contrast. Horizontal grating added, surround only,  $0^\circ$  and  $180^\circ$  phase: no effect on suppression. Horizontal grating added to centre and surround: suppression occurred in both phase relations, and depended on surround contrast. No facilitation occurred in any condition. Our results suggest that gain-control processes pooling over orientation

are also involved in contrast-contrast phenomena, but only interact among themselves and do not interact with orientation-tuned processes.

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◆ **Direction specific contrast gain control**

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The perceived contrast of a central patch of visual texture depends upon the contrast of surrounding texture such that a high-contrast surround reduces the apparent contrast of the centre (Chubb et al. 1989 *Proceedings of the National Academy of Sciences of the USA* 86 9631–9635). This reduction is orientation and spatial-frequency specific. In our study the centre and surround contained drifting samples of random visual texture. Centres drifted to the left. We used a 2AFC paradigm to determine the effect of surround direction on apparent centre contrast. Five directional differences between the centre and surround were tested (0°, 45°, 90°, 135°, and 180°) and it was found that as directional difference decreased, the apparent centre contrast decreased. This supports the suggestion that contrast gain control is tuned for direction of motion.

◆ **Gain-control and integration processes in line-coding and edge-coding mechanisms**

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Lines and edges have broad spatial-frequency spectra, and mechanisms which code them probably combine signals from different spatial-frequency ranges. To investigate these coding processes, we had viewers judge the orientation of spatially localised stimuli, each of which comprised two spatially superimposed components drawn from different spatial-frequency ranges. Orientation judgments were used because of existing evidence that such judgments reflect processes which combine signals from different frequency ranges. One component of each stimulus was always a medium-frequency 'edge' (first derivative of a Gaussian bar, half-amplitude bandwidth 1.7 octaves centred on 6.5 cycles deg<sup>-1</sup>). The second component was either a low-frequency 'edge' (same bandwidth centred on 1.3 cycles deg<sup>-1</sup>) or a low-frequency 'line' (Gaussian bar, low-pass spectrum falling to half-amplitude at 1.3 cycles deg<sup>-1</sup>). Masking tests (one component varied in orientation, the other a constant orientation mask) showed mutual masking between components for both line-edge and edge-edge combinations. Cue-integration tests (both components varied in orientation) indicated that the masked signals generated by line and edge components in line-edge combinations are kept separate up to the level of decision processes, while the masked signals from the edge components in edge-edge combinations are merged prior to decision levels. The results are consistent with the proposal that line-coding and edge-coding mechanisms share a common contrast-gain-control process, but use separate, phase-sensitive summing processes to integrate signals from different spatial-frequency ranges.

◆ **Contrast facilitation by collinear flanks is abolished by non-collinear flanks**

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The contrast detection threshold for a Gabor patch is reduced by the presence of collinear flanking patches (Polat and Sagi, 1993 *Vision Research* 33 993–999). We confirmed this effect with patches of 13.3 cycles deg<sup>-1</sup> grating, identical to those used by Polat and Sagi, with a distance of 3 wavelengths between the centres of the target patch and each of the flanks. However, this facilitation was abolished by additional flanks which formed an annulus of grating completely surrounding the target. An annulus missing the collinear flanks had no significant effect on detection. Opposite-contrast-polarity flanks also had no consistent effect. These findings are compatible with a model in which second-order collector units contribute to target detection. These collector units receive excitatory input from first-order units with collinear receptive fields, but receive inhibitory inputs from non-collinear units.

## ILLUSIONS

◆ **Classifying Illusions**

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For any science, classification of phenomena and selected objects is very important—as in the Periodic Table of the chemical elements, and the Linnean System for biological species. Indeed, inductive generalisations and deductive arguments depend on classifications. Classifying phenomena of illusions should similarly be useful for understanding, and for designing experiments.

I attempt a classification of phenomena of illusions, in terms of kinds of appearances and broad kinds of causes. As many of these are controversial the classification is necessarily tentative. This may serve at least for discussion, and hopefully for suggesting defining experiments.

Kinds	Causes			
	Physics	Physiology	Cognition	
	Disturbances between light source and objects or between objects and the eyes	Disturbance of neural channels, cross-talk, spontaneous neural activity and many more	Inappropriate rules, eg perspective on a plane setting constancy scaling inappropriately	Inappropriate object-knowledge: past probabilities misleading present perception
	<b>Optics</b>	<b>Signals</b>	<b>Rules</b>	<b>Knowledge</b>
<b>Ambiguities</b>	shadows, cataract, haze	retinal rivalry, migraine patterns	figure-ground, size-distance	hollow face, Necker cube
<b>Distortion</b>	astigmatism, mirages	Café Wall, Pulfrich pendulum	Müller-Lyer, Hering, Ponzó	size-weight (smaller-heavier)
<b>Paradox</b>	looking-glass (oneself doubled)	aftereffects of motion	Penrose triangle, devil's fork	Magritte mirror (painting)
<b>Fiction</b>	rainbow, moiré patterns	afterimages, Mach bands	Kanizsa triangle, filling scotomas	faces in the fire, ink blots

- ◆ **A neural mechanism detecting depth order and contrast polarity at illusory contours**  
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In previous reports we suggested that monkey area V2 includes neurons which detect the depth order at illusory (occluding) contours, some showing this sensitivity independently of the luminance contrast at the contour, others preferring certain combinations of figure-ground direction and contrast polarity. We explained this sensitivity in terms of a model which uses 'end-stopped cells' for the detection of occlusion cues (line ends, corners). Depending on the excitatory part of their receptive fields ('simple' or 'complex'), these neurons are expected to be selective (or nonselective) for different types and contrast polarities of occlusion cues.

We therefore studied the responses of end-stopped cells in areas V1 ( $n = 39$ ) and V2 ( $n = 70$ ) of the alert monkey to light and dark bars and edges of opposite contrast polarity. We defined sensitivity to stimulus type and contrast polarity quantitatively by the responses to these four stimulus conditions. We found that 33% (36/109) of the end-stopped cells gave similar responses to all four stimulus types, 24% (26/109) preferred pairs of stimuli (bar and edge), and 43% (47/109) preferred one stimulus type. No statistical difference was found between areas V1 and V2. The results suggest that end-stopped cells vary considerably in their selectivities for stimulus type and contrast polarity, and that end-stopped cells from area V1 are just as likely as those from area V2 to contribute to mechanisms detecting depth order and contrast polarity at occluding contours. [Supported by SNF grant #5002-044891.]

- ◆ **Dynamic dependence of the scintillating grid illusion: Equivalence of afferent and efferent motion conditions**  
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In the scintillating grid illusion (SGI) apparent dark spots are perceived within bright disks superimposed on a grey Hermann grid as flashing with each flick of the eye (Schrauf et al, 1997 *Vision Research* 37 1033–1038). With steady fixation, stimulation must be brief (210–350 ms) for the illusion to occur. The dynamic dependence of the SGI was studied for a pattern consisting of a matrix of  $12 \times 8$  intersections (21.6 deg high  $\times$  14.4 deg wide). The stimulus pattern was either moved smoothly with fixed gaze centred on the pattern (afferent motion) or the eyes tracked a

small target that moved rightward through the horizontal midline of the stationary stimulus pattern (efferent motion). In both conditions, six speeds (from 2.33 to 13.39 deg s<sup>-1</sup>, in steps of 2.13 deg s<sup>-1</sup>) were used. The strength of the SGI was rated on a 5-point scale (5 maximal, 1 no effect). Mean ratings depended inversely on speed under both conditions, ie they were 4.2 (afferent) and 4.3 (efferent) for the lowest speed, decreasing monotonically with increasing speed to 1.6 and 1.5 at the highest speed. The results which show a strong SGI with slow retinal image displacement may be related to the Filehne illusion which likewise shows an inverse dependence on target speed (Ehrenstein et al, 1990 *Perception* **19** 411–412).

◆ **Defining the context in line-length illusion**

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In the parallel-lines illusion, a long contextual line (eg 105 mm) induces a robust overestimation of a proximal shorter line (eg 60 mm). We attempted to define the effective contextual stimulus for the induction of this line-length illusion. The variables of interest were the organisation of the contextual stimulus and contextual-stimulus motion. We employed solid and segmented contextual lines as well as contextual lines containing twelve non-collinear segments (experiment 1). The segmented non-collinear contextual lines differed in the organisation of the twelve segments. In experiment 2, we introduced motion of contextual stimuli. For solid and segmented collinear contextual lines, the entire contextual stimulus moved while the judged line was stationary. For the non-collinear segmented contextual stimuli, half of the contextual-stimulus elements moved while half remained stationary. Finally, we included three levels of motion of contextual-line segments (experiment 3).

The data indicate that line-length illusions can be induced by both solid and segmented collinear contextual lines. Additionally, a contextual stimulus composed of two non-collinear segments induced an illusion even when half of the stimulus moved and half was stationary. We conclude that (i) neither a solid contextual line nor collinearity of contextual elements are required to induce length illusion, (ii) the organisation of segments within the contextual stimulus is more important than the location of the endpoints of the stimulus in illusion induction, (iii) neither complete nor partial contextual-line movement diminishes the illusion, and (iv) the inferred organisation of the contextual segments is consistent with an object-based description of attention.

◆ **Perceptual segmentation and neuronal grouping in tilt illusions**

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Tilt illusion, which is the misjudgment of bar orientation in the presence of another intersecting bar, seems to result from an inherent property of cortical mechanisms underlying global perception of bar orientation. We examined how perceptual segmentation affects the amount of apparent tilt, in order to investigate whether neuronal populations are functionally grouped together and are relevant to the global perception of bar orientation. A series of visual stimuli whose segmentation was determined by contrast, color and stereo disparity was shown to human subjects, and the amount of apparent tilt measured quantitatively. The results indicate that the amount of apparent tilt is independent of perceptual segmentation but dependent on contrast. For further analyses, we developed a network model consisting of V1 neurons and a process for grouping the neuronal activities. The simulations of the model indicated that most V1 neurons show responses which correspond to the tilt effects induced by the local geometry of the stimulus configuration and the receptive-field structure. Grouping V1 neurons by excluding the bar intersections, the model reproduced the apparent bar orientations in good quantitative agreement with the results of comparable psychophysical experiments, including the different apparent tilts induced by contrast variation. The results suggest that the tilt illusion perceived with intersecting bars depends on the local geometry of stimulus configuration and receptive-field structure, rather than on global aspects of image segmentation.

**OBJECTS AND SYMMETRY**

◆ **Robustness and sensitivity to noise in visual detection of bilateral mirror symmetry**

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We examined the effects of three different types of perturbation on symmetry detection in patterns consisting of forty dots. In the case of parallel noise, symmetric dots were displaced over a small

distance in a direction parallel to the axis of symmetry (which could be vertical, horizontal, left-diagonal, or right-diagonal, in separate blocks). In the case of perpendicular noise, symmetric dots were displaced in a direction perpendicular to the axis of symmetry, whereas in the case of random noise, they were displaced in a completely random direction. Robustness of symmetry detection to five levels of noise for each of these three types of noise was tested by asking one group of observers to discriminate between symmetric patterns (either perfect or perturbed) and completely random patterns. Sensitivity was tested by asking another group of observers to discriminate between perfectly symmetric patterns and all others (perturbed symmetric or random). Stimulus patterns were presented for 150 ms. In the (perfect or perturbed) symmetry versus random discrimination task, the proportion of symmetry responses did not decrease differentially with noise level across the three noise types. In the perfect versus perturbed symmetry discrimination task, sensitivity was lower for perpendicular perturbations than for the other two noise types. Perturbations were easier to detect with a vertical axis than with a horizontal axis, but this effect interacted with noise type. Oblique orientations yielded intermediate performance levels across all noise types. Results are discussed in terms of current symmetry-detection models.

◆ **Detection of bilateral symmetry: interaction of convexity and closure**

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We studied the speed with which observers could detect bilateral (reflectional) symmetry in drawings that incorporated symmetric contours within single objects or across different objects. This factor, called objectness or closure, is known to affect speed of symmetry detection, producing a single object advantage. Praeganz is also a grouping factor that affects symmetry detection and interacts with closure (Bertamini, Friedenberg, and Kubovy, 1997 *Acta Psychologica* 95 119–140). Another important grouping factor, namely convexity, is known to affect comparisons between contours (Gibson, 1994 *Journal of Experimental Psychology: Human Perception and Performance* 20 203–207).

We tested how convexity interacts with closure, under the hypothesis that both should speed up symmetry detection because of their power to group contours into objects. We used two types of contours, forming convex, eg < >, or concave, eg > <, shapes around the axis of reflection. Results show that convexity affects detection of symmetry, but only because it produces a strong crossover interaction with the effect of closure,  $F_{1,13} = 21.2$ ,  $p < 0.001$ . Our interpretation of these results suggests an hierarchy where convexity is secondary (or relative to) closure.

◆ **Scenes, objects, parts: A reference frame hierarchy?**

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When human observers have to judge which of two vertices is higher in the visual field, they perform this task faster when both vertices belong to a single object than when they belong to two separate objects (two-object cost). An explanation for this difference is the assumption that the human visual system derives routinely two types of reference frames: (i) a scene-based frame, which describes the relative location of the objects; (ii) an object-based frame which describes the location of the parts of a single object relative to each other. From this assumption it follows that the height difference between the vertices of a single object is directly represented in the object-based frame, whereas the height difference between the vertices of two separate objects is only indirectly available. The transformation that is necessary to make this height difference explicit is responsible for the observed two-object cost.

In our present research, we addressed the question whether this hierarchy of frames of reference extends to the parts of single objects. Are parts of an object assigned individual reference frames as well? We hypothesised that the presence of deep concave cusps decomposes an object into such parts. Therefore, when the vertices of a single object are on the opposite sides of a deep concave cusp, the height judgment task should yield slower reaction times than when the vertices are not separated by a concave cusp. We indeed found this effect: two-part judgments are 40 ms slower than single-part judgments.

◆ **The differential effects of simultaneous and successive axis orientation cuing on the detection of bilateral symmetry in dot patterns**

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Corballis and Roldan (1975 *Journal of Experimental Psychology: Human Perception and Performance* 1 221–230) obtained speeded judgments of whether dot patterns were bilaterally symmetrical

about, or translated across, a line. Reaction times were shortest for vertical lines, increasing as the line's angle with vertical increased:  $90^\circ$  (vertical)  $> 45^\circ = 135^\circ > 0^\circ$ . Because almost identical results occurred with trials blocked by axis orientation, Corballis and Roldan concluded that subjects cannot prepare by rotating a mental frame of reference in advance. Since most other symmetry studies have found that  $90^\circ > 0^\circ > 45^\circ = 135^\circ$ , the axis line may have made oblique judgments easier than otherwise; or translated rather than random nonsymmetrical patterns may have induced mental rotation. Also, blocking trials may have been ineffective because blocking cannot provide incremental benefits over those already provided by the axis lines. Four experiments show that cue lines produce an advantage but only in the absence of axis blocking: that blocking reduces RTs significantly more than when a cue line is present without blocking; that the type of nonsymmetrical foil makes no difference; and that the usual axis orientation ordering of  $90^\circ > 0^\circ > 45^\circ = 135^\circ$  is markedly attenuated by simultaneous but not successive axis lines. Simultaneous axis line cues thus provide larger benefits to diagonal than  $0^\circ$  axis processing, compared to successive or no cue conditions. These results are inconsistent with the view that axis cue lines and axis blocking are equivalent treatments. Instead, it appears that unblocked line cues require finite processing time and, under blocking, subjects can prepare for the expected orientation. There was no suggestion anywhere of the  $V > D > H$  axis ordering which Corballis and Roldan (1975) reported.

◆ **From spatial filters to mirror symmetry: New findings and a new model**

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We have a limited understanding of how our visual system extracts mirror symmetry from spatially oriented filters. Recent studies argue that structure oriented either parallel or perpendicular to the axis of symmetry is important. However, symmetry is defined by a continuum of mirror orientations of which parallel and perpendicular are only special cases. We report experiments where symmetry detection was measured at selected mirror orientations.

Observers detected symmetry in random-noise patterns filtered to remove all but narrow bands of mirror orientations. The orientation content was systematically varied over the full continuum. Correct detection rates of 75% were estimated in a 2AFC task where varying degrees of phase jitter determined performance.

In line with previous results, resistance to phase jitter is worst with structure parallel to the symmetry axis and best with structure perpendicular to it. However, the key new finding is that performance approximates a quarter-cycle sine function as orientation varies from parallel to perpendicular. We model the results in terms of the pooled response of mirror pairs of oriented filters with adjacent positions on either side of the symmetry axis. The critical feature is that spacing between filters depends on their aspect ratio so as to minimise overlap. Filters parallel to the axis integrate less information and have a lower density of independent symmetry samples than their perpendicular counterparts. This predicts the observed sine relationship between performance and mirror orientation. It also predicts that the size of the symmetry-integration area covaries with orientation content; we are currently testing the latter prediction.

**WAYFINDING**

◆ **Speed can influence aim-point judgments even before illusory depth cues enter the picture**

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Recent work indicates that viewers can judge self-motion direction accurately in the azimuth dimension and that illusory depth cues can influence heading perception when appropriate extra-retinal pursuit information is unavailable (Banks et al. 1996 *Vision Research* 36 431–443; Beusmans and Richards, 1994 *Perception* 23 Supplement, 19).

In two experiments, we measured directional judgments for movements varying in the elevation dimension, as occurs when aircraft approach a runway. In experiment 1, observers estimated aim-point elevation during self-motion simulations. Trajectories ranging from a  $6^\circ$  climb to a  $6^\circ$  sink were simulated, with three different speeds. 'Ground' scenes (containing texture in the lower visual field) were compared to 'sky' scenes (containing upper-field texture). Estimates varied monotonically with actual aim-point elevations. Fast movements elicited steeper estimates than did slow movements along equivalent trajectories. Movements approaching the ground or sky elicited steeper estimates than equivalent movements away from each texture. In experiment 2 aim-point estimates in scenes containing veridical depth cues were compared with those in scenes containing

illusory cues. Normal, veridical scenes displayed a rectilinear structure, whereas 'Ames' scenes duplicated the projected image of the normal scenes but were painted on a surface whose slant was reversed to render depth cues misleading. Ames scenes elicited directional errors consistent with the perceptual interpretation of the illusory cues. Notable findings are that camera speed influenced directional aim-point estimation, that altitude change was more salient during approach toward the ground or sky, and that pictorial cues influenced viewers' use of optic flow even when appropriate extraretinal information was available.

◆ **Lane changing without visual feedback?**

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Many well-learned and complex visuomotor tasks like grasping and bicycle riding are performed effortlessly despite little or no explicit knowledge of the required motor movements. Researchers disagree about the extent to which movement control depends on sensory feedback although it is often suggested that driving manoeuvres like lane changing or positional control can be completed without continuous visual feedback. Recently we showed that most drivers are unable to perform both phases of a lane change (pulling out and straightening the car), in the total absence of visual feedback (Wallis et al, 1997 *Perception* 26 Supplement, 100).

In a new series of experiments we sought to distinguish the mode of control for these two phases during a lane change. Subjects drove in a simulated, naturalistic environment projected on a 180 deg screen, using a force-feedback steering wheel. Subjects were required to complete the manoeuvre within a total distance of 80 m (velocity 72 km h<sup>-1</sup>, duration 4 s). In condition (a), vision was occluded 0.5 s after initiation of the manoeuvre for 1.5 s, preventing visual feedback throughout the first phase. In condition (b), vision was occluded after completion of the first phase until the end of the trial, preventing any further feedback.

In condition (a), temporary withdrawal of vision led to a production of significantly larger steering-wheel amplitudes, with a consequent overshoot in lateral position ( $p < 0.001$ ). Under condition (b), an exaggerated, complementary steering phase was observed. These results indicate that manoeuvres like lane correction or overtaking can be characterised by two distinct phases, each of which must be preceded by a critical period of visual feedback used to initiate the subsequent steering phase.

◆ **A model of visual navigation: how to explain 'place cells' and 'view cells' activities**

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We are using mobile robots with a moving CCD camera to simulate animal behaviour models (an animat). Our main concern is to understand how animals select, learn, and use visual cues to navigate in a complex visual environment. Our first interest was about place recognition. Since correlation between global panoramic views is inefficient when the animat is far away from the learned location, we have separated the 'what' (recognition of a local snapshot) and 'where' information in a model that tries to mimic the temporal and parietal ways of image processing in the mammalian brain. We have shown that a plastic merging of this information (performed in a simplified model of the hippocampus) allows construction of a robust representation of a place that can then be used to learn sensorimotor associations. They allow our robot to reach a goal whatever its original location in the test room is.

The activity of our simulated 'place cells' is very similar to that recorded in rat hippocampus. Moreover, we have shown that our robot's performance is really improved if instead of trying to give a single label for each landmark (local snapshot), we leave it to associate several labels to each of them. The choice of the relevant interpretation is then performed on the basis of the merged information. We have also shown the same model accounts for 'view cells' activities recorded in the hippocampus of primates and not in that of rats. This can be simply explained by a reduction of the animal field of view. In our system, the neurons that learned the merged representation of 'what' and 'where' information are able to recognise a view of a room whatever the distance and the orientation from the learned location is (the system only needs the view to be present in the panoramic image taken). Work in progress concerns the addition of top-down processes to bias the 'what' and 'where' activities according to the a priori knowledge of the system. We think those 'realistic' simulations are very important for better understanding of the integration problems of the current models of visual processing.

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◆ **Effects of exocentric information on performance of egocentric way-finding**

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When we move around in an unfamiliar environment, we use exocentric information such as a road map or a car-navigation system to help our way-finding based on real-time egocentric information. It has not been thoroughly understood, however, how the exocentric information interacts with the egocentric information in order to achieve appropriate navigation. We simulated way-finding in a real-world environment by a maze with the egocentric view in a virtual-reality display system. We investigated effects of concurrent or prior exocentric information on performance in a task where subjects are asked to reach a goal in the virtual-reality maze.

Although the concurrent exocentric information improved performance in general, there was no statistically significant improvement of performance by presenting the position of the observer superposed on the exocentric view as implemented in the car-navigation system. When false exocentric information was presented concurrently, performance was significantly worse than when no exocentric information was presented. It simulates a situation of losing ourselves in a real-world environment. On the other hand, performance to reach a goal in a maze did not depend on whether prior presentation of the maze was egocentric or exocentric for both the maze with many landmarks and that without any landmark. This suggests that we create a common representation of environment as a working memory for navigation.

◆ **Effect of object velocity on the discrimination of curvilinear from rectilinear self-motion**

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The flow pattern on the retinae generated by self motion is affected by objects that move independently of the observer. How does the velocity of the object affect the ability to determine the path of self-motion? We used a temporal 2AFC staircase procedure, without feedback, to determine the threshold angular speed required to discriminate curvilinear from rectilinear simulated self-motion. In some blocks a simulated object was present, in others there was not. The object consisted of a collection of dots that moved in depth toward and away from the observer. Observer and object velocity were manipulated. Results showed that the critical factor was not object speed per se, but rather the speed of the object relative to the speed of the observer; thresholds increased with relative object speed. When no object was present, thresholds increased with observer speed, but the effect of observer speed varied among observers when an object was present. Results can be explained in terms of the detectability of the rotational component relative to the translational component in the retinal flow pattern. The relative contribution of the rotational component, due to curvilinear self-motion, decreases with object and observer speed.

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## TUESDAY and WEDNESDAY

### POSTERS A

#### ATTENTION AND SEARCH

##### ◆ The conjunction of features in visual-search tasks

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In a conjunction search task, one target element differs, in half of the trials, from distractors in a combination of two features. Observers indicate whether or not a target is present. Usually, search times increase linearly with the number of items displayed, at a defined slope. Treisman and Sato (1990 *Journal of Experimental Psychology: Human Perception and Performance* 16 459–478) proposed that two features contribute additively and independently to the mean slope (of target-present and target-absent trials) of the conjunction task; hence both features are processed separately. We systematically tested many conjunction tasks to investigate this additivity assumption.

Each trial consisted of 6, 10, or 14 Gabor patches; features were 'movements', 'colour', 'contrast', 'orientation', 'spatial frequency', and/or 'stereoscopic depth'. Target and distractors differed in a conjunction of two features. To assess the additivity assumption, the differences between mean conjunction slopes were calculated for each feature pair. If the additivity assumption holds, these differences should be equal.

Differences were found not to be equal, hence we could not replicate the additive effect of features on the mean conjunction slope. Single features seem to contribute differently to different conjunctions. If both features are not processed separately in conjunction tasks, then observers might have restricted their search to elements defined by only one feature type. It is not clear, however, which feature the subjects might have chosen, since even for each individual observer no single feature led to constantly small conjunction slopes. This indicates that the choice of the searched feature type might change from condition to condition. Alternatively, the combination of two features might lead to conjunction tasks with new properties not inherent in the single features.

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##### ◆ Adaptation of fixation duration to changes in stimulus characteristics during visual search

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In search tasks that require multiple fixations, fixation durations in difficult tasks are longer than in easier tasks. We performed an experiment with the object of establishing whether fixation duration is determined by the immediate visual stimulus or is set on the basis of expectations about the task gathered during previous fixations. In a display containing 25 items placed on a hexagonal grid, subjects had to look for a single O (target) among 24 Cs (distractors). Eye movements were recorded and used on-line to trigger changes in gap size and manipulate item visibility. Item locations were visually marked but subjects could only see the item at the location at which they were directing their gaze. We compared fixation durations made when distractors had small (difficult task) or large (easy task) gaps for the entire length of the trial with ones made in trials in which gap size changed from small to large (or vice versa) after 10 fixations; 25 trials of each of these four conditions were randomly interleaved.

On average, when distractors had small gaps, fixations lasted about 75–100 ms longer than when gaps were large. When gap size changed during a trial, fixation duration also changed. Interestingly, this change was gradual rather than instantaneous and could take up to 4 fixations (ie well over 1 s). Thus the duration of a fixation is not directly determined by the immediate visual stimulus, but appears to be set on the basis of demands during previous fixations. This suggests that fixation duration is determined by a mechanism working in parallel with that performing the discrimination task.

◆ **Parallel processing of collinearity and luminance and of collinearity and colour in a visual-search task**

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Treisman's (1988 *Quarterly Journal of Experimental Psychology A* 40 201–237) original position that features (eg colour or form) are processed in a parallel fashion, producing flat search functions with increasing number of distractors, and conjunctions (eg colour and form) are processed serially, where an increase in the number of distractors results in a concomitant increase in reaction times, has been shown to be untenable. It is now clear that conjunctions may be processed in a parallel fashion as well (Duncan and Humphreys, 1989 *Psychological Review* 96 433–458). Gilchrist et al (1997 *Journal of Experimental Psychology: Human Perception and Performance* 23 464–480) investigated collinearity and luminance in a visual-search task, and found that opposite polarity contrast of paired elements did not disrupt pre-attentive grouping when the elements had collinear edges. This result supports the idea of two separate and independent modules dealing with edge information and luminance information as suggested by Grossberg and Mingolla (1985 *Perception & Psychophysics* 38 141–171).

We sought to extend this finding by demonstrating independence between collinearity and colour. We used the same experimental procedure as Gilchrist et al (1997) in which subjects have to search for two horizontally arranged elements (circles or squares) amongst increasing number of distractors, consisting of vertically arranged elements. In the achromatic condition, the two elements were either of the same (both black or both white) or opposite (one black and one white) polarity contrast. In the colour condition, the two elements were either of the same (both red or both green) or opposite (one green and one red) polarity equiluminous colour.

The results in the achromatic condition were consistent with the original Gilchrist study. The slopes of the target-present trials were comparable and relatively flat in all conditions apart from the one in which the target was defined by contrast-opponent circles. The same was true for the chromatic conditions, suggesting that collinearity and colour are also processed in parallel. The data of the target-absent trials, however, showed a much less clear pattern and seemed to indicate a more serial processing mode for contrast-opponent, collinear stimuli. These results are discussed in terms of strategy effects.

◆ **Analytic implementation of the guided-search model allows comparisons with signal detection models in target-localisation accuracy tasks**

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In the last 10 years, models of visual search have moved away from the original serial/parallel dichotomy. Recent work has been divided in broad terms into two groups. A first group of experiments measuring response times as a function of set size has been consistent with a two-stage model where a parallel system guides a serial search stage [guided-search model (Wolfe, 1994 *Psychonomic Bulletin and Review* 1 202–238)]. A second group of experiments measuring search accuracy in briefly presented displays has been quantitatively predicted by models based on signal detection theory (SDT) that consist of noisy parallel processing.

These two types of models are fundamentally different; however, progress towards achieving a consensus in the field has been hampered by the difficulty associated with directly comparing these two models. First, the two models have been developed for different experimental paradigms: SDT models for search accuracy and the guided-search model for response-time studies. Second, current implementations of the guided-search model generate predictions with the use of computationally time-consuming Monte Carlo simulations, a method that precludes fitting the model quantitatively to human data.

We present an extension of the guided-search model to generate predictions for a target-localisation-accuracy task as a function of set size. Our implementation consists of analytic mathematical expressions that allow quantitative fitting of the model to the human data in a time-efficient manner. The development of explicit analytic expressions for the guided-search model comparable to those for the SDT model will allow the direct and quantitative comparison of the ability of the two models to explain human search performance in target-localisation tasks.

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◆ **Selective processing of elemental features: beyond space-based and object-based attention mechanisms**

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A negative-priming paradigm was used to investigate the processing of an ignored feature while a second, relevant feature is selected. In the prime display of experiment 1 two features (colour and orientation) were combined within the same object (a red vertical bar), and the task was to discriminate either the colour or the orientation of the stimulus depending on an instruction cue. In experiment 2 the same features were segregated in different objects. The prime display consisted of three stimuli arranged horizontally (flankers task), and a colour or orientation discrimination was to be performed on the central stimulus (a red circle flanked by gray vertical bars). In both experiments the probe display was represented by an individual stimulus defined by a single feature (a red circle or a gray vertical bar).

Results showed a typical negative-priming effect. When the feature in the probe display was the same as the ignored feature in the prime display, probe response times were increased, suggesting that the internal representation of the ignored feature is inhibited during selection.

The results indicate the existence of an attention mechanism able to select single features within and between objects. This selective mechanism should thus be added to attention mechanisms operating on spatial regions or on integrated objects.

◆ **Characteristics of bottom-up processing in feature-defined multiple-target search tasks**

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In a typical feature-search task, a target pops out. In the guided-search model of visual search, the pop-out is explained by assuming bottom-up processing of a feature map on which a singleton was given the highest activation (Wolfe, 1994 *Psychonomic Bulletin and Review* 1 202-238). However, it has also been shown that top-down information such as knowledge of target feature is effective even in feature search (Muller et al, 1996 *Perception & Psychophysics* 57 1-17).

The purpose of this study was to examine the effect of top-down information on modulation of bottom-up activity in feature search. Three modified feature-search tasks were used: (i) target detection, (ii) target discrimination, and (iii) an homogeneity judgment. Top-down information on a target was assumed to vary with the task. Efficiency of bottom-up information was manipulated by varying the number of targets in a display, which ranged from none to all. Results from the target-detection task (experiment 1) showed that reaction time (RT) for target(s) in a single-target condition was longer than that in multiple-target conditions, suggesting that a feature singleton is not necessarily one of the most useful bottom-up sources of information for visual search. RT as a function of the number of targets in a display varied with the task (experiments 2 and 3), in spite of the same search displays being used. These results suggest that top-down processing is involved in feature search and that the weighting of it depends on the task.

◆ **Quantitative measurement of visual attention by analysing microsaccades**

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It has been demonstrated in many studies that the attentional state has a great influence on observers' performance. However, an objective estimation of the attentional state has not been proposed. To establish a procedure for the quantitative measurement of visual attention (VA), we analysed microsaccades, which are small involuntary eye movements, under the following three experimental conditions: (i) VA was focused on the foveal object, (ii) VA was dispersed in the parafoveal visual field, and (iii) VA was focused on one of the parafoveal objects.

The results showed that the frequency and amplitude of the microsaccades were markedly reduced when VA was focused on the foveal object. The frequency of the microsaccades was greater when VA was dispersed rather than focused on the parafoveal object, although the mean amplitude of the microsaccades was similar for both conditions. Microsaccades occur more frequently when VA is not focused, and the amplitude of the microsaccades decreases when VA is focused.

Our finding demonstrates the influence of VA on involuntary eye movements; hence eye movements may be used as an indicator of the attentional state, whether VA is focused or not.

◆ **Effects of an identical singleton distractor on attentional control in visual feature search**

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Three experiments were conducted to examine the effect of an identical singleton distractor to a target with respect to the target-defining feature on attentional control in orientation-search display. The subject's task was to search for an orientation-defined target and to respond to a to-be-reported attribute of the target. A search display, composed of a target and non-targets, was preceded by an identical distractor. Stimulus onset asynchrony (SOA) between the distractor and target, similarity between the target and non-target, and the number of non-targets in the display were varied as independent variables. Reaction time (RT) to the target was the dependent variable. In both high-similarity and low-similarity conditions, RT decreased with increasing SOA until 200 ms and was constant at longer SOAs (experiments 1 and 2). This result suggests that interference from an identical distractor was eliminated within 200 ms of its presentation. In the low-similarity condition, RT was independent of the number of non-targets (experiment 1). In the high-similarity condition, RT increased as a function of the number of non-targets within 200 ms of SOA (experiment 2), while RT was independent of the number of non-targets under longer SOAs (experiment 3). These results clearly show that serial target search was involved when attention was captured by the identical distractor in the high-similarity condition. Implications and possible mechanisms of the serial target search are discussed in terms of recent models of visual search and attentional capture.

◆ **Effects of positional uncertainty on the identification time of simple visual patterns**

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Identification of visual patterns is not instantaneous. An interesting question is whether even more time is required when we are uncertain about the spatial position of the pattern. We studied the effect of positional uncertainty and exposure duration on contrast threshold for the identification of the orientation ( $5^\circ$  or  $180^\circ$  vs vertical) of grating patches. The duration of the display was varied, and the target appeared either in a fixed location at the centre of the field or its location was randomly varied within an area of  $3 \text{ deg} \times 3 \text{ deg}$ . In the absence of distractors, the increase of contrast sensitivity with exposure duration was similar for the fixed-location and varied-location conditions. In the presence of distractors, the increase of performance was independent of positional uncertainty if the orientation difference was  $180^\circ$ . For these conditions, the improvement of performance with exposure time can be explained solely by temporal integration. No active search is needed. However, for an orientation difference of  $5^\circ$  between the target and distractors, the performance improved more steeply when the spatial position of the target was randomly varied than when it was fixed. The results suggest that decision processes that determine performance when the target is presented in an empty background do not require time. With distractors the dissimilarity of the target and distractors plays an important role in determining performance. Specifically, when the orientation difference is in order of orientation discrimination thresholds, the observer requires time to find the target.

◆ **Effects of practice and feedback on the detection of embedded figures**

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Studies on perceptual learning have shown that several perceptual performances may be improved through training or practice. Some results suggest that perceptual learning does not require any feedback or correction of errors but the effect of training is stronger if feedback is given. In the present study we investigated the effect of training with and without error feedback on the detection of embedded figures.

One hundred and seventy pairs of whole and segmented figures were used as stimuli. Half of them were positive items, ie the searched part actually was contained in the whole. The other half were negative items without the searched part. The stimuli were shown on a computer screen. The subjects were asked to decide whether or not the whole figure contained the simultaneously presented part figure and to give their response by pressing one of two buttons. Response latency and error rate were recorded. Eighty-four subjects took part in three sessions, each session consisting of these one hundred and seventy items. To test the effect of practice the results within

the three sessions were compared. In the feedback condition subjects were given information about their number of errors after every ten trials, whereas in the no-feedback condition subjects received no information on their errors. The effect of feedback was tested by comparing these two conditions.

The results show a clear effect of practice on the subjects' performance: the mean reaction time and the error rate for positive as well as for negative items decreased over the three sessions. Feedback resulted in more accurate but slower reactions. Contrary to the expectations practice in the feedback condition had no stronger effect than in the no-feedback condition. These findings are discussed with respect to practice effects found in other perceptual tasks.

◆ **Do visual-search tasks reveal an early site for the perceptual creation of illusory surfaces?**

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It has been reported that visual search for a Kanizsa illusory square (in an array of distractors which do not induce illusory surfaces) is parallel, so that search times are almost independent of the number of distractors [Davis and Driver, 1994 *Nature (London)* 371 791–793]. This result was interpreted as evidence for an early site for the perceptual creation of illusory surfaces, supposedly before the site at which pre-attentive pop-out occurs. However, it is possible that pop-out in this search task is caused by a property of the inducers (such as their collinearity) rather than by the pre-attentive creation of an illusory surface (which may occur at a later stage of visual processing) (Gurnsey et al, 1996 *Perception* 25 861–874). In addition, the immediate change from the pre-field placeholder array discs to the pacmen in the search array might have produced other cues to pop-out, and as apparent expanding motion. Our study had two conditions, one a replication of the task of searching for a Kanizsa square, the other a similar task in which the Kanizsa inducers (and those of the distractors) were replaced by line corners (which created similar collinearity cues, but not similar illusory surfaces). We introduced a delay between placeholder offset and search field onset, and removed from the search a tray placeholders which did not form part of a target or distractor, so that the number of potential items in the search varied. Over three experimental sessions, search times in both conditions reduced. However, even in the third session, there were significant effects of number of distractors for the Kanizsa targets (target-absent slope, 46 ms/item; target-present slope, 15 ms/item). Search functions for the line-corner targets had shallower slopes (target-absent slope, 18 ms/item; target-present slope, 3 ms/item). Our findings suggest that targets defined by collinearity alone can generate parallel search functions, but that Kanizsa targets do not, where two possible sources of artifact are removed.

◆ **Visual search in photo-realistic scenes**

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Visual search was extended from the domain of polygonal figures presented on a uniform field to photo-realistic scenes containing target objects in dense, naturalistic backgrounds. The target in a trial was a computer-rendered rock protruding in depth from a 'wall' of rocks of roughly similar size but different shapes. Subjects responded 'present' when one rock appeared closer than the rest, owing to occlusions or cast shadows, and 'absent' when all rocks appeared to be at the same depth.

Results show that cast shadows can significantly decrease reaction times compared to scenes with no cast shadows, in which the target was revealed only by occlusions of rocks behind it. A control experiment showed that cast shadows can be utilised even for displays involving rocks of several achromatic surface colours (dark through light), in which the shadow cast by the target rock was not the darkest region in the scene. Finally, in contrast with reports of experiments by others involving polygonal figures, we found no evidence for an effect of illumination direction (above vs below) on search times.

◆ **Effect of knowledge of the dimension on conjunction search**

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We examined the effect of knowledge of the particular dimension in which a target differs from the non-target. Nakayama and Silverman [1986 *Nature (London)* 320 264–265] indicated that conjunction search for stereo and colour is parallel. However, we reported that the conjunction

target defined by stereo and colour did not pop-out (Nakao and Mori, 1997 *Perception* 26 Supplement, 92). In our experiment, when the subjects knew the target properties, there was a significant effect of set size, although search times were short; and when the subjects were asked to search for the odd one target, search times were long and increased as a function of set size. These results suggest that conjunction target defined by stereo and colour is serially searched. However, it is still unclear why the target is searched rapidly when the subjects know the target properties in conjunction search for stereo and colour. In this experiment, different visual-search times were measured in accordance with previous presentation or non-presentation of target property of location. When the subjects had the knowledge of target location, search time was shorter than when they had the knowledge of another target dimension. This result suggests that directing attention to specific locations is easier than directing attention to particular features.

◆ **Dissociation between attentional and monitoring resources in rapid serial visual presentation (RSVP)**

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The object of this experiment was to determine whether letter size (1.4 deg or 0.7 deg) and kind (Roman, Hiragana, or Kanji) influence two indexes in a rapid serial visual presentation (RSVP): the mean ratio of reports as an indicator of attentional control, and the confidence rating score as that of monitoring. Each of 16–24 items was presented in rapid succession in the same location at a rate of 11.11 letters  $s^{-1}$ . The task was to look for and report a white letter (125  $cd\ m^{-2}$ ) appearing in an array of black letters (0.2  $cd\ m^{-2}$ ), at the centre of a gray field (48.4  $cd\ m^{-2}$ ), and to assign a confidence rating (1: “could hardly see” to 5: “could easily see”). The mean ratio of reports showed that more target-intrusion errors were found with complicated Kanji than with simple Roman and Hiragana, and that more post-target intrusion errors resulted with Hiragana than with Roman. By contrast, it was found that the confidence level with Roman was higher for 0.7 deg than for 1.4 deg letters, and that the confidence levels with Roman and Hiragana were higher than with Kanji. These findings suggest that monitoring resources would monitor the sizes of letters, but that attentional resources could not use this information, and support those of Nishiura (1998 *Japanese Journal of Psychology* in press), which indicated a dissociation between attentional and monitoring resources.

◆ **Visual marking of locations or feature maps? Evidence from within-dimension defined conjunctions**

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Recently, Watson and Humphreys proposed that the selection of new visual events can be aided by the top-down inhibition of old information—visual marking (VM), and that the mechanisms of marking differ for static and moving stimuli. Stationary stimuli are marked by location-based inhibition, whereas moving stimuli are marked via inhibition applied at the level of whole feature maps. Here we provide a test of this ‘two-mechanism’ account. We show that static items can be marked even when old and new stimuli contain the same features, and so cannot be distinguished by activation within a unique feature map. However, moving old items could not be marked unless they possessed a unique feature (colour). Manipulations of grouping strength, both within and between distractor sets, did not affect the basic findings. The results support the existence of two mechanisms for VM and counter an object-based inhibition explanation of performance.

◆ **Peripheral pop-out detection is set-size dependent**

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Subjects were tested on orientation and colour pop-out tasks with arrays of  $3 \times 3$ ,  $5 \times 5$ , or  $7 \times 7$  elements. Orientation pop-out stimuli were arrays of vertical white bars on a black background with a diagonal target element present on half of the trials. Colour pop-out stimuli consisted of  $60^\circ$ -oriented bars with blue distractor and yellow target elements on a gray background. The arrays were presented centrally or peripherally in the right or left hemifield, so that the distance of their centres from the fixation cross was 0–2.5–6.5 deg. Subjects performed about equally well on all array sizes as long as the array was presented centrally, confirming classical results (Treisman and Gelade, 1980 *Cognitive Psychology* 12 97–136). However, if the presentation was lateral there was a great difference between performance with larger and smaller arrays. There are two sources of this array size effect: (i) Target eccentricity (the target appeared, on average, more centrally for smaller array sizes). This is demonstrated by comparing performance for

different target locations with the same array size. (ii) Target location uncertainty (larger arrays have more possible target locations). We found that performance is better for smaller arrays even when comparing pop-out for elements which physically appeared at about the same location on the screen.

◆ **Consistent versus varied distractors can affect conjunction search**

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We explored the effects of practice on a conjunction search as a function of distractor heterogeneity. We reasoned that when two types of distractors are present in each trial, search would be less efficient if their identity varied from trial to trial than if the two distractors were the same throughout the session. We also reasoned that practice would benefit the search in the latter condition more than in the former and that search for the more heterogeneous display would benefit more from practice.

Observers searched for a colour  $\times$  shape conjunction, a red 'A', amid 5 to 25 distractors. A target was present on half of the trials. There were three distractor conditions: (a) blue 'A' and red 'N'; (b) 'A' of 8 different colours and 8 different red letters; (c) each trial had a given combination of 2 distractors [whereas in condition (b) each trial had many distractors, half letters and half colours]. For each condition, fifteen observers performed 4 blocks of 250 trials each.

Detecting the presence of the target was faster than detecting its absence; search time increased as the display contained more items, and decreased progressively across blocks. Importantly, search improved more for condition (a) than (c), and (b) improved the least. Furthermore, only in condition (a) was there evidence of 'guided search'. These findings, which confirmed our hypothesis, are discussed in terms of uncertainty within and between trials, and the possibility of grouping via distractor inhibition.

◆ **Uniform connectedness and topological structure in object-based attentional selection**

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Uniform connected (UC) regions are connected regions with homogeneous surface property, which have been shown to play a privileged role in attentional selection. A representation of a UC region is assumed to be insensitive to the shape of the region. The object of this study was to examine the validity of this assumption from the following aspects: (i) whether UC advantage holds even with complex, concave UC regions, and (ii) whether the UC advantage with complex UC regions depends on topological structure of the regions. Stimuli were complex filled objects composed of a connected set of rectangles with short sticks attached at two corners. They were either UC (connected and homogeneous texture), non-UC (connected but heterogeneous texture), or separated (one part missing). Subjects made speeded comparative judgments on the number of sticks. Euclidean distance between the two stick locations was identical; thus differences in response times reflect the effect of UC regions to which sticks were attached. In experiment 1, objects were used with their components linearly connected (a J-like shape); and in experiment 2, objects had their components branched (an H-like shape). With J-like objects (experiment 1), response times were shorter with UC objects than with non-UC or separated objects. By contrast, with H-like objects (experiment 2), there was no such UC advantage. Complex and concave UC regions can function as an object for attentional selection, but the UC advantage depends on topological structure of the UC regions, suggesting that UC representations are not insensitive to shape information.

◆ **Use of emergent properties like 'guide' for within-dimension conjunction processing**

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We studied the possibility that subjects can guide their search through a stimulus defined by a within-dimension conjunction (colour  $\times$  colour). We carried out three experiments in which we manipulated the presence of emergent information. In experiment 1, we used a target defined by a green square over a red square. Their intersection was yellow and distractors were red over green. In experiment 2, target and distractors were the same as in the previous experiment except that in this case the intersection had the same colour as the upper square. Finally, experiment 3 was a control in which the elements were formed by the same squares but in this case they were adjacent. Ten subjects performed each experiment and carried out 4 blocks of 288 trials each.

The results showed that the presence of emergent properties (experiment 2) facilitated the performance of subjects. In this case the search was efficient showing that this kind of information may be used as a guide for attention. These results are important for the 'guided-search model' of Wolfe (1994 *Psychonomic Bulletin and Review* 1 202–238) in which the guided search is possible only when the target is defined by between-dimension conjunctions.

◆ **Inhibitory tagging to moving items**

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In a serial-search task, it is not necessary to return attention to a location that has been confirmed. Klein [1988 *Nature (London)* 334 430–431] demonstrated that reaction times for detection of small probes increased at the locations where there had previously been distractor items in serial-search tasks. However, subsequent studies do not support the results of Klein's study (eg Wolfe and Pokorny, 1990 *Perception & Psychophysics* 48 357–362). We found in our previous study that the inhibition was observed only when the distractor items were maintained until detection of probes.

In this study, we examined whether the effect of distractor continuity occurred because of object-based tagging. Sixteen subjects were required to respond in probe-detection tasks, which followed the search tasks. Search items were shifted after the response for search task. Reaction times for probes increased both at the locations where distractors had been before the shift and at the locations where distractors were presented after the shift. These results indicated the existence of environment-based and object-based tagging. Thus the effect of distractor continuity might not be explained by object-based tagging.

◆ **Active versus passive processing of biological motion**

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We examined biological-motion processing as a function of motion quality (smoothness) and attentional load. Observers viewed a display of randomly moving dots and tried to determine the direction of heading (left versus right) of a point-light walker embedded within the dot mask. Motion quality was manipulated by inserting blank frames of either 0, 40, or 80 ms between successive walker frames. Attentional load was manipulated by presenting a concurrent task in which observers detected a changing rectangle among a flickering array of nonchanging rectangles. This task can only be performed with the use of focused attention (Rensink, 1996 *Perception* 25 Supplement, 2).

In the full-attention condition, observers were told to ignore the flickering rectangles and to concentrate on the walker task. Here, direction discrimination remained above 80% across all ISIs, consistent with previous findings [Thornton and Shiffrar, 1996 *Investigative Ophthalmology & Visual Science* 37(4) S742]. In the divided-attention condition, observers performed the change-detection task and the walker task concurrently. When the motion of the walker was smooth (0 ms ISI), direction discrimination was relatively unaffected (94%). At 40 ms ISI, however, accuracy dropped dramatically (66%) and reached chance levels by 80 ms (53%). These results suggest a shift in the nature of biological-motion processing, from passive detection at very short ISIs to some form of active tracking at longer ISIs (Cavanagh, 1991 *Spatial Vision* 5 303–309).

◆ **Selective sensitivity reduction in chromatic and luminance channels by lowered visual attention**

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It is known that visual attention changes the detectability of visual stimuli. In this study, we investigated the reduction of chromatic and luminance sensitivity at the parafovea when visual attention was directed to the fovea. In experiment 1, we measured increment-threshold spectral sensitivity functions at 4 deg in the peripheral visual field while the observer performed a visual attention task at the fovea. The task was to find a number of rings which had two discontinuous positions. Two small rings were used as task stimuli and each ring had four possible discontinuous positions. The test stimulus of 1.2 deg diameter was presented either to the right or the left of the centre on a background white field of 62 deg × 44 deg, 146 cd m<sup>-2</sup>. We found that sensitivity was reduced for all test wavelengths, and that two peaks at 543 nm and 599 nm of the spectral sensitivity function, which were prominent under the no-task condition, disappeared under the task condition. In experiment 2, we measured contrast sensitivity functions (CSFs) for chromatic and

luminance gratings in a 2-deg stimulus window under the same visual-attention task condition. The surrounding field was  $30 \text{ deg} \times 20 \text{ deg}$ ,  $32.5 \text{ cd m}^{-2}$ . We found that both chromatic and luminance contrast sensitivities were reduced for all frequencies, and that greater reduction occurred in the low-frequency region of less than  $2 \text{ cycles deg}^{-1}$  for the chromatic CSF. The present results indicate that visual attention has selective effects on the chromatic and luminance mechanisms, which indicates that visual attention may affect an early stage of the visual system.

◆ **Parallel processing of two simultaneously presented foveal stimuli**

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The ventral or 'what' cortical system (details and object identification) is associated with foveal vision, and the dorsal or 'where' system (movement detection and object localisation) with peripheral vision. In previous experiments it was shown that, when two stimuli are presented simultaneously in fovea and periphery, much parallel processing of the peripheral stimulus takes place without slowing down response times on primary foveal task. The present experiment was designed to examine whether parallel processing also occurs when both stimuli are presented foveally. A memory comparison task (varied mapping) was used as primary foveal task. Two target letters had to be compared with one stimulus letter, presented for 150 ms randomly at one of four positions equidistant from the fixation point (all within 2 deg visual angle). A manual target-present or target-absent response was required. The secondary task was the identification of an arrow, pointing upwards or downwards (voice key response 'high' or 'low'), presented for 150 ms randomly at  $-35$ ,  $-15$ ,  $0$  (at fixation point),  $15$ , or  $35$  deg eccentricity (east-west meridian). A precue indicated whether the trial was a foveal single, secondary single, or dual task trial. Results showed an equal amount of parallel processing for foveal and peripheral arrows, and no difference in error percentage. Contrary to current notions of spatial attention, an arrow presented at the centre of the focus of attention and an arrow presented in the periphery interfered about equally with foveal task processing. Parallel processing being independent of retinal locus suggested operation of the dorsal system in the fovea as well.

◆ **Neuromagnetically revealed activity related to visual pop-out stimuli**

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Neuromagnetic fields elicited by visual pop-out stimuli were measured. Three stimulus conditions were used: a colour pop-out, an orientation pop-out, and a homogeneous condition. We tried to investigate the pop-out phenomenon making an effort to exclude top-down factors as far as possible. Subjects were not given a priori information and overt reactions were not required. When the magnetic fields evoked under the pop-out conditions were compared with those evoked under the homogeneous condition, a difference was seen in the region of 200 to 270 ms latency. The latency of the difference occurred later in the orientation pop-out conditions than that in the colour pop-out conditions. The brain activity estimated in common with the three conditions was around the basal regions of the occipito-temporal lobes, suggesting the ventral stream of visual pattern information processing. On the other hand, the difference of the magnetic fields at about 200–270 ms suggested activity around the parietal cortex only under the pop-out conditions. It can be considered that preparatory mechanisms for controlling visuospatial attention may exist around the parietal cortex on the dorsal pathway. The activity tended to be emphasised under another condition where the subjects were instructed to search a pop-out stimulus.

◆ **Spatial attention affects acuity and texture segregation**

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We manipulated attention by peripherally precueing target location, which ranged from 0 to 12 deg of eccentricity. If spatial resolution is enhanced at the attended location, performance would be differentially affected depending on the spatial resolution demands of the tasks. Whereas an enhanced spatial resolution would benefit acuity judgments at all eccentricities and texture segregation at the periphery, it would impair texture segregation at foveal locations, where the spatial filters are too small for the scale of the texture.

To test the acuity performance, naive observers judged whether the gap was on the right or left side of a Landolt square, or the direction of the Vernier offset. The target was presented alone.

In texture segregation tests, naive observers indicated the interval containing a texture target (2AFC), whose lines differed from the background lines by 90°. Performance was compared for precued trials (50%) and for neutral trials (50%). The cue did not convey information about the correct response. Display duration did not allow eye movements to take place.

Acuity performance was significantly faster and more accurate for the cued than neutral trials at all eccentricities, for both the Landolt-square and the Vernier targets. In contrast, for texture segregation the attentional effect interacted with eccentricity: Cueing improved performance at all locations except at fovea, where performance was impaired. These results support the hypothesis that attention enhances spatial resolution, even in tasks considered to be 'pre-attentive'.

◆ **Spatiotemporal characteristics of object-based attention**

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Faster and/or more accurate performance has been reported when two judgments are required on one object instead of on two objects (same-object effect). This has been taken as evidence for object-based allocation of attention.

To examine spatiotemporal characteristics of object-based attention, we devised a new task in which simultaneous counting judgment was required at multiple locations. We examined whether the same-object effect would be observed under different spatiotemporal constraints. Subjects were presented with two objects (non-intersecting curved lines) and multiple dots, and asked to report the number of target dots (ie one or two) that were connected to the objects. When two target dots were presented, the metric distance between them was kept constant irrespective of whether they were parts of the same or different objects. The stimulus onset asynchrony between object and dot presentation was manipulated to test the temporal characteristics, and the number of total dots (including non-targets) was manipulated to test the spatial characteristics.

The results revealed that the same-object effect in the performance of target counting was observed under limited spatiotemporal constraints: the reaction times for same-object conditions were faster than for different-object conditions only when the spatial load (the total number of dots) was large and the objects appeared in advance of the dots by at least 250 ms. However, this effect was not observed when the spatial load was small and when the objects and dots were presented at the same time. These results suggest that the object-based attentional selection does not occur mandatorily, but only under favourable spatiotemporal environments.

◆ **Pre-information effects on pop-out**

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Attentional effects on early vision can be explained by two types of mechanisms: (1) Attention might influence early visual processing itself, lowering thresholds for target features or increasing selectivity. (2) Attention might suppress features or elements that are not attended to. In the latter case attention would not need to influence early visual areas but could just process their output information. If attention works with a mechanism of type 1, pre-information about the type of the target should result in increased salience of the target, thus increasing performance. Pre-information about the type of distractors should increase *their* salience, but should not help in target detection. If attention works with a mechanism of type 2, pre-information about the type of distractors should be even more efficient than that about the target type.

In a forced-choice paradigm with backward masking, detection rates for three different presentation times were measured, from which detection threshold values were computed. This was done for four conditions: without any pre-information, or with information about target, or distractor type, or both. Both targets and distractors were chosen from a pool of five different shapes. For untrained subjects only pre-information about target type increased performance but pre-information about distractor type did not. This is in line with the predictions of mechanisms of type 1. During extended training, however, subjects could learn to exploit pre-information about the distractor type.

**SPATIAL CONTRAST; IMAGE PROCESSING**

◆ **Perceived location of bars and edges in broad-band 1-D images: experiment and computational model**

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We compared the ability of zero-crossing and contrast-energy models to predict the perceived location of features in 1-D images. Each image had the amplitude spectrum of a square-wave (fundamental frequency  $0.5 \text{ cycle deg}^{-1}$ ), subjected to different amounts of Gaussian blurring and phase shift,  $\phi$ , to create a large family of test images. For each image, observers moved a cursor dot to mark the location and polarity of all edge and bar features seen. Subjects consistently saw a single edge when  $\phi = 0^\circ$  or  $180^\circ$  (square-wave phase) and a bar bounded by two edges at all other phases. Edge and bar positions shifted systematically with phase, especially at larger blurs. These results could not be predicted by peaks of contrast energy, since there was only one energy peak, and it had the same fixed position for all images.

We considered a generalised Marr-Hildreth model in which features are located at zero crossings in the output of a filter whose amplitude spectrum has a slope  $Z$  on a log-log plot, smoothed by a Gaussian with standard deviation (scale)  $S$ . The best-fitting slope and scale were estimated for edges (even filter) and bars (odd filter) for each level of blur and contrast. The number, polarity, and location of the observed features were closely predicted by this general model. Estimated slopes  $Z$  were close to 2 for the even filter and 1 for the odd filter, irrespective of blur, but the filter scale was not critical. Thus perceived features are well predicted by locating edges at zero crossings in the 2nd derivative of the stimulus, and bars at zero crossings in the 1st derivative of the stimulus (peaks and troughs in the luminance profile).

◆ **Observers' performance in a 'crowded' visual task**

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We measured the percentage of correct responses in a task in which observers were required to detect the orientation of a central Landolt C surrounded by several types of distractors: Landolt C's, bars, and rectangular gratings of different spatial frequencies. All types of distractors and separations between the target and distractors were randomly interleaved and presented during the same experiment. The only difference in the experimental procedures was that in one experimental set the observer was asked to report one of four possible orientations of the target (left, right, top, bottom), while in another experimental set the choice was to be made between only two orientations (eg left, right). In the former case, we obtained inhibitory areas corresponding to the size of a minimal resolved target for a particular observer (cf Flom, 1991 *Problems in Optometry* 3 237-257), but they were about twice as large as those obtained in the latter case. We consider possible mechanisms underlying these differences in the sizes of the inhibitory areas obtained in the two sets of experiments. One of the hypotheses is that the human visual system may perform a spatial-frequency analysis when detecting the orientation of the Landolt C at the resolution limit.

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◆ **Looking for a line: task-dependence in long-range perceptual spatial interactions**

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When three Gabor patches are presented in a collinear configuration, contrast sensitivity for the central patch tends to be enhanced (Polat and Sagi, 1994 *Vision Research* 34 73-78). This phenomenon, which is thought to reflect contour integration processes, was investigated here in the context of changing task demands: Does the act of looking for a collinear relationship between a set of line segments modulate the strength of the interaction between them?

Stimuli were constructed from a central patch of variable contrast and orientation, and a flanking set of four high-contrast patches, each separated from the centre by three wavelengths. These were arranged to form two diagonally intersecting virtual lines (ie an X configuration). The two patches on each of the diagonals could have a Vernier offset of zero (aligned) or slightly above threshold (misaligned). Subjects performed a dual two-interval forced-choice task. The primary task was to detect alignment of the pair of patches on one pre-designated diagonal while ignoring the other diagonal. The secondary task was to detect the presence of the central patch. It was predicted that the enhancement due to collinearity would be greater when the central patch had the same orientation as the designated diagonal, compared to when it was oriented with the ignored diagonal.

Results largely confirmed the predictions, suggesting two conclusions: long-range interactions between spatial filters may indeed play a functional role in contour integration; furthermore, the pattern of these interactions appears to be task-dependent and under top-down control.

◆ **Detection and recognition of gratings defined by modulations of luminance and contrast: separate labelled channels?**

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Human vision can detect spatial structure (and motion) that is defined by spatial variations in intensity (luminance modulation, LM) and local contrast of a carrier pattern (contrast modulation, CM). CM gratings cannot be detected by linear spatial filters sensitive to LM, so several models have proposed separate linear and nonlinear pathways for LM and CM. However, some cells in visual cortex are responsive to both LM and CM gratings, perhaps implying a common mechanism. The ability to distinguish two patterns perfectly at threshold is often taken as a sign of separate, perceptually labelled mechanisms, so we asked whether this was true for LM and CM.

LM patterns were produced by adding sinusoidal gratings to static, 2-D, binary noise of 40% contrast. In CM patterns the noise contrast was modulated sinusoidally around a mean of 40%. In the first experiment, observers had to say which of two stimulus intervals contained a grating (the detection task) and to identify it as LM or CM (the recognition task). A signal detection model based on independent, labelled mechanisms predicts equal percent correct scores for the two tasks. The second experiment was aimed to assess detection and recognition in separate 2AFC tasks. Here the detection model predicts  $d'$  (recognition) =  $\sqrt{2}d'$  (detection). In both experiments the trends were similar to those predicted by independent channels, but with a slight deficit for recognition compared with detection performance. Taken in conjunction with our previous experiments (Schofield and Georgeson, 1997 *Perception* 26 Supplement, 3), where we found no facilitation between near-threshold LM and CM gratings, these results favour the separate-channels model, but perhaps their labelling is imperfect.

◆ **Three target bisection and alignment thresholds at different stimulus orientations**

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Three target bisection and alignment thresholds were measured as a function of spatial separation of stimuli presented at horizontal, vertical, and oblique (45°) orientations. The targets were bright ( $14 \text{ cd m}^{-2}$ ) 2 min of arc points on a blank background. The separation between the outer points of the stimuli varied from 10 to 60 min of arc for each task and orientation. A two-alternative forced-choice method was used to evaluate the thresholds in all cases. The bisection thresholds were similar and increased approximately linearly with the increase in spatial separation of the stimuli by a constant factor of 0.016 for all stimulus orientations. The alignment thresholds were similar only at small spatial separations of the stimuli (10 s of arc at 10 min of arc). However, at large separations (60 min of arc), thresholds for the stimuli presented at oblique orientations were about 30 s of arc higher than those at the horizontal and vertical orientations. Alignment thresholds at the horizontal and vertical orientations increased approximately linearly with increases in the spatial separation of stimuli by a constant factor of 0.006. In the case of stimuli presented at an oblique orientation this factor was 0.016. The results obtained are discussed in terms of the different spatial mechanisms underlying the evaluation of displacement in the bisection and alignment tasks under the different stimulus conditions.

◆ **Automated assessment of the visual contrast-sensitivity function in the hooded rat**

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The spatial contrast-sensitivity function (CSF) is a sensitive, quantitative behavioural test for assessing spatial visual function that is comparable across species. Rat vision is widely assumed too poor for meaningful psychophysical assessments, and the perceptual characteristics of vision in rats, despite their extensive laboratory use, have been rarely studied. We have developed an automated method for rapid assessment of the hooded rat's CSF using a standard computer monitor for stimulus display and an infrared touch screen as response detector. Sine-wave gratings, varying in contrast and spatial frequency, were presented in a six-alternative forced-choice task;

a rat's nose-poke to the target stimulus resulted in reinforcement (water), and nose-pokes to other locations repeated the trial with a short aversive time-out. Spatial frequencies assessed were in the range of 0.041 to 0.78 cycle deg<sup>-1</sup>; at each spatial frequency tested, stimulus contrast changed according to a simple adaptive procedure. Psychometric functions were determined by fitting a logistic function to the binary response data with the use of a maximum-likelihood fitting procedure (L O Harvey Jr, 1997 *Spatial Vision* 11 121–129), and the point of inflection was taken as the threshold. The CSFs obtained had the typical inverse-U shape. Peak sensitivity was 7% Michelson contrast occurring at 0.10 cycle deg<sup>-1</sup> and acuity was 1.1 cycles deg<sup>-1</sup>, similar to previous data. We consider this procedure a valid method for rapid determination of the rat's CSF and a rigorous tool for spatial vision assessment after experimental manipulations of the visual system.

◆ **Masking effect on the right-angle judgment**

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We measured the accuracy with which subjects judged a 90° angle at three orientations (0°, 45°, and 90°) of the principal axis of the stimulus. The stimuli, consisting of three bright dots (0.3 min of arc in diameter) or two lines (0.3 min of arc wide) sharing one common end-point, were displayed on a monitor. Subjects were requested to adjust the two segments of a stimulus to form a right angle. The angle between the segments was changed with the panel keys by simultaneous and symmetrical movements of the segments in 10 min of arc steps. The masking stimulus, an angle formed by an additional pair of bright lines, shared the same apex point with the test angle. The angle of the masking stimulus ranged from 0° to 180°. The experiments were carried out in a dark room. Monocular viewing was used. The errors of the subjects' judgments were estimated as functions of: (i) the masking angle size, and (ii) stimulus orientation. The greatest error values were recorded at 90° stimulus orientation in the regions of 60°–80° and 100°–120° of the masking angle. The test angle seemed to be bigger if the masking angle was less than 90°, and smaller if it was larger than 90°. The masking angle made of three dots showed negligible influence on the right-angle judgment. Predictions of a combined model of spatial filtering and visual-field anisotropy have been found in quantitative and qualitative agreement with the experimental data obtained.

◆ **Psychophysical measurements of the spatial-frequency spectrum of internal noise in the human visual system**

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The detection of a sine-wave grating, ie threshold contrast  $R_s(F)$ , strongly depends on the spatial frequency of the test grating,  $F$ . The threshold contrast of a grating depends on  $F$  because the internal noise in the visual system has a non-uniform distribution of energy across spatial frequency. The results of psychophysical experiments permit us to estimate the spatial-frequency spectrum of the internal noise  $N_n(F) = N_1/F^2 + N_0$ , where  $N_0$  and  $N_1$  are constants determined experimentally. The threshold contrast of a sine-wave grating at photopic light levels is  $R_s(F) = k[N_n(F)/s]^{1/2}/K(F)$ , where  $s$  is the critical size of the area on the retina which permits the resolution of the grating of a given frequency, and  $k$  is a constant. For spatial frequencies up to 25 cycles deg<sup>-1</sup>, the changes in  $K(F)$  are small and may be neglected. For spatial frequencies below 2 cycles deg<sup>-1</sup>,  $N_n(F)$  is approximately proportional to  $1/F^2$  and therefore  $R_s(F)$  is proportional to  $1/F$ . For frequencies above 2 cycles deg<sup>-1</sup>  $N_n(F)$  changes insignificantly. However, the increase in frequency results in an increase of the unresolved part of grating as a large part of the grating occupies the parafovea, which has lower resolution. Therefore,  $s$  decreases in proportion to  $F^2$  and in place of  $R_s(F)$  we have  $R_s(F) - F$ . The phenomenon is observed only in photopic vision, where the factor limiting threshold contrast is internal noise. On the other hand, in suprathreshold contrast-matching experiments the contrast of the matched gratings in comparison to the contrast of the reference grating hardly depends on  $F$ .  
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◆ **Spatial localisation in relation to real and imaginary references**

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We studied the observer's ability to determine the spatial position of a vertical line in relation to a reference line or an imaginary centre of a spatial interval defined by two parallel bars. It is known that the precision of spatial localisation decreases with the distance separating the test probe from the reference object (Westheimer and McKee, 1977 *Vision Research* 17 941–947). The

main question addressed by this study was whether this deterioration of spatial localisation is identical for real and imaginary reference objects, or whether it is different for two different forms of local signs.

Two vertical bars (0.3 by 18.4 min of arc) separated by a horizontal gap (0.4 deg) were continuously visible on a display screen viewed at the distance of 5.6 m. In half the presentations the centre of the spatial interval was marked by a vertical bar and in the rest it was not physically specified. The probe line was presented for 114 ms under the reference configuration at various distances (from 0 to 2.9 deg) from it. The observer's task in each trial was to specify in which direction, to the left or to the right, the probe was displaced from the centre of the reference configuration.

The results demonstrated that the localisation precision deteriorated linearly with the distance between the test line and the reference configuration (Pearson's product-moment correlation was  $r = 0.995$  and  $r = 0.991$  for the real and imaginary centre, respectively). The slopes of the best fitting linear functions were practically identical for both experimental conditions. ANOVA revealed no difference in the accuracy of localisation of physically marked or unmarked conditions ( $F_{1,28} = 0.39$ ,  $p < 0.539$ ). We conclude that local signs formed by an imaginary process do not differ from local signs defined by singular points of a luminance distribution, at least within the spatiotemporal limits examined.

◆ **Second-order feature extraction in the visual cortex: selective and invariant sensitivity of neurons to the shape and orientation of cruciform and corner figures**

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In area 17 of the cat visual cortex nearly all units have a definite selectivity to orientation of a single light bar flashing in the receptive field or moving across it. An effective system for image processing needs also units with selectivity to lines crossing at different angles. Many neurons (56/174) that we studied in the cat striate cortex significantly (by 3.2 times on average) increased their responses to cross-like or corner figures flashing in the receptive field as compared with the single light bar of preferred orientation. We found 71.4% of these neurons to be selective to the configuration and orientation of these figures, with all possible types of invariance of the neuron's selectivity to form and/or orientation: neurons with selectivity to form of the figures and invariance to their orientation and, vice versa, units invariant to configuration but selective to orientation. Some cells (18/56) were invariant both to form and orientation of the cross-like or corner figure but sensitive to the appearance of any such figure in the receptive field. Characteristics of tuning to the shape of the figure (an angle between its lines) were about the same for a cross and a corner. We found a direct relation between the orientation-tuning width and selectivity for bars, crosses, and corners. Most cells sensitive to crosses (35/46) responded to the figure with angles of 45° or 90° between the lines. The remainder (11/46) responded to crosses with angles of 68°. We suggest that the studied units are suited for the selection of crosses or corners and play an important role in feature extraction and processing in the striate cortex.

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◆ **Spatiotemporal dynamics of contour integration: psychophysics and physiological correlates**

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Recent psychophysical and physiological studies suggest that lateral intracortical interactions subserve contour integration. Little is known, however, about the dynamics of this process. We investigated, through psychophysics and intracellular recordings in cat visual cortex, the dynamics of intracortical interactions, using sequential presentations of oriented spatial configurations of Gabor patches at varying ISIs, spatial separations, and directions. Two major findings emerge from our psychophysical experiments: (i) The apparent speed of sequentially presented high-contrast Gabor patches is much faster for collinear as compared to parallel configurations. This effect is quite large for high reference speeds (64 deg s<sup>-1</sup>) and decreases as reference speed decreases. (ii) Contrast thresholds for the detection of a target Gabor patch are modulated by the sequential presentation of remote Gabor inducers, as compared to thresholds for the target alone. The thresholds increase for small spatial separations but decrease at large separations (~2 deg) and short ISIs (16.6 ms), suggesting both an inhibitory and facilitatory influence of remote stimulation on sensitivity.

Intracellular recordings in cat visual cortex under similar conditions indicate that visual stimulation in regions surrounding the classical receptive field modulates the membrane potential suggesting the existence of an extended synaptic integration field. The observation that the latency of the postsynaptic potential increases linearly with the eccentricity of visual stimulation relative to the RF suggests that slow propagation of activity through horizontal intracortical connections is responsible for the buildup of a latency basin characteristic of each recorded RF. We propose that the perceptual phenomena reported herein can be accounted for by the summation of direct feedforward visual inputs and lateral activation through intracortical connections, which is optimised when both sources are appropriately temporally synchronised.

◆ **Probability summation for detecting multiple patches of grating**

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When components of a compound pattern stimulate different visual mechanisms, psychophysical performance typically improves by a small amount consistent with probability summation. In spatial vision, compound stimuli have been made from (a) components with different spatial frequencies (sf) or orientations, and (b) gratings with variable spatial extent [Graham, 1989 *Visual Pattern Analysis* (Oxford: Oxford University Press)]. In (a), typically only a small number of components have been used; and in (b), full psychometric functions are rarely shown, and interpretation is difficult because sensitivity is not always uniform across the stimulated region. We tackled these limitations in the following way. Using a 2AFC technique and the method of constant stimuli we measured psychometric functions for detecting 100 ms presentations of circular sine-phase patches of grating centred on up to four corners of an imaginary square surrounding a fixation point. Grating components were windowed by raised cosine functions with half-height diameters of either 3.75 deg or 2.5 deg and their centres placed 4.24 deg from the fixation point. Orientations were 0°, -45°, or 45°, and spatial frequency was 1 or 5 cycles deg<sup>-1</sup>. Various combinations of these component patches produced compound stimuli made from 4, 8, or 16 components. Thus, our compound stimuli varied in: (1) position alone; (2) spatial frequency and position; (3) orientation and position; (4) spatial frequency, orientation, and position; and (5) orientation and spatial frequency. Predictions using (i) probabilistic summation of individual psychometric functions, and (ii) the Quick pooling formula, were consistent with probability summation amongst independent detectors sensitive to each of the components in the compound.

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◆ **Approximation of curvature in human vision**

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In psychophysical experiments, the subjects observed monocularly a segment of (i) a circle, (ii) an exponential spiral, or (iii) a sinusoidal-type curve generated on a monitor, and resolved the trajectory of the invisible interval of the curve by adjusting the position of the test spot situated at a distance from the end of the stimulus.

The task of the subjects was to place the spot in the position of intersection of the invisible segment of the curve with an imaginary horizontal line. The subject's error was always positive but varied with the type of curvature and the individual. The value decreased gradually with the stimulus length (5° to 180°) and increased with the distance between the stimulus and the test spot (15°–60°). The region of error modulation (0–30 min of arc) was a characteristic of visual precision in curvature discrimination and approximation task. To model the law of visual approximation, five types of trajectories have been checked: (a) chord, (b) tangent, (c) tangent =  $K$  trajectory, (d) curvature at the end point, and (e) averaged curvature of the stimulus.

The calculated curves (a, b, c, d, e) have been compared with the experimental ones. The tangent =  $K$  trajectory yielded the results closest to the experimental data of the four subjects. The coefficient  $K$  has been found empirically. Biological significance of the trajectory tangent =  $K$  is an object of further studies.

◆ **Spatial filter combination in edge-computation revealed by spatial summation**

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Contemporary models of human spatial vision consider extraction of image spatial features as being performed in two basic stages: (a) processing by orientation-selective and spatial-frequency (SF)-selective channels, and (b) combining of channel outputs to determine the features.

Spatial organisation of feature extraction was studied by measuring the contrast threshold for form identification of different sorts of complex gratings of variable width. In most experiments the test stimuli consisted of two SF components— $F$  and  $3F$ , the irrelevant stimuli consisted of the component  $F$  only. The width of the component  $F$ , determined as the doubled space constant of a Gaussian aperture, was fixed as  $2.7/F$  while the width of the component  $3F$  was varied. The results showed that the size of the spatial summation zone was determined by the period of the third harmonic ( $1/3F$ ) when the contrast of  $F$  was below some critical value and determined by the period of the fundamental harmonic ( $1/F$ ) at higher contrasts of this harmonic. This critical contrast was found to be lower at zero spatial phase between  $F$  and  $3F$ , and higher at  $180^\circ$  phase. When the test stimuli consisted of components  $F$  and  $5F$  the summation zone size was found to be independent of the contrast of the fundamental harmonic and determined by the period of the fifth harmonic ( $1/5F$ ). Adding the component  $3F$  to both the test and the irrelevant stimuli made the summation zone size contrast-dependent again. This size was determined by the period of the fifth harmonic ( $1/5F$ ) at lower contrasts of  $F + 3F$  and determined by the period of the fundamental harmonic ( $1/F$ ) at higher contrasts. The results suggest that: (i) channels tuned to different SFs combine their outputs if their preferable SFs do not differ by more than 1.5–2.0 octaves and when channel activity exceeds a critical level; (ii) this level is phase-dependent; (iii) channels tuned to very different SFs can also combine their outputs but this depends on the activity in the channel(s) tuned to intermediate SFs; (iv) the receptive-field size of combining channels tuned to different SFs is the same and is determined by the period of the component of lowest SF.

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◆ **Artificial scotomas shrink the dynamic aftereffect but do not alter spatial summation**

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Exposure to an artificial scotoma, a small uniform patch within a dynamic random-noise background, results in alterations in the response properties of striate cortical neurons. When the dynamic noise is replaced by a homogeneous background, a dynamic aftereffect (DAE) can be visualised in the location of the artificial scotoma. In previously performed experiments at 6 deg eccentricity, we discovered a dramatic shrinkage (nearly 1 deg) in the perceived size of the DAE relative to the inducing artificial scotoma. Shrinkage in the DAE is probably induced from the edges of the artificial scotoma and may represent a depression in the suprathreshold response profile of cortical neurons following adaptation to the dynamic noise.

Spatial summation in the peripheral retina is thought to reflect the receptive-field size of underlying neural mechanisms. We determined spatial summation at the centre of the DAE. We fitted two-line functions to the contrast detection thresholds of line targets of different widths and found the same summation values as in the control conditions (6.4 min). However, receptive-field size may only be altered near the edge of the artificial scotoma. We now report that spatial summation measured near the edge of the artificial scotoma is also unchanged. Taken together, our findings suggest that (i) viewing an artificial scotoma does not influence the size of the receptive fields that determine spatial summation, and (ii) the perceived size of the DAE may not be processed by the same neural mechanism that determines the area of complete spatial summation.

◆ **'Labelled lines' as a Ryleian category error**

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The concept of 'labelled lines' is used frequently in modern psychophysics to explain a variety of phenomena, including stimulus identification at detection threshold and perceived stimulus quality. A label may be defined as "a hypothetical 'extra process' that accompanies a sensory message and gives a clue to its origin" [Morgan, 1977 *Molyneux's Question* (Cambridge: Cambridge University Press) p.141]. However, the nature of the mysterious 'extra process' has never been clarified.

Sensory information leads to 'representations', which interact with each other as part of the cognitive 'semantic network' and ultimately have a causal role in affecting behaviour. A distinction must, however, be made between the representation (the vehicle or medium) and its content (the meaningful information contained within it) [eg Dretske, 1995 *Naturalizing the Mind* (Cambridge, MA: MIT Press)]. I propose here that this distinction maps onto that between 'labels' and Morgan's 'sensory messages': the former refers to the medium and the latter to the content. Thus the theory of labelled lines assumes that information is available not only about the content but also about the medium by which the message is conveyed. An example of such use is the idea that information is coded as position in anatomical topographic maps (Konishi, 1990 *Cold Spring Harbor Symposia* 55 575–584).

Given that the medium and the message are two different categories of entity, to treat them both as (equivalently accessible types of) 'information' would be to commit a category error, in the sense made famous by Ryle [1949 *The Concept of Mind* (London: Hutchinson)].

◆ **Flanking effect in three-target bisection and alignment tasks**

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To investigate different spatial mechanisms underlying the precise assessment of displacement in three-target bisection and alignment, thresholds were measured with the presentation of flanking targets on both sides of the stimuli. The targets were bright ( $14 \text{ cd m}^{-2}$ ) 2 min of arc points on a blank background. The separation between the outer points of the stimuli was constant (60 min of arc) while the distance between outer points and flanks varied from 10 to 50 min of arc. The bisection and alignment thresholds were measured for stimuli presented at horizontal, vertical, and oblique ( $45^\circ$ ) orientations. A two-alternative forced-choice method was used to evaluate thresholds. Flanks had a weak effect on the bisection thresholds at the small flanking distance (10 min of arc), whereas increasing the separation of flanks caused substantial reduction of bisection thresholds (up to 20–30 s of arc from 60 s of arc), irrespective of stimulus orientation. There was no significant effect of flanking on alignment thresholds for stimuli presented at horizontal and vertical orientations. However, flanks reduced alignment thresholds strongly (20–30 s of arc) for stimuli presented at oblique orientations.

◆ **Eye transfer function and spatial scale selection**

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Our ability to perceive fine details of the environment depends on visual acuity. Acuity is not uniform in the visual field, but declines progressively from the fovea to the periphery. In spite of a large body of psychophysical research describing in a precise way the distribution of visual acuity in the visual field, it is not clear what exactly the human eye perceives outside the fovea. The goal of this research was to simulate what the eye perceives in the various areas of the visual field. Under photopic luminance viewing conditions, two main factors determine visual resolution: the quality of the optics of the eye and the ability of the retina to resolve the image details. These two factors define the transfer function of the eye. The resolution of the eye can be modelled by a space-variant low-pass filter with variable kernel at different eccentricity. If  $I(k_1, k_2)$  is the input scene, and  $F(k_1, k_2)$  the impulse response of the visual system, the result of the visual filtering is written:

$$O(k_1, k_2) = \sum_{uv} I(k_1 - u, k_2 - v) \cdot F(k_1, k_2, u, v) = H(k_1, k_2) \circ I(k_1, k_2),$$

with

$$H = g_1^c \circ g_1^a \circ g_2^c \circ g_2^a,$$

and where  $g_i^c$  and  $g_i^a$  are computed respectively by:

$$y^c(k_i) = x(k_i) + \lambda(k_1, k_2) \cdot y^c(k-1) \quad \text{and} \quad y^a(k_i) = x(k_i) + \lambda(k_1, k_2) \cdot y^a(k+1),$$

and where  $\lambda$  is the space-variant parameter that is a function of retinal eccentricity

$$\lambda(k_1, k_2) = \epsilon(k_1^2, k_2^2),$$

computed from psychophysical measures of visual acuity. Results of the simulation suggest that, under ecological viewing conditions, the eye transfer function contributes to the 'prior entry' of global information in the visual system. The global precedence principle, which holds that global scene configuration tends to dominate local feature processing in human perception, is reconsidered.

◆ **Investigation of contrast sensitivity in myopes and emmetropes in low photopic and mesopic conditions**

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This investigation was stimulated by our previous findings of higher contrast thresholds for negative-contrast stimuli in myopes under photopic conditions (1995 *Perception* 24 Supplement, 86) and some anamnestic data for myopes for low vision under mesopic conditions. To examine

this we measured contrast thresholds for recognition of letters by the staircase method. The stimuli, Cyrillic letters (size 30 min of arc), were generated by Cambridge Research Systems and one of the characters was presented for 150 ms on a grey background with either positive or negative contrast. The brightness of the background (Hewlett Packard computer monitor) had one of four different values: 0.6, 1.6, 2.6, 3.6  $\text{cd m}^{-2}$ . The subjects were divided into three groups and all had normal or corrected-to-normal visual acuity (1.0). The first group consisted of emmetropes with a mean age of 25 years, the second group of myopes (5 D on the average) with a mean age of 25.6 years, and the third group of myopes (2.5 D on the average) with a mean age of 22 years. Observation was monocular. Two-tailed unpaired and paired Student *t*-tests were used for statistical analyses. The data obtained with all four levels of background brightness indicated that emmetropes had lower contrast thresholds for negative contrast than for positive contrast ( $p < 0.01$ ). The second group, with a degree of myopia of 5 D, produced the opposite results—lower thresholds for positive contrast and both thresholds for negative and positive contrasts were higher in comparison with emmetropes ( $p < 0.01$ ). Very interesting were the results of the third group. They were the same as the results of emmetropes, only their thresholds for negative contrast were not as low. These results showed the tendency towards decreasing contrast sensitivity for negative contrast in myopes according to the degree of myopia.

◆ **Simultaneous comparison of vertical line lengths**

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Comparative judgments of simultaneous stimuli produce space errors. Here, two kinds of comparison were used to study space errors: first, a comparison by relation when the compared stimuli are very close together, and second, a repeated successive comparison when the compared stimuli are far apart (the eyes move a number of times from one stimulus to the other). The aim was to test whether there was a change in the kind of comparison when stimuli were close and far apart, by checking if there was a corresponding change in the differential thresholds. Two vertical lines were presented simultaneously for length comparison. The method of constant stimuli was used. Subjects reported which of the two lines appeared longer. The individual points of subjective equality were calculated by a variation of the method of transitions. The results show that errors progressively increase as the distance between the two lines increases. Differential thresholds were low when the two lines were close, and large when the two lines were far apart. The two kinds of comparison mentioned above seem to account for this result.

◆ **Spatial distribution of intrinsic connections in area 18 of the cat**

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We investigated the spatial and laminar distributions of the population of cells sending axons to single cortical columns of area 18 in the cat. Injection sites corresponded to different regions of the visuotopic map. 3-D reconstruction of labelled cell regions was performed with the use of serial frontal brain sections.

Retrogradely labelled (mainly pyramidal) cells were found in the supra-granular (II, III) and infra-granular (V, VI) layers and in the top of the granular (IV) layer. As in area 17, the regions with labelled cells in the supra-granular and infra-granular layers lay in register. The tangential distribution of labelling was elongated in a rostrocaudal direction (along the projection of the vertical meridian of the visual field). The dimensions of the labelled area were: length up to 5 mm, width 0.2 to 1.5 mm. Similar elongated regions of labelled cells were obtained in area 18 when we injected single columns in area 17.

Considering that all the investigated columns are very unlikely to share a common orientation preference we conclude that in cat area 18 there is no relation between orientation selectivity and the arrangement of the horizontal connections, as shown previously (Bosking et al. 1997 *Journal of Neuroscience* 17 2112–2127) in tree shrew's striate cortex.

◆ **The estimates of dimension for an image as a dynamic system**

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The processing of spatial patterns by the human visual system is followed by a sequence of eye movements from one point to another. The latter forms a set of trajectories of spatial inspection of these patterns by an observer. It may reflect the result of finding the hidden periodicity in

spatial-pattern structure. The pattern is treated here as a nonlinear dynamic system with some finite dimension  $d$  that could be used as a measure of complexity of the visual pattern. To estimate the dimension  $d$  for some images the correlation method of Nicolis and Prigogine [1989, *Exploring Complexity. An Introduction* (New York: W H Freeman)] was applied. The computer generated the test images which were artificial gray-scale images of different objects on one hand and reproduced art production copies—on the other. It was found that the values of  $d$  vary in the range from 0.6 to 7. This reflects the observer's understanding of the complexity of perceived images. The minimal value of  $d$  corresponds to the simple geometrical binary objects with blurred borders and increases as pattern complexity grows. For instance a face photograph without background has the value of  $d$  approximately equal to 2.1. The essential influence of the background on the dimension-estimating process was also determined. The value  $d = 7$  supports this conclusion since it was obtained for the blank noise image of the polygraph technology process.

◆ **Detection of collinear dots in noise**

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The visual system is adept at detecting visual patterns embedded in random noise. Moulden [1994 *Higher-Order Processing in the Visual System* Eds G R Bock, J A Goode (Chichester: John Wiley) pp 170–192] measured detection of collinear line elements (the 'target') as a function of the number of noise elements. As the number of target elements increased up to 7, performance improved rapidly, with subsequent improvement beyond this point occurring more gradually. Previously, we reported that this change in the rate of improvement was not observed if adjacent noise elements corresponding to each target element were removed to compensate for the local increase in element density associated with superposition of target elements [Tripathy, Mussap, and Barlow, 1996 *Perception* 25 Supplement, 3]. In the present experiments with dot elements, detection limits were compared for two methods of removing proximal noise elements: when proximal noise dots were removed from within the two co-axial quadrants relative to the target dots (ie  $\pm 45$  deg off the axis of collinearity), performance deteriorated significantly; when proximal dots were removed from within the two orthogonal quadrants relative to the target dots, performance improved significantly. This pattern of results suggests that collinearity-detecting mechanisms treat noise dots close to the axis of collinearity as signal dots, thus increasing the effective number of target dots.

◆ **Evidence for curvilinear interpolation from dot-misalignment judgments**

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In three experiments, interpolation between dots was studied with a new, forced-directional-response (FDR) paradigm. After a 150 ms stimulus exposure, subjects indicated the direction of displacement of a centrally given variable dot  $v$ , with respect to two reference dots  $r$ , regardless of the co-presence of two more remote context dots  $c$ . The  $r$  and  $c$  dots always formed together a segment of a regular dot polygon, the (outer) angle of which was varied within and over experiments between  $90^\circ$  and  $180^\circ$ . In experiment 1 stimuli were presented horizontally, in experiment 2 vertically, and in experiment 3 both orientations were presented in a mixed manner. Displacements of  $v$  were either orthogonally off-line relative to the two  $r$  dots (the experimental conditions), or on-line between the two  $r$  dots (control conditions). Bias, evidencing curvilinear interpolation, was in that way established for the experimental stimuli under extreme angle conditions, more saliently under the horizontal orientation conditions. The data supported Koffka's interpolation guess, rather than Bouma's one. The data are discussed with respect to the quantification of the Gestalt law of good continuation, while the FDR paradigm is contrasted with the traditional methodology based on template matching.

◆ **Space error in length estimation of static and evolving horizontal lines**

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We investigated spatial anisotropy in the perception of the length of static and evolving stimuli. Classical experiments with static stimuli (usually lines) show overestimation in the left area of the visual space. Our aim was to replicate this result with non-static stimuli. Eighty subjects were asked to estimate the length of lines that appeared for a short time (0.75–3 s) on the left or right side of a screen. Lines could be stationary or evolving; in the latter case they either symmetrically

lengthened from 0 to 84 mm or shrunk from 84 mm to 0. Each line was compared to a stationary line appearing after a brief ISI (2.1 s) on the other side of the screen. The method of constant stimuli was applied. Results confirmed the left–right asymmetry for static lines. In contrast, the effect disappeared for evolving lines. The absence of the spatial localisation effect for evolving lines seems to suggest the following hypothesis: the difference in the metric evaluation exhibited by the ‘centre’ that governs size estimation in visual fields acts in a different way for stimuli in movement or for stimuli that require greater cognitive resources.

- ◆ **A common pathway for spatial localisation of luminance-defined and contrast-defined blobs**  
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Luminance-defined and contrast-defined stimuli are thought to be processed independently in the motion system (Derrington and Badcock, 1985 *Vision Research* 25 1869–1878), with the mechanism supporting motion of contrast-defined stimuli being more sluggish (Derrington, Badcock, and Henning, 1993 *Vision Research* 33 1785–1794). We examined these two suggestions with respect to the visual encoding of relative spatial position.

Thresholds for a three-blob alignment task were measured with stimuli which were 10 dB above detection threshold for a range of exposure durations (27 to 400 ms). Blob stimuli were constructed from dynamic random-dot noise and circularly symmetric Gaussian envelopes ( $sd=0.5$  deg). The outer reference blobs were separated vertically by 6 deg. and judgments were made about the relative position of a central test blob. Alignment thresholds were obtained from psychometric functions generated by a self-paced method of constant stimuli. To address the issue of independence, a ‘mixed’ condition where test and reference stimuli were of different type—luminance-defined reference and contrast-defined test blobs, or vice versa—was tested. Alignment thresholds were on average similar for all stimuli—luminance-defined, contrast-defined, and mixed. The effect of exposure duration on alignment thresholds, which was slight (power function with exponent of about  $-0.15$ ), was similar for all stimuli, as was the effect of increasing signal strength (from 1.5 to 12 dB above detection threshold).

These findings do not support the need to propose separate first-order and second-order visual pathways in order to encode relative spatial localisation information for separated stimuli. [Supported by the Australian Research Council.]

- ◆ **Orientation tuning estimated by notch-filtered noise masking**  
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We measured orientation bandwidths of human luminance-detection mechanisms in conditions free from off-orientation looking. This was done by means of a simultaneous spatial masking technique with Gabor test stimuli and two-dimensional filtered noise masks. In the presence of a high-contrast mask, the detection of a test stimulus may be subserved by a mechanism whose preferred orientation differs from the orientation of the test stimulus. This off-orientation looking will narrow estimates of the bandwidth of the detection mechanism. Off-orientation looking can be prevented by the use of appropriately filtered noise to mask the test stimulus. We used two-dimensional spatial noise with a  $1/f$  amplitude spectrum. This noise was filtered to remove an orientation notch about the test stimulus; that is the Fourier representation of the noise contained no energy at the centre orientation of the test stimulus nor for a (variable) range either side. If only a single mechanism subserves detection, the masking obtained with notched noise (symmetrical about the test) would be equal to the sum of masking obtained with noise consisting only of obliques either side of the test. We show that this is not the case; rather that masking obtained with notched noise was greater than the sum of masking obtained with obliques, demonstrating the presence of off-orientation looking. Using symmetrically notched noise to force the visual system to use a single mechanism for detection, we found orientation bandwidths (half width at half-height) of 30 deg.

- ◆ **Orientation effect in the length estimation**  
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In previous experiments, we noticed that subjects tended to overestimate the length of moving amodal objects (rods presented with their end points), while the length in otherwise the same but static stimulation was judged correctly. One possible explanation is that the path of the end

points was overestimated, which produced overestimation of the length of the object. In the following experiments, the effect of motion on length estimation was measured in a similar experimental situation. The object, a bright dot on a dark computer screen, was moving along a straight path. The task was to estimate the length of the object path, by adjusting a straight line on the screen. In four conditions, the orientation of the object path and of the tool were varied both vertically and horizontally. In general, subjects were sensitive to the change of the length of object path. Also, they did not overestimate, but rather underestimated the lengths presented. Another unexpected result was that orientation of the path was not a significant factor in the estimation of length. There are several explanations of these illusions that are based on the orientation effect. It seems that there is no such effect in the estimation of the path of moving objects. When the path and the tool were of different orientation, no significant difference was found. Though this is in accordance with constancy principles, it is still in contradiction to the horizontal-vertical effect.

◆ **'Phase filtering' disrupts continuity through spatial scale of local image structure**

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Using a variety of manipulations, in particular 'phase filtering', I present images that show that recognition of blocked images (coarsely-sampled and quantised) is restored—perceptually unmasked—under conditions where the occurrence of spatial-frequency masking would conventionally be predicted. Image structure is locally continuous through spatial scale in natural images. I show that it is the uninterrupted flow through scale of image structure that plays the crucial role in perceptual masking by blocking, and not the relatively weak masking of low spatial-frequency image-components by spectrally adjacent high-frequency components associated with the blocking.

'Local-phase structure' may provide a general definition of image structure, and is related to local maxima in the energy function of the image. Regions of local-phase structure, for most image-intensity functions, flow smoothly and continuously through spatial scale, and extend over differing ranges of spatial frequencies. For many structural features of an image that can be characterised by local-phase structure, the phase structure changes position in space as it traverses scale. The perceived location of a feature is often at the finest scale that local-phase structure associated with the feature occurs. This finding, together with an account of the effect of image-blocking on local-phase structure, offers a plausible explanation for the perceptual unmasking of blocked images that is a consequence of low-pass or band-reject filtering: disruption of phase structure that is otherwise continuous through scale.

◆ **Temporal dynamics and laminar organisation of orientation tuning in monkey primary visual cortex**

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We studied how orientation tuning dynamics vary across V1 laminae to gain an understanding of the cortical architecture and circuitry mediating the generation of orientation tuning in monkey primary visual cortex. Orientation tuning dynamics were measured by the technique of reverse correlation in the orientation domain [Ringach et al, 1997 *Nature (London)* **387** 281–284]. The following results were obtained: (a) The sharpest orientation selective cells are located outside layer 4C. (b) Some cells exhibit a peak suppression of their response at an angle lying *between* the preferred orientation of the cell and the orientation orthogonal to the optimal; the orientation tuning profile of these neurons resembles a Mexican hat in the orientation domain and we refer to them as exhibiting *flank suppression*. Cells with this type of response are found outside layer 4C. (c) There is a strong correlation between orientation tuning bandwidth and the degree of flank suppression. Flank suppression increases with decreasing orientation tuning bandwidth. (d) The input-output delay time at which cortical cells are best tuned varies across layers. The shortest times are found in layer 4C $\alpha$  ( $\approx 45$  ms). The longest times are found in layer 2 ( $\approx 70$  ms) and layer 6 ( $\approx 65$  ms). Our results suggest that a significant amount of intracortical processing takes place to bring the broadly tuned responses in layer 4C to sharply tuned responses in the output layers of the cortex. Furthermore, sharply tuned cells exhibit flank suppression, an effect difficult to reconcile with Hubel and Wiesel's model of orientation selectivity.

◆ **Perceived motion of multi-component plaid patterns depends on local mechanisms**

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When two sinusoidal gratings of similar spatial frequency, temporal frequency, and contrast are added, they appear to form a rigid 'plaid' pattern moving in a direction determined either by reconciling the constraints implied by the motions of the 1-D component gratings [Adelson and Movshon, 1982 *Nature (London)* 300 523–525] or by summing their vectors (Wilson et al. 1992 *Visual Neuroscience* 9 79–97). The perceived motion of plaid patterns can also be predicted from the motions of their local features. When a sinusoidally phase-reversing grating is added to a symmetrical plaid pattern with the same horizontal period, the grating components predict an appearance of transparent motions in opposite directions. When the phases of the component gratings are appropriate, analysis of local features segregates the pattern into rows of blobs that appear to move in opposite directions.

Four-component patterns made from spatial frequencies between 1 and 20 cycles deg<sup>-1</sup> all appear to be segregated in this way. When direction-discrimination performance was measured with small low-contrast patches of these patterns, observers always reported the pattern to move in the direction predicted by the local features in the centre of the patch. This suggests that the motion of 2-D patterns is determined by local mechanisms.

**CONTRAST, INTERACTIONS AND GAIN CONTROL; CONTRAST DETECTION AND ADAPTATION**

◆ **The time-course of contrast adaptation and discrimination**

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Clifford and Langley showed that while the perceived speed of a maintained stimulus declined as a function of time, sensitivity to modulations of velocity increased. We asked if analogous effects occur in perceived contrast: does sensitivity for temporal contrast modulations of a moving stimulus improve over time? Using a 2AFC procedure, subjects were asked to detect a subtractive or additive contrast burst presented in one of two spatially displaced windows. The windows contained (one) sinusoidal grating at 60% contrast, moving in opposite directions but with equal frequency. Contrast bursts were introduced at 1.0 s intervals and lasted for 100 ms. Each motion sequence took 22 s to complete. There were 32 motion sequences per session split into positive and negative bursts of the same magnitude. Each motion sequence was separated by a 30 s delay. During each session, and across different motion sequences, the spatial location and direction of motion were varied. Temporal sampling was also offset by 500 ms. For intermediate grating frequencies (eg 3.0 cycles deg<sup>-1</sup>, 6.0 Hz), little or no improvements in contrast modulation sensitivity were found after 0.5 s. However, for low spatial and high temporal frequencies (eg 0.7 cycle deg<sup>-1</sup>, 17.0 Hz), sensitivity for the contrast modulations was found to improve over time as a function of modulation depth: larger modulations were discernible (at the 90%-correct level) after 0.5 s, but smaller modulations took longer to detect at the same level of accuracy. Collectively, our data show that contrast/speed discriminability improves as the perceived magnitude of contrast/speed declines. These data may be explained by a logarithmic encoding strategy. One beneficial effect of logarithmic encoding is the minimisation of quantisation noise. From this, it is posited that adaptation reflects an optimisation strategy used by the visual system: one that strives to preserve visual information given limitations in neural transmission.

◆ **Masking by compound gratings described by an image-sequence-discrimination model**

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Ahumada and Beard (1997 *Perception* 26 Supplement, 24) calibrated an image-sequence-discrimination model to masking conditions where the target and masker were the same spatially. Masking was based on local contrast energy so that compound-grating masking is greater than that of either component alone, and masking is nearly independent of mask frequency.

Detection thresholds were measured for a 12 ms target in the presence of a 700 ms mask. Targets were 1, 3, or 9 cycle deg<sup>-1</sup> sine-wave gratings. Masks were one grating or two gratings combined in peaks-subtract phase. The target was presented in 17 temporal positions, before,

during, and after the mask. Peak masking was found near mask onset and offset for 1 and 3 cycle  $\text{deg}^{-1}$  targets, while masking was more uniform during the mask for the 9 cycle  $\text{deg}^{-1}$  target. In general, combination maskers were not significantly more effective than the more effective single-component mask. Also there was much less masking when the mask frequency differed from that of the target.

By altering the model so that much of the masking is caused by a point nonlinearity rather than local contrast energy, the model can predict the results without the complexity of spatial-frequency channels.

◆ **Two stages of adaptation and orientation coding revealed by comparison of the tilt aftereffect and threshold elevation**

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In previous experiments on the tilt aftereffect (TAE), we found strong crossover effects, in that adapting gratings composed of luminance-modulated (LM) binary spatial noise induced a TAE on contrast-modulated (CM) test gratings and vice versa. Little or no TAE was seen after adaptation to LM and CM superimposed at opposite orientations. Both results suggested a common mechanism processing the orientation of LM and CM patterns.

Here we test the idea that separate channels sensitive to LM and CM may feed the common, integrative stage. In a 2AFC detection experiment, subjects adapted to and were tested on CM, LM, and luminance-only (LO) gratings of 1 cycle  $\text{deg}^{-1}$ . All adapting gratings had modulation depths 8 times threshold. An additional control condition was provided by unmodulated noise (N). Noise contrast was 45% for all relevant gratings. Initial adaptation lasted 3 min, with 2 s top-up between trials. Test intervals were presented sequentially for 300 ms with a 500 ms ISI. After adaptation, thresholds were raised by different amounts up to about 6 dB. Unlike the TAE results, threshold elevation was specific for LM and CM: adapting and testing to the same type of grating produced significant loss of sensitivity, but adapting to LM and testing to CM (or vice versa) produced little change. These results support the idea of an initial cue-specific stage, containing separate LM and CM channels, and strengthen our earlier contention that the adaptation responsible for the TAE takes place largely in the integrative stage fed by these channels.

◆ **Encoding of statistically significant differences by the retina**

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Given the limited dynamic range of the retinal output signal (the ganglion cell spike discharges transmitted by the optic nerve), it is fruitful to view several retinal processes as 'serving' to attenuate wasteful neural activity, eg responses to light signals of low biological information value. Well-known examples are (i) classical light-adaptation, ie decreases in gain (response amplitude per photo-isomerisation) with increasing mean illumination; (ii) spatiotemporal differentiation, preserving large response amplitudes only near spatial and temporal borders; (iii) the near-instantaneous gain decrease of ganglion cells exposed to high spatial contrasts. Much less generally appreciated are the adaptational mechanisms attenuating responses to light fluctuations that occur with high probability over time. These mechanisms, based on synaptic plasticity in the neural network, adjust retinal gain according to the statistics of temporal contrast sampled over tens of seconds (rather than seconds or fractions thereof as for the light response itself). They depress ganglion cell responses to quantal fluctuations and to image contrasts falling in a range of contrasts that have occurred frequently over the preceding period, as shown first in amphibians (Donner et al, 1990 *Journal of General Physiology* 95 733–753; 1991 *Neuroscience Research* 15 Supplement, S175–S184) and recently confirmed in rabbit [Smirnakis et al, 1997 *Nature (London)* 386 69–73]. When set by quantal fluctuations, these gain mechanisms implement 'square-root' or 'de Vries–Rose' adaptation, ensuring that a threshold response always signals a contrast of constant statistical significance. We have developed this idea further, analysing the fluctuation-dependent gain as function of different conditioning light sequences in frog retinal ganglion cells.

◆ **Electrophysiological and psychophysical measurements of spatial-frequency characteristics in suprathreshold conditions**

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In suprathreshold experiments we measured spatial-frequency characteristics (SFC) with the presence or absence of additive noise in electrophysiological and psychophysical experiments. In electrophysiological experiments, amplitude of the main VEP components was plotted against spatial frequency of the gratings. Adding stationary visual noise strongly reduces the early components and, at low spatial frequencies, increases the late negative wave (N180). The amplitude of the late positive component (P240) had a maximum at  $1.8 \text{ cycles deg}^{-1}$  with two typical slopes in the low-frequency and high-frequency ranges. Adding noise slightly reduces amplitude of the P2 component, and shifts maximum of the SFC to lower frequencies. The bandwidth of P2 SFC becomes narrower, as the responses to the high frequencies are smaller. In psychophysical experiments observers were asked to estimate the subjective contrast of gratings presented in electrophysiological experiments. A six-grade scale was used: '0'—grating invisible, '5'—best visibility. Each grating was presented until verbal response was obtained. The average subjective contrast was plotted versus spatial frequency. The resulting curves were similar to P2 SFC of the VEP. Adding noise shifts SFC tuning both VEP and subjective estimation to low frequencies. Present results are discussed from the viewpoint which is based on the correlation between the late positive component of VEP (P2) and pattern recognition.

◆ **Stimulus-energy transform within early visual stages**

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This study was aimed at describing how the early visual stages transform the contrast energy of threshold stimuli into the energy of stimulus responses. For this purpose, the threshold summation of incremental stimuli—disks presented foveally on a background of  $30 \text{ cd m}^{-2}$ —was examined. The stimulus-contrast energy (the product of the squared detection contrast, stimulus duration, and area) as a function of stimulus duration and area formed a concave surface with a minimum at a stimulus of 0.057 s duration and  $0.011 \text{ deg}^2$  area.

To describe the data obtained, a recently proposed model for contrast detection (Manahilov and Simpson, *Biological Cybernetics* submitted) was employed. This model assumes that the response energy is a constant at detection threshold. With this assumption, the predicted stimulus energy at threshold satisfactorily describes the data obtained.

This assumption allowed us also to express the efficiency of the early visual stages by the ratio of the response energy to the stimulus-contrast energy. Thus, the stimulus detected at a minimal contrast energy is processed most effectively by the early visual stages. The data analysis in the frequency domain showed that the stimulus-contrast energy equals the sum of the response energy and the lost energy which is filtered by the early visual stages. Thus, the determined energy balance reflects a law of energy conservation for threshold vision.

This energy approach revealed that the constancy of the product of detection contrast, stimulus duration, and area in complete spatiotemporal summation is not due to the constancy of stimulus-light energy. Rather, it reflects the specific changes of the stimulus amplitude–frequency spectrum and the constancy of the stimulus-response energy.

◆ **Analysis of contrast experiments when corrected for intraocular scatter**

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We are all familiar with the contrast experiments in which identical grays in a display appear lighter on a black surround and darker on a white surround. When we calculate the actual stimulus on the retina after scatter in the human eye we find the white surround has increased the retinal irradiance of the enclosed gray area. Scatter affected the gray in the black surround much less. In order to make a new display with equal gray areas on the retina, we must substantially darken the gray in white part of the display. With such stimuli we have equal irradiance gray areas on the retina. Measurements of such displays show that simultaneous contrast is a much larger effect than otherwise measured.

This paper deals with the influence of scattered light on a variety of different contrast phenomena. Some examples, such as the simultaneous-contrast experiments described above, show that scattered light reduces the apparent magnitude of the underlying mechanism. Correcting for scatter makes molehills into mountains.

In other examples, such as White's effect, the scattered light makes the phenomenon much larger than corresponding displays with equal retinal radiances. Correcting for scatter makes mountains into molehills.

◆ **Effects of noise carrier spectrum on sensitivity to luminance and contrast modulations are different: further evidence for separate mechanisms**

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Modulation sensitivity functions (MSFs) for luminance modulation (LM) and contrast modulation (CM) of binary, 2-D, visual 'white' noise have similar shapes. However, overall sensitivity to LM falls with increasing noise contrast, owing to masking, whereas sensitivity to CM increases with noise contrast, consistent with the noise acting as a more effective carrier. Other experiments also suggest that separate mechanisms exist for LM and CM (Schofield and Georgeson, 1997 *Perception* 26 Supplement, 3).

We show here that the two mechanisms behave quite differently in the presence of non-white noise samples. Two additional types of noise were employed: '1/*F*-noise' (spectral amplitude falls with increasing spatial frequency) and '*F*-noise' (amplitude rises in proportion to frequency). The shapes of MSFs for LM were found to be highly dependent on the spectral content of the noise such that sensitivity was lowest at frequencies where the power of the noise was greatest. This is consistent with spatial-frequency-specific masking. Sensitivity functions for CM were very different, being low-pass irrespective of noise type. Although the two carriers had the same rms contrast (0.2), average sensitivity in *F*-noise was higher than that in 1/*F*-noise. This suggests that high-frequency components play the dominant role as carriers for the CM signal. These components have a higher power in *F*-noise than in 1/*F*-noise which would explain why *F*-noise is the more effective carrier.

◆ **Electrophysiological measurements of the spatial-frequency spectrum of internal noise in the visual system**

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Human VEPs were recorded with the use of sine-wave gratings (0.3–18 cycles deg<sup>-1</sup>) with and without quasi-white noise. This approach makes it possible to calculate the value of internal noise [A Skoczenski and A Norcia, 1998 *Nature (London)* 391 697–700]. We proposed to measure the spatial-frequency spectrum of internal noise. These measurements are based on the following definitions: the amplitude of evoked potentials  $V(F)$  depends on the spatial frequency  $F$  of a sine-wave grating;  $V(F)$  for gratings with superimposed noise increases with contrast  $R(F)$  and decreases with increasing external noise, ie  $V(F) = kR(F)/(n_e^2 + n_i^2)^{1/2}$ , where  $n_e^2$ ,  $n_i^2$  are variances of the external and internal noise and  $k$  is a constant. According to the match filtering model of the visual system (N N Krasilnikov, 1958 *Tekhnika Televideniya* 25 26–43), variances of external and internal noise, determining threshold contrast  $R_s(F)$ , are directly proportional to corresponding spectral intensities  $N_{ext}$ ,  $N_{int}(F)$  at the spatial frequency of a grating. Therefore  $V(F) = AR_s(F)/[N_{ext} + N_{int}(F)]^{1/2}$ , where  $A$  is a constant determined from the experiment. The possible non-uniformity of the spatial-frequency characteristic  $K(F)$  of the primary visual system is neglected, as the suprathreshold measurements (contrast-matching functions) are practically flat across spatial frequencies (M A Georgeson and G D Sullivan, 1975 *Journal of Physiology* 252 627–656). We established that the spectral density of internal noise increases with decreasing spatial frequency. The internal noise of the visual system is 'coloured' and most of its energy is concentrated in the low-frequency part of the spectrum.

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◆ **Recovery kinetics of the human-rod ERG a-wave during dark adaptation**

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The physiological basis of the relatively slow adaptation of our visual system to low levels of illumination following intense exposures is an interesting question. We have developed a system to study human-rod activity through the analysis of the rising phase of the a-wave of the electroretinogram (ERG). With this method, we are able to obtain measurements of the changes in the maximal response ( $a_{max}$ ) and sensitivity of the rod system in the course of dark adaptation following retinal bleaches.

The a-wave was recorded from human volunteers with normal vision with a DTL fibre electrode and a Ganzfeld flash stimulator. Ethical approval was obtained from the Cambridge Human Biology Ethics Committee. Dark-adapted control responses to a range of flash intensities were recorded prior to exposure of the retina to bleaching light. Rod-isolated responses were obtained by using photopically matched blue and red flash stimuli with subsequent subtraction of the red-flash response. The time course of recovery of the a-wave from a partial or full retinal bleach was monitored with a series of bright and dim test flashes. We observe that the time for  $a_{\max}$  to recover shifts to longer times in an approximately linear relation to the size of the bleach. The form of recovery is qualitatively similar to that in psychophysical studies of visual-sensitivity recovery from retinal bleaches, and we conclude that in dark adaptation there is a close correlation between the recovery of rod-photoreceptor activity and the recovery of overall visual sensitivity.

◆ **Choice reaction times to contrast increments at different spatial frequencies**

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Choice reaction times (CRTs) and contrast increment thresholds were measured for contrast differences in sine gratings of 2, 4, and 8 cycles  $\text{deg}^{-1}$  at low pedestal contrasts (0–0.048). The observer's task was to indicate as quickly as possible which of two gratings presented side by side had higher contrast. Both gratings had the same spatial frequency but one had a constant pedestal contrast and the other had an increment added to the pedestal contrast. The percentage of correct responses and median correct CRTs were calculated for ten increments added to each pedestal contrast. Contrast increment thresholds, obtained by fitting a Weibull function to the psychometric functions, were higher for 8 than for 2 and 4 cycle  $\text{deg}^{-1}$  gratings at low pedestal contrasts, but the increasing portions of the dipper functions merged at higher pedestals. CRTs corresponding to threshold contrast increments behaved in a similar manner as the increment thresholds. These findings suggest, first, that processing time depends on pedestal contrast since CRTs were not equal when error rates were equal, and second, that processing time for contrast discrimination is slower for high spatial frequencies at low contrast levels but roughly independent of spatial frequency at higher contrast levels, since CRTs increased with spatial frequency at low pedestals but were approximately equal for all frequencies at higher pedestals.

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◆ **Nonlinearities and the pedestal effect**

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Psychophysical and physiological evidence suggests that luminance patterns are independently analysed in 'channels' responding to different bands of spatial frequency. There are, however, interactions among stimuli falling well outside the usual estimates of channels' bandwidths (Henning, Hertz, and Broadbent, 1975 *Vision Research* 15 887–899). We examined whether the masking results of Henning et al are consistent with independent channels. We postulated, before the channels, a point nonlinearity which would introduce distortion products that might produce the observed interactions between stimuli two octaves apart in spatial frequency.

Standard 2AFC masking experiments determined whether possible distortion products of a 4.185 cycle  $\text{deg}^{-1}$  masking sinusoid revealed their presence through effects on the detection of a sinusoidal signal at the frequency of the second harmonic of the masker—8.37 cycles  $\text{deg}^{-1}$ . The signal and masker were horizontally oriented and the signal was in phase, out of phase, or in quadrature with the putative second-order distortion product of the masker. Significant interactions between signal and masker were observed: for a wide range of masker contrasts, signal detection was facilitated by the masking stimulus. However, the shapes of the functions relating detection performance to masker contrast, as well as the effects of relative phase, were inconsistent with the notion that distortion products were responsible for the interactions observed.

◆ **The influence of adapting luminance distribution on brightness response function**

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It is well known that the visual system preserves a high contrast sensitivity over a wide range of light levels by adaptation to the mean luminance. In natural environments, not only the mean

but also higher-order statistics of luminance distribution vary considerably across scenes (Richards, 1982 *Applied Optics* 212 2569–2582; van Hateren, 1997 *Vision Research* 37 3407–3416). This fact raises the question whether vision adapts to higher-order statistics to achieve efficient use of its limited operating range.

The present study addresses the issue of what statistics of the intensity distribution determine the state of brightness adaptation. The perceived brightness for a flash stimulus under various adaptation conditions was measured by psychophysical methods of brightness matching and magnitude estimation. The adaptation conditions differed from each other either in the luminance distribution and/or the temporal waveform, both of which were defined on a logarithmic scale. It was found that the slopes of the brightness response functions were shallower than those obtained under the steady adapting field. The adaptation effect was influenced primarily by the variance of the adapting luminance distribution rather than by the shape of the distribution or the temporal waveform. This suggests the existence of an adaptation mechanism which regulates sensitivity on the basis of the variance information over some prior period.

## ILLUSIONS

### ◆ Effect of shape on verticality judgments with single and double frameworks

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Two experiments were performed to study the influence of shape on visual orientation illusions, in which inducing stimuli with curved borders were used so as to reduce local information about orientation.

In the first experiment, a wavy curved border frame with the same global characteristics as a square was compared with a standard (straight lines) rod-and-frame illusion (RFI) display. The frame was presented in central view at 11°, 22°, and 33°, while the rod orientation was varied between 8° clockwise and 8° counterclockwise; a forced-choice method was used to determine the subjective vertical. Rod settings varied according to frame orientation with an angular function similar to the RFI, but shifted towards the direction opposite to frame orientation (indirect effect), indicating the stronger effect of the diagonal virtual axis of this figure.

In the second experiment, an inner upright frame was added to obtain a double curved border frame or a double square frame. The aim was to examine the effectiveness of the curved frame in producing the inversion of the effect obtained in a previous work and explained by Rock's hierarchical-organisation hypothesis. This proposes that the orientation of an object is influenced only by the nearest surrounding framework. The results confirmed the predicted inversion of the effect; no difference between the straight and curved line frames was found, supporting the idea that hierarchical-organisation effects are due to global mechanisms of shape analysis.

### ◆ Parallel coding of transparent subjective surfaces is governed by Metelli luminance conditions

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A recent controversy addressed whether modal completion of subjective figures arises only for single, attended stimuli or alternatively can proceed for multiple stimuli simultaneously. Several previous attempts to resolve this issue involved human visual search for modally completed figures. However, several of the paradigms employed in those studies has subsequently been reported to contain potential confounds.

Here we exploit a feature of the modal completion of apparently transparent surfaces, namely its sensitivity to the luminance configuration of elements in the display, to devise a new test for parallel coding of modal completion. Results from six experiments indicate that modal completion proceeds rapidly and automatically for several stimuli simultaneously. Moreover, we show that such coding only arises for stimuli where the luminance configuration of the inducing elements is consistent with the presence of a partly camouflaged, transparent surface. These findings suggest that parallel visual processing embodies a tacit knowledge of transparent-surface optics.

### ◆ Brightness contrast and exposure time effects on the Oppel–Kundt illusion

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We examined the extent to which manipulating stimulus brightness and presentation time affects the perceived extent of Oppel–Kundt figures. Observers with normal or corrected-to-normal vision judged pairs of Oppel–Kundt figures that consisted either of an equal number of lines, or of two solids of the same dimensions, in a forced-choice comparison task where the only difference between the two stimuli consisted of a brightness contrast. The stimuli (lines or solid bars)

varied in brightness in steps from 13%, 33%, 53%, 73%, to 93% gray scale, and were presented in all possible pairings. All pairs of stimuli were judged at the exposure times of 100 ms, 500 ms, and 1000 ms. The results showed that the brighter stimuli were perceived as longer for both lines and solid bars, and that as brightness contrast increased so did the probability that subjects would respond this way. Analysis of the presentation times showed the presence of a linear regression, indicating that brighter stimuli appear as longer at all three exposure times, with the 100 ms time yielding the largest Oppel-Kundt illusion. This finding leads us to the question whether the dividing lines within the extent of the 'typical' Oppel-Kundt figure are the major determining factor in perceiving the illusion; this is discussed in terms of the magnocellular and parvocellular processes as contributing physiological mechanisms in the generation the Oppel-Kundt illusion.

◆ **Surface lightness is based on anchoring within surface groups**

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Perception of surface lightness is based on relative luminance values, it is widely agreed. But specific gray values can be derived from relative luminance values only when an anchoring rule is given. For simple images, the rules of anchoring have been well worked out and shown to agree with virtually all the empirical data. Basically there are two rules, one involving relative luminance (the highest luminance appears white) and one involving relative area (the darker region appears lighter as its area is enlarged, as long as its area exceeds that of the highest luminance).

A complex image can be treated as a set of surface groups, where a surface group is composed of two or more surfaces that belong together, as defined by Gestalt grouping principles. A given target surface typically belongs to more than one group and a lightness value can be computed for it within each group using the same rules that apply to simple images. The perceived lightness of the surface, as represented by human matching data, is a weighted average of the several lightness values computed within each of the groups to which it belongs. This formula is highly effective in predicting the pattern of errors shown by human observers throughout the entire literature on surface lightness, including a wide range of recently-celebrated illusions, and several new critical tests.

◆ **A quantitative measure of illusion of curvature**

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An equilateral triangle or square inscribed in a circle were used as stimuli in psychophysical experiments. The stimuli were seen on a monitor as bright figures made of thin lines (0.7 min of arc). The triangles and squares had either straight sides or curved ones of various radii that made the internal angles of the figures vary in appearance. For subjects, the arcs of the circumscribed circles appeared to be puffy owing to perceptual distortions. Viewing the stimulus monocularly and by manipulating the panel keys, subjects adjusted the curvature of the arcs to reduce the illusion to zero. The corrections of the subjects were considered as a measure of the illusion strength. Ten subjects showed approximately the same results. The illusion increased gradually with the size of the stimulus (diameter of the circle, 7–70 min of arc): 2–11 min of arc for triangles, and 2–20 min of arc for squares of the right-sided type. Also the illusion increased with the internal angle (10–80 deg) of the figures: 12–20 min of arc for triangles and 20–35 min of arc for squares of the stimuli up to 1 deg in diameter. The results obtained can be interpreted in terms of spatial filtering. A neurophysiological filter model with dynamic characteristics (Bulatov et al, 1997 *Biological Cybernetics* 77 395–406) has been applied to the experimental data. A quantitative and qualitative correspondence between the data and predictions of the model have been found in the study.

◆ **Equivalent homogenous context intensity depends on average intensity, contrast range, and relative target intensity of complex context patterns**

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Most theories of context effects in brightness perception assume that the effect of context can be mapped into a scalar which is somehow used to compute a target's brightness in relation to the context. This implies that for every target in a complex context there exists a homogenous context which is equivalent to the complex context. Furthermore, independence of target intensity and context influence is often assumed.

We compared several methods for finding equivalent homogenous context patterns and tested whether equivalent context intensity is independent of the target and how it depends on the contrast range of pattern intensities and average intensity of complex context patterns.

Data show a significant dependence of the homogenous equivalent context on (i) average intensity of complex context patterns, (ii) contrast range of context pattern intensities, and (iii) position of context pattern contrast range relative to target intensity. As long as the target intensity is within the range of context pattern intensities there also is a strong target intensity dependence. Neither local averaging rules for normalisation nor taking the highest luminance as white and computing the target intensity ratio with respect to this standard can explain the results.

◆ **How illusory lines interact with real Gabor patches**

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Illusory contours do not represent physical luminance or colour edges, but we perceive them as such. In psychophysical experiments we studied the interactions between these lines and Gaussian-truncated gratings.

Two 'pacmen' (dark circles with a sector removed) formed the illusory line. The same circles rotated by 90° were used as a control condition. A Gabor patch was inserted at the midpoint on the illusory line and at the corresponding place in the control figure. We measured the detection thresholds of the Gabor patch using a 2AFC paradigm with a staircase procedure. In one set of experiments we varied the phase of the Gabor patch (0°–180°), and in the other set we changed the separation between the two pacmen.

In both the test and control conditions we observed a decrease in the detection thresholds relative to those obtained on the homogeneous background. But observers showed different changes in detection of the Gabor patch depending on its phase. For one observer, there were no significant differences for all phases tested: the thresholds were lower when the illusory line was seen relative to the control condition. Another observer, however, showed lower thresholds when the Gabor patch had a sine-wave profile, but for the cosine-wave Gabor patch this difference disappeared. With increasing separation between the pacmen, thresholds increased in the presence of the illusory line, but did not change significantly in the control condition. The results show that the perception of illusory lines varies among observers: the line may be seen as a light or dark edge and interact in different ways with real objects.

◆ **Figural completion in occlusion phenomena: Effect of contour orientation**

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There are some two-dimensional line patterns that can be seen as figures arranged in depth so that one figure partly occludes another. Available data show no prevailing principle which predicts what will be seen behind the occluding figure, ie how the perceptual system completes a partly occluded figure. Sometimes, the principle of local factors prevails: the occluded part will be completed so that the contours of visible parts continue monotonically after intersection with the contour of the occluding figure until they connect to each other. Sometimes, the principle of global factors prevails: the occluded part will be completed so that the whole figure attains the greatest possible symmetry.

The basic idea of this study is that whether local or global factors prevail depends on contour orientation. It is assumed that the partly-occluded figure will be completed so that the contour of the occluded part reaches vertical and/or horizontal orientation. Sometimes this coincides with local and sometimes with global factors. A collection of fourteen patterns (each set in eight orientations) was presented in the experiment. The subjects were asked to draw the contours of the occluded parts of figures. The results partly confirmed the contour orientation-hypothesis. In cases where local and global factors diverge into different solutions, contour orientation becomes the prevailing factor and the vertical–horizontal orientations of completed figures are significantly preferred over the oblique. However, if local and global factors converge into the same solution, then this solution remains dominant irrespective of orientation.

◆ **Instability of the Necker cube: Influence of orientation and configuration**

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Kubovy and Claessens (unpublished) observed that the instability of the Necker cube (NC) varied with the cube's orientation. We explored this phenomenon by briefly (300 ms) presenting five types of NCs at seven counterclockwise tilts (in 22.5° steps). Let 1.0 be the length of the sides of the two square faces of each cube. If the lower left-hand corner of the left-low face of the cube is at the origin, then the coordinates of the lower left-hand corner of the right-up face of the five types of cube are: (i) (0.5; 0.5), ii) (0.34; 0.34), iii) (0.167; 0.167), (iv) (0.5; 0.34), (v) (0.5; 0.167). We found two principal effects: (a) the shorter the projection of the orthogonals (the lines in depth) of a cube, the less stable it was; (b) the greater the asymmetry of a cube, the greater was the shift of maximal instability toward larger tilts.

We discuss two hypotheses: (a) that the probability of seeing a given organisation is directly related to the probability of the viewer interpreting this organisation as a cube seen from above; (b) that reversals of the NC are analogous to apparent motion.

◆ **Intentional organisation and colour appearance**

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Perceptual organisation is an important factor in colour vision. Assimilation occurs when an intentional effort is needed to disambiguate among possible perceptual groupings [Agostini and Proffitt, 1992 *Investigative Ophthalmology & Visual Science* 33(4)]. We studied a new version of White's illusion, where target gray patches could be intentionally grouped with other gray patches aligned with either the black or white stripes of the White's pattern. We found that the targets appeared lighter when they were intentionally organised in phase with the black stripes of the White's pattern and darker when they were intentionally organised in phase with the white stripes. This finding supports the idea that intentional perceptual organisation influences colour appearance.

◆ **Expansion of partially occluded figures as due to optical-geometrical illusions**

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In a previous report (Purghe and Olivero, 1997 *Perception* 26 Supplement, 49) we claimed that size effects originally attributed to amodal completion (phenomenal shrinkage of partially occluded figures and expansion of the modally visible parts of such figures) might be due to the same mechanisms that are responsible for the emergence of classical optical-geometrical illusions. As to the effects of expansions, the best candidates might be the mechanisms underlying the horizontal-vertical illusion as well as those underlying the Lipps illusion (elongation of a square lacking one of its four sides).

In order to test which of the two above-mentioned illusions matches more closely the expansion of modally visible parts of partially occluded figures we carried out two experiments. The first experiment was run with the method of adjustment on nine patterns (a square and eight variants of a similar square-like figure). There were twenty subjects, aged 19 to 30 years. The second experiment was aimed at testing the microgenesis of the expansion by the method of constant stimuli, with twenty-four subjects, aged 19 to 24 years. Exposure times varied from 30 to 1000 ms. Four different patterns were used.

The results converge in showing that the expansion of the square in the Lipps illusion is significantly stronger than that measured in amodal-completion condition (a square touching a rectangular 'occluder'). Therefore the expansion of the modally visible parts of an occluded figure cannot be simply explained in terms of perceptual absence of the occluded edge. On the contrary, the time function of the horizontal-vertical illusion seems to follow rather closely that of the 'occluded' square. Our conclusion is that the latter illusion and the expansion of partially occluded figures might be the outcome of the same visual mechanisms.

◆ **The relationship between perceived brightness and contrast threshold in illusory figures**

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We investigated the relationship between changes in contrast thresholds on illusory contours and the brightness changes perceived on these contours.

We measured the perceived brightness in the gaps of a Kanizsa square, where an illusory figure is perceived, and in the gaps of an outline square by determining the point of subjective equality with the background for a small line target presented in the gap. White inducers were displayed on a gray background. We also determined the decrement and increment thresholds for detecting the same target in these two configurations. While the gap appeared to be brighter than the background, there was no significant difference between increment and decrement thresholds, which means that the perceived brightness in the gap does not act like a simple contrast pedestal on the detection of the target. This implies that brightness and luminance are processed at different levels.

To investigate possible top-down influences of figural completion we compared the increment thresholds obtained in a closed configuration (same as above) to thresholds in an open configuration where only two sides of the square were outlined by the inducers. Contrast thresholds for both configurations were significantly lower than in the control configuration, where the target was displayed alone. We found no difference in increment thresholds between the open and the closed configuration, which suggests that later processing stages, in which the unity of the square is established, have no influence on contrast thresholds.

◆ **Inducer luminance affects the strength of illusory contours in the Ehrenstein figure**

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We studied the effect of luminance of the inducing lines on the strength and clarity of illusory contour in an Ehrenstein figure using a subthreshold summation paradigm as presented previously (Tassi, Pardieu, and Bonnet, 1995 *Perception* 24 Supplement, 127). The figure consisted of four bright lines (inducers). The inducers were presented in eight different luminances ranging from 4 cd m<sup>-2</sup> to 20 cd m<sup>-2</sup>. The threshold of a white real line superimposed on the illusory contour and joining two inducer ends was measured for each luminance condition, with a forced-choice (left-right) procedure. Each figure presented the same gap size (1.6 deg) for which the length of the real line joining the ends of two inducers was 1.1 deg. All figures presented the same inducer length (2.5 deg). The results obtained in each condition and compared with the control condition, where the real line was presented alone, show a decrease in threshold of the real line and an increase in clarity of apparent contour with increasing inducer luminance. When the real line was superimposed on the illusory contour, its threshold was lower than in the control condition, and decreased quasi-linearly with the increment of inducer luminance. Thus, it seems that dipole cells involved in the illusory-contour formation, as suggested previously by Tassi et al, in agreement with the Grossberg and Mingolla model (Grossberg and Mingolla, 1985 *Psychological Review* 92 173-211; Grossberg, 1994 *Perception & Psychophysics* 55 48-120), respond to luminance variation.

◆ **Modal and amodal completion in the Poggendorff illusion**

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We measured the strength of the Poggendorff illusion in configurations containing solid surfaces as opposed to usual parallels. Surface, oblique-line, and background luminances were manipulated separately to create two types of configurations: (a) consistent with the amodal completion of oblique lines behind the surface; and (b) consistent with modal completion of the obliques in front of the surface. The perceived misalignment of oblique lines in these configurations was judged by naive subjects by a paired comparison procedure.

Configurations that allow for modal completion of oblique lines in front of the surface were judged as drastically less misaligned compared to the configurations in which oblique lines were completed amodally. The contrast of the oblique-line segments relative to the background also affected the size of the illusion: oblique-line segments having lower contrast relative to the background appeared more aligned. This effect was especially pronounced in configurations compatible with amodal completion. The marked difference in the size of illusion between conditions favouring amodal versus modal completion is consistent with the claims that the perceived spatial layout is a major determinant of the Poggendorff illusion.

◆ **Approaching the perception of illumination**

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Very few experimental studies have considered the problem of 'if and how' environmental illumination is perceived. More often researchers have addressed their attention to illumination in relation to the perception of surface colours. We are trying to turn over the problem by considering how surface colours influence the perceived luminosity of an environment. Until now, we have been concerned with achromatic representations of a 3-D world. In experiment 1, we address the 'if' problem by asking two groups of observers to judge the global luminosity of two sets of computer displayed 3-D scenes on a 1:100 scale. The between-subjects independent variable (*G*) was the depicted object: in one set of stimuli it was a cube, in the other set it was a more complex solid with angles and curved surfaces. The within-subjects independent variables were: *A*, the luminance of the sky (2 levels); *B*, the luminance of the ground (2 levels); *C*, the contrast between the surfaces of the object (4 levels); *D*, the presence of a cast shadow (2 levels). Besides foreseeable interactions, we found reliable *G-A-B*, *A-C*, *B-C*, and *G-D* interactions. In experiment 2 we have started to address the 'how' problem by performing a matching task where other observers had to match the surfaces of the same two sets of 3-D scenes and the surfaces of flat Mondrian renderings of those scenes on a 20-step grey scale. This experiment was designed to measure the lightness/brightness evaluation differences between 3-D scenes and flat scenes.

◆ **Perceptual belongingness and spatial propagation of lightness contrast**

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Agostini and Proffitt (1993 *Perception* **22** 263–272) showed that perceptual belongingness (the subsumption of some set of elements into a perceived whole) can cause simultaneous lightness contrast (SLC) to be seen in configurations in which the inducing elements are not adjacent to the target. The aim of this work was to measure the strength of belongingness in determining SLC when the numbers of inducing and induced elements are manipulated in Agostini and Proffitt-type configurations.

Observers had to perform a nulling task. They adjusted the luminance of the gray dots organised with the black inducer dots to cancel the illusion and attain a subjective match with the gray dots organised with the white inducer dots. We found that even when there are few inducer elements, perceptual belongingness causes SLC to spatially propagate on all the gray induced dots. Simple lateral inhibition or retinex theories cannot account for the effects observed in these configurations. Higher-level processes must be factored in to explain lightness contrast.

◆ **The Café Wall revisited**

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We have suggested (Gregory and Heard, 1979 *Perception* **8** 365–380) that the long illusory wedges of the Café Wall figure are given by small-scale wedges produced by pulling together of each half-rectangle where there is luminance contrast across the neutral luminance 'mortar' lines. Another possibility that has been suggested is that 'feature detectors' mis-signal at the right angles to the vertical edges. What happens if right angles are avoided? Results are reported.

## NEURAL MODELLING

◆ **A bio-inspired novelty detector for camera motion control**

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Using a photoreceptor model and a model of retinal processing, we have implemented on the Rolling Vision Sphere, our active vision platform, a novelty detector. The photoreceptor model, inspired by Prokopowicz and Cooper (1995 *International Journal of Computer Vision* **16** 191–204), is an IIR low-pass filter followed by a Naka–Rushton light-adaptation filter. We compare this model of photoreceptor with a more accurate but computationally demanding model. The retinal processing model, inspired by Beaudot (1994, PhD dissertation), implements a model of the outer and the inner plexiform layers. The resulting image is used to control the saccadic mechanism

of a quick, mobile vision platform (500 deg s<sup>-1</sup> and 40 000 deg s<sup>-2</sup>). The system is able to detect an object moving and centres on it. We compare the performance of our system in terms of robustness and efficiency with classical approaches.

◆ **Perspectives on cognitive computational aspects for neuromorphic vision**

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The cortex processes the various attributes of a viewed object—colour, shape, texture, depth, etc—and adapts to the information structure of the environment to integrate them into a recognisable whole. We describe a parallel, dynamical system designed to integrate model-based and data-driven approaches to image recognition through an artificial neural network (ANN). The tight intercoupling and dynamic interplay between high and low levels of visual analysis results in the verification of hypotheses formed and reformed during the image recognition process. This process assists the cerebral cortex in determining and interpreting the objects being viewed. The architectural and functional characteristics of this neuromorphic network have been designed to emulate the cerebral cortex in the light of neurobiological considerations. Each of the dimensional segments of the multilayered, multidimensional parallel-feedback ANN processes the various but interrelated attributes and characteristics of the viewed object. The outputs of these networks are fed into another ANN which infers the object's attributes. The work described here bridges the gap between different levels of neuronal discoveries and cognitive explanations through the use of distinctive characteristics of cognitive neuro-vision. Some computational aspects for the network's implementation onto a machine are also provided.

◆ **Reverse correlation analysis and direction selectivity of simple cortical cells**

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White-noise stimuli and reverse correlation analysis (RCA) are widely used to determine the spatiotemporal structure of the receptive fields (RFs) of simple cortical cells. When RCA is applied to simple-cell responses to white noise, a large body of data shows that direction-selective (DS) cells tend to have inseparable spatiotemporal RFs while non-DS cells tend to have separable RFs. Yet a number of DS cells also have separable RFs as estimated by RCA, a fact that threatens the validity of current models of direction selectivity based on inseparable spatiotemporal RFs.

Here, the results of a simulation study aimed at determining the compatibility of direction selectivity with separable RFs as estimated by RCA are reported. In the simulations, model cells with a variety of spatiotemporal RFs were presented with both moving bars and white noise. Responses to moving bars were used to produce post-stimulus time histograms that would indicate the DS of the cell, and responses to white noise were subjected to RCA to obtain  $X-T$  plots. Across the entire set of simulations, we were able to reproduce the expected results (DS cells producing inseparable  $X-T$  plots and non-DS cells producing separable  $X-T$  plots) as well as the exceptional cases of DS cells producing separable  $X-T$  plots. We discuss the implications of these results for models of direction selectivity in simple cortical cells.

◆ **Models of visual information processing in the human visual system at threshold conditions**

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Starting from statistical decision theory and the procedures of optimal (Bayesian) image processing, three functional models of visual information processing in the human visual system at threshold conditions have been developed. These three models differ in their algorithms and structural organisation. In the first model, optimal image processing is assumed to operate according to the Zigert-Kotelnikov algorithm; in the second model—the correlation algorithm; and in the third a 'matched filtering' algorithm. All possible variants of optimal processing of visual information are exhausted by these three models. In these models we have taken into account the inaccuracy of memorising complex figures. The models are created as working computer algorithms. The mathematical formulation of this approach was reported by one of us previously (Krasilnikov, 1958 *Tekhnika Televideniya* 25 26–43). We tested these three models using the method of comparative (human–computer) measurements of the probability of correctly identifying the image in noise. In our experiments we used images of different complexity: black-and-white (letters, Landolt C) and half-tone (faces, aeroplanes, cars). Identification by all these models and by eight trained observers coincides within the limits of measurement error of about 4%.

Thus, the experiments have demonstrated the efficiency of the model. However, the method used in our experiments in principle does not make it possible to give preference to any one of the three models. This problem requires further investigations by the other methods.

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◆ **Grating-optical diffractive image preprocessing in human vision**

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Diffraction and quantisation (pulse coding) transforms the light entering through the cones and passing through the oscillating nuclear layers of the human retina. This transformation results in a reciprocal Fourier space in the Fresnel near-field behind the grating. Such oscillating 3-D multilayer phase grating structures act as spatiotemporal frequency and spectral filters, preprocessing the image in Fourier space. This process separates the physical-stimulus parameters (intensity and wavelength) into three exit chromatically tuned adapted RGB colour channels. It also processes the multiple ranges of objects in 3-D space into either spatial frequencies or temporal phase differences in the reciprocal Fourier space. The resulting patchwise differentiation by Fourier analysis identifies local features (fine structures), and the integration by Fourier synthesis identifies global features (coarse structures). The elements of spatiotemporal and spectral diffractive optical filtering are illustrated here with centrosymmetric multilayer gratings. The cellular 3-D gratings are interpreted as cortical modulators. Such cortical modulators are important for coincidence detection (pattern segmentation), binding of multimodal stimulus parameters, and spectral/spatiotemporal correlation analysis in the processing of complex images. The results indicate that spectral time and spatial-frequency analyses seem to be orthogonal to each other, similar to what occurs in auditory systems. Thus, this cellular diffractive 3-D grating is a key component in cortical 4-D spatiotemporal processing.

◆ **A new method to distinguish between signal-detection and threshold theories: evidence in favour of high-threshold theory**

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It is now well-established that human observers in detection/discrimination experiments can rank judgments according to their degree of certainty. We have recently provided additional evidence (Logvinenko and Vityaev, 1994 *Perception* 23 Supplement, 49) showing that discriminative judgments for perceived numerosity obey the transitivity law. However, this was the case only when the stimuli to be discriminated were different. Surprisingly, when the two stimuli in a pair were the same, the judgments were intransitive. This finding has a strong implication for theories of detection/discrimination since many such theories, including signal-detection theory and low-threshold theory, predict transitivity for both different and identical stimulus pairs. The only exception is high-threshold theory which predicts transitivity for pairs composed of different stimuli and intransitivity for pairs of identical stimuli.

We have followed up this investigation with a new experiment on the numerosity discrimination of random-dot patterns with five more subjects. The experimental design and the method of statistical analysis were the same as in our previous experiment. In agreement with our previous result the observers' judgments were found to be transitive for different pairs and intransitive for identical pairs. These results are favourable to high-threshold theory but not to signal-detection theory or low-threshold theory. To account for the data obtained, an alternative interpretation is proposed in terms of fuzzy numbers, developed in fuzzy mathematics.

◆ **Local and global aspects of information processing in the outer retina**

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In the vertebrate outer retina different types of cones are selectively coupled to different kinds of horizontal cells. Horizontal cells form large networks that are electrically coupled in the dark-adapted state and uncoupled with light adaptation. Signal propagation in these networks changes with the state of adaptation. A mathematical model of signal propagation has been evaluated by cell recordings in turtle retina and simulation studies. Morphology of horizontal cells is another factor that influences signal propagation. Its effect has been studied by the same methods.

In the light-adapted retina local processes seem to be more important than global ones. Colour processing is determined by local negative feedback of horizontal cells to cones and bipolars. Recordings of a turtle bipolar cell are interpreted by a simulation model that suggests an important influence of H3 horizontal cells on colour-specific behaviour of the bipolar.

The selective coupling of cones to horizontal cells leads to different colour signals in the retinae of different species. Simulation studies support the cascade model of Stell as an explanation of colour-specific reactions of turtle and carp horizontal cells. Primate horizontal cells do not show similar colour-specific reactions. Their role in colour processing can be seen in the modulation of cone output. Another simulation model suggests that the pedicles of red and green cones react in a monophasic way to stimuli of different wavelengths while pedicles of blue cones generate a biphasic output to coloured stimuli.

◆ **Weber–Fechner adaptation in vertebrate photoreceptors**

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The ergocity theorem from statistical mechanics has been used to solve the adaptation problem in vertebrate photoreceptors under non-bleaching conditions. In these receptors, the reduction in sensitivity follows the century-old Weber–Fechner formula  $I_0/(I + I_0)$ , where  $I$  is the background intensity and  $I_0$  an adjusting parameter. For the first time, the exact value of  $I_0$  for a given photoreceptor can be calculated from the geometry of the outer segment and the decay time constant of the current response to single photon or small flashes. A compartment model was built, based on the well-known different geometries of the rod and cone outer segments. For the cones, each of the thousands of lamellae that make up the outer segment was considered a separate compartment; for the rods, the finite lifetime of the excited biochemical molecules controlling the dark current and the diffusion coefficients of these molecules were used to define an 'operational compartment'. If, inside these compartments, the single photon response can be characterised by a response having maximal amplitude, a sharp rising edge, and decaying exponentially with a time constant  $\tau$ , then the value of  $I_0$  is simply  $N/\tau$ . A Mathematica program was used to simulate the Poisson stochastic process and the result provided a perfect fit for the  $I_0/(I + I_0)$  Weber–Fechner relation. When compared to experimentally obtained values for the receptors of many vertebrate species, the values of  $I_0$  that the model outputs are within experimental errors. The model is also able to predict the absolute sensitivity of rods and cones in many species and the rules for a photoreceptor whose sensitivity would be temperature-independent, a desirable feature for cold-blooded vertebrates.

◆ **Feature contrast explained by cortical geometry**

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Detection performance in feature contrast usually decreases towards the periphery, but at least for the feature of orientation a central performance drop can also be observed (Kehrer, 1987 *Spatial Vision* 2 247–261). By scaling the whole stimulus, the drop also gets scaled. These findings are usually explained by filter models with several degrees of freedom. We believe that the distance between the cortical representations of target and adjacent distractors completely determines the detection rate. Therefore, we propose a model assuming only isotropic lateral interaction in V1. This model has only two parameters:  $s$  determines the cortical coupling width distribution and  $a$  comes with the retino-cortical mapping model  $\log(a + z)$ .

We measured detection rates for a single line with orientation contrast at 48 positions and three viewing distances with backward masking, resulting in both peripheral and central performance loss. The model fits the experimental detection rate well when parametrised to  $s = 3 - 7$  mm and  $a = 1 - 2$  deg. Unlike classical filter models, these two values can be checked for anatomical validity. In particular, our  $a$  parameter is exactly in the range observed for human V1.

We also repeated the experiment using isoluminant colours which generally confirmed the results in the previous high-contrast condition. This is an additional cue for a spatial (P channel) explanation based on a very regular computational architecture within V1, where only the retino-cortical mapping is responsible for the nonhomogeneity in performance. The central performance loss can therefore be explained by cortical distances that are too large to be bridged, and the peripheral loss by very small distances on V1 exceeding its resolution.

## TEMPORAL PROCESSES

### ◆ Masking and the integration of spatial frequencies

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It has been suggested that spatial-frequency information is preferentially integrated from coarse to fine through time. A direct prediction of this coarse-to-fine preference would be that the harmonics of a square wave presented separately and in rapid succession from coarse to fine should be more readily integrated to form a square wave than its converse, fine to coarse. When a comparison is made between an  $F/3F/5F$  presentation order with a  $5F/3F/F$  order, the former order leads to more incorrect detection reports of a square wave but the latter is favoured in judgments of square-wave resemblance (reported at ARVO 1998). The first experiment presented here replicated this fine-to-coarse preference for square-wave resemblance with the first two harmonics of a square wave. Two possible masking explanations for these results are then examined: the differential masking effects of the flat-spectrum noise patch which delineated the two intervals,  $F/3F$  and  $3F/F$ ; and the differential forward and backward masking effect of the  $F$  on the  $3F$ . It was found that neither masking explanation could account for the fine-to-coarse preference in experiment 1 and that reported previously. The results are discussed in terms of a flexible integration mechanism.

### ◆ A central component of delay in processing high spatial frequencies?

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Both reaction time (RT) and the visually evoked potential (VEP) are delayed in response to stimuli of high spatial frequency (SF) but the mechanism of delay is still a matter of controversy. Hence, it is surprising that no attention has been paid to the reported higher rate of RT increase in comparison with the VEP latency increase at higher stimulus SFs (Musselwhite and Jeffreys, 1985 *Vision Research* 25 1545–1555; Strasburger et al. 1988 *Applied Optics* 27 1069–1088).

We recorded both VEP and RT under stimulation with sinusoidal gratings with SFs of 0.5, 5, or 12 cycles  $\text{deg}^{-1}$  and contrast ranging from 2.5% to 50%. VEP latency was measured at the peak of the early negative wave of the Laplacian derivation from Oz against two lateral electrodes. Consistent with previous findings, both VEP latency and RT increased with the increase of grating SF and with the decrease of grating contrast. It was found, in addition, that RT and VEP latency increased by approximately the same amount at 0.5 and 5 cycles  $\text{deg}^{-1}$ , thus suggesting that the main source of the RT delay at 5 cycles  $\text{deg}^{-1}$  in comparison with RT at 0.5 cycle  $\text{deg}^{-1}$  is of peripheral origin. However, in comparison with the data at 0.5 and 5 cycles  $\text{deg}^{-1}$ , RT at 12 cycles  $\text{deg}^{-1}$  increased much more than VEP latency. Although the effect was particularly strong at low contrast levels, the prolonged RT at 12 cycles  $\text{deg}^{-1}$  could not be explained by factors such as monitor MTF, reduced subjects' contrast sensitivity, or uncertainty effects at this SF. We conclude that the RT delay at high SFs involves a substantial central component in addition to the peripheral delay.

### ◆ Spatiotemporal interactions in VEPs and contrast sensitivity; on-off vs reversal

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Many visual-evoked-potential (VEP) studies now use on-off and reversal stimulation to account for the sustained/transient dichotomy. For example, we have shown that on-off is more appropriate for chromatic VEPs. Here we compare contrast sensitivity and VEP responses to onset-offset and reversal of achromatic gratings, deriving 3-D spatiotemporal tuning functions with ranges of 0.75 to 12.5 cycles  $\text{deg}^{-1}$  and 12 to 20 Hz.

At all temporal frequencies, the reversal VEP is dramatically reduced in the middle of the spatial-frequency range (around 3 cycles  $\text{deg}^{-1}$ ). The on-off VEPs exhibit a virtually unimodal spatial tuning function at 16 Hz. However, a small notch appears at other rates, so that both on-off and reversal functions possess lower and higher spatial-frequency branches. They differ most markedly at low temporal frequencies, where the low-spatial-frequency branch is enhanced with on-off but attenuated with reversal presentation. The high-spatial-frequency branches are relatively immune to changes in temporal frequency.

Unlike the VEP, contrast sensitivity hardly changes with temporal frequency although, as classical psychophysics predicts, low-spatial-frequency sensitivity reduces with on-off. The (suprathreshold)

changes in the VEP cannot be attributed to (threshold) differences in psychophysics. It is important to take these results into account if the VEP is to be used to monitor spatial vision (eg in clinical studies). It is clear that, at low spatial frequencies, the two forms of stimulation tap different mechanisms and are probably mediated by different populations of nerve fibres.

◆ **Precision of the rotating Pulfrich technique for determining visual latency difference is significantly greater if viewing distance is varied than if angular velocity is varied**

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We compared two versions of the rotating Pulfrich technique described by Nickalls (1986 *Vision Research* 26 367–372; 1996 *Vision Research* 36 2865–2872) for determining visual latency difference: (technique A) varying viewing distance from the centre of rotation to the eyes and keeping target angular velocity constant ( $33 \text{ rev min}^{-1}$ ), and (technique B) varying angular velocity and keeping viewing distance constant (180 cm).

All subjects observed (tracked) the same black vertical thin rod rotating clockwise on a horizontal turntable with a neutral optical density filter ( $\text{OD} = 0.7, 1.0, 1.3$ ) in front of the right eye for both techniques. Mean luminances of front screen and background were  $92$  and  $108 \text{ cd m}^{-2}$ , respectively. In both techniques the same visual endpoint was used, namely when the target appeared not to rotate but to only move back and forth from side to side along a flat path.

We obtained the following results ( $n = 10$  for all graphs):

Technique A: OD 0.7 ( $7.19 \pm 0.49$  ms); OD 1.0 ( $8.06 \pm 0.89$  ms); OD 1.3 ( $9.05 \pm 0.94$  ms).

Technique B: OD 0.7 ( $6.69 \pm 1.99$  ms); OD 1.0 ( $8.80 \pm 1.78$  ms); OD 1.3 ( $9.95 \pm 1.91$  ms).

These show (a) the mean visual latency differences for a given neutral density filter associated with each technique were not significantly different, (b) the precision (SD) associated with technique A was 2–4 times better than that associated with technique B, and (c) for each technique the mean latency difference increased similarly with an increase in optical density. These results further validate the Nickalls formula for determining visual latency difference by this technique.

◆ **Psychophysical evidence for a geometrical module in the magnocellular pathway**

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On the basis of a neuropathological study, Davidoff and Warrington (1993 *Neuropsychologia* 31 83–93) suggested that, besides a shape module in the parvocellular pathway, a geometrical module has to be present in the magnocellular pathway. This module is responsible for the detection of 'secondary' contours (eg subjective contours). Rogers and Ramachandran (1998 *Vision Research* 38 71–77) used high-frequency flickering for exclusively stimulating the magnocellular pathway. Their results might be taken as evidence for the existence of the geometry module postulated by Davidoff and Warrington.

In the experiment reported here high-frequency flickering has also been used. In an eight-by-eight grid of dots, a set of three, four, or five dots was flickered in antiphase. Subjects had to press a button when they could detect the occurrence of a four-dot configuration for two possible conditions: the constant global form condition (the dots formed a straight line in random orientations) and the variable global form condition (the dots formed triangles, squares, or pentagons). The prediction was that the four dots could still be perceived during high-frequency flickering in the variable global form condition, whereas this should not be the case for the constant global form condition. This prediction was confirmed, corroborating the hypothesis of the existence of a magnocellular, geometrical module.

◆ **Visual illusions and travelling alpha-waves evoked by flicker with alpha frequency**

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The aim of the study was to obtain some experimental evidence for the 'scanning hypothesis' that links EEG alpha-activity with rhythmically spreading waves in the visual cortex. Forty healthy persons were studied. Through closed lids, flicker stimulation with a frequency matched to the individual's alpha-rhythm was presented. All subjects perceived clear illusory visual objects (ring or circle, spiral or spiral spring, grid). A ring or a circle was perceived most often, a three-dimensional spiral less often, and a curved grid infrequently. Individual optimal stimulation frequency for evoking these illusions was significantly correlated with the individual dominant

alpha-frequency. The probability of evoking the ring and spiral illusions was the highest at this frequency, while that for the grid illusion was maximal for frequencies that differed by  $\pm 1-2$  Hz. Under the same conditions 10 typical trajectories of the travelling EEG alpha-waves on the human scalp were revealed and a significant inter-relation between occipito-frontal trajectory and illusions of a ring or a spiral was found. Dependence of the effects obtained on the interaction of a spreading alpha-wave with cortical excitation evoked by flashes is discussed. Quasi-stroboscopic perceptual fixation of the spreading cortical wave of alpha-rhythm due to summation with isorhythmic cortical excitation after flicker can perceptually 'stop' the alpha-wave at some moment of its spreading and can make it suprathreshold and visible. Data obtained provide evidence that an alpha-wave in the visual cortex is a reflection of the spreading process, thus confirming the 'scanning' hypothesis.

#### **BINOCULAR STEREOPSIS AND STEREO MECHANISMS**

- ◆ **Binding of suppression zones in binocular rivalry by synchronised contrast modulation**  
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Binocular rivalry with large stimuli is typically piecemeal, with many small suppression zones. We showed (1998, ARVO) that random contrast modulation of one eye's stimulus promotes cooperativity, causing these zones to predominate jointly as a larger ensemble. The current data explore spatial and temporal aspects of this effect. Two collinear grating patches were presented to the left eye and random-dot patches to the right eye. Contrast modulation (25 Hz) was either synchronous (identical modulation) or asynchronous (independent modulation). In 60-s trials, subjects monitored grating predominance (left, right, or both gratings) using key presses, with proportion of conjoint predominance measured. Strong elevations of conjoint predominance occur with synchronised modulation, relative to unsynchronised. This effect is weakened by collinear and orthogonal grating orientations, by spatial-phase differences, and by temporal-phase lags between otherwise identical contrast modulations. Increasing the spatial separation of the gratings eliminated the effect at 7.5 deg. At this separation, inserting an identical 'bridge' grating between the outer two restored the full elevation of conjoint predominance, but only when the bridge was collinear and synchronised with the outer two. As suppression zones are thought to correspond to the visual field of cortical hypercolumns, lateral connections between columns probably underlie these data. Further, as modulating stimulus contrast will induce a modulating cortical response, elevations in conjoint predominance may reflect the binding of the gratings into a perceptual ensemble. This is consistent with the recent 'temporal correlation hypothesis', also thought to be based on lateral cortical connections.

- ◆ **The fine structure of neuronal connections in the cat area 17**  
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The functional properties (orientational, directional selectivity, etc) of the striate cortex neurons and the distribution of these properties over the cortex surface are well known. At least some of these properties are based on the spatial structure of intrinsic horizontal connections.

Our aim was to investigate the connections of the single orientational column—the functional unit of the striate cortex. Single cortical columns representing different parts of the visual field (from  $-25$  deg to  $+10$  deg) were microiontophoretically injected with horseradish peroxidase. 3-D reconstruction of the region of retrogradely labelled cells was performed with the use of serial frontal brain sections.

It was found that (i) the orientation of elongated labelled-cell region for columns located in the transition zone between areas 17 and 18 and for those outside this zone is different, (ii) labelled cells were mainly arranged in two parallel rows running approximately perpendicular to the 17–18 border, (iii) in relation to the position of the injected column the labelled-cell region usually was asymmetric: extended either towards the visual-field midline projection, or in the opposite direction. The first asymmetry type was obtained for the columns receiving callosal projections from the non-corresponding regions of other cortical hemifield, the other was found for columns receiving projections from the corresponding regions. The neuronal connections found by us may offer an explanation of the basic phenomena of stereopsis and periphery effects.

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◆ **Estimator reliability predicts perception of cue-conflict stimuli**

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The human perceptual system often has several methods available for constructing a representation (percept) of the environment. Each method defines an estimator, and each estimator's reliability depends on the calculation it uses and the noise in the signal measurements that go into the calculation. Assuming that the system knows the reliability of each estimator and weights estimates optimally according to the reliabilities, one can predict the percept that results in a cue-conflict situation. We developed such a modified weak fusion model for surface slant perception. Specifically, we examined the geometric effect (apparent slant from horizontal magnification of one eye's image) and the induced effect (slant from vertical magnification). Ogle reported that slant-nulling settings increase systematically with viewing distance in the geometric and induced effects. Gillam, Rogers, and colleagues reported that estimated slant increases with distance in the geometric effect, but not in the induced effect.

We first attempted to replicate the slant-nulling and slant-estimation experiments. The results were consistent with the literature. Next, we analysed the available signals and modeled perceived slant using estimator reliabilities. The model explains the apparent contradiction in the literature. Moreover, if eye position is manipulated appropriately, the model predicts that apparent slant will increase with distance for vertical, but not horizontal, magnification. This remarkable prediction was confirmed experimentally.

◆ **Depth perception induced by three types of vertical disparity**

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Recently, Erkelens and van Ee (1998 *Vision Research* in press) proposed a model of depth perception based on head-centric disparities. The model uses local horizontal disparity together with a measure of the global vertical-disparity field to accurately derive head-centric distance throughout the visual field. Three types of vertical-disparity fields influence depth perception. Two of these fields are induced by vertical scale and shear transformations between the half-images. The third field is a product of multiplication of the other two fields.

The effects of the three types of vertical-disparity fields on depth perception were measured on four subjects. A multiplied vertical shear-scale field is perceived as a convex or a concave cylinder with a vertical axis. A similar percept can be induced by applying only a horizontal-disparity field, namely by an affine horizontal scale transformation. Vertical scale and shear induce the same types of depth percept as horizontal scale and shear, respectively. Different amounts of horizontal and vertical disparity which give the same type of percept were combined in one stimulus. We measured the amount of horizontal disparity necessary to cancel a certain amount of vertical disparity. The ratios between horizontal and vertical disparities differed from those predicted by the model. The differences between the predicted and the measured ratios depended on the subject and the type of vertical disparity. The different ratios suggest that the three vertical-disparity fields are processed separately by the visual system.

◆ **Characterising the 'Venetian blind' effect**

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In the 'Venetian blind' effect, an illusory rotation resembling that of a partially opened Venetian blind is perceived when a vertically oriented rectangular-wave grating is binocularly viewed with a neutral density filter, artificial pupil, cylindrical lens, or spherical lens over one eye (Cibis and Haber, 1951 *Journal of the Optical Society of America* 41 676-683).

Eight hundred vertically oriented rectangular-wave grating stereograms, each consisting of a standard image presented to one eye and a geometrically identical variable image presented to the other eye, were presented to each of four subjects. On each trial, the side on which the variable image appeared was randomly selected, along with its average luminance level and Michelson contrast level. A map was produced of the probability of seeing a multi-axis rotation such that, for any light vertical bar, the side of the bar which appeared to be closer to the subject was on the same side as the variable image (ie light bar rotation was 'changewise').

Significant main effects and an interaction effect were found for Michelson contrast and average luminance. For variable images whose contrast was greater than or equal to that of the standard image, light bar rotation was changewise for low luminances and counter-changewise for high luminances. For variable images whose contrast was less than that of the standard image, light bar rotation was changewise at all luminances ( $p < 0.0001$ ).

The model proposed by Cibis and Haber fails to predict these results, since that model requires that the luminance level of dark bars be subthreshold.

◆ **Surface constraint: a new approach for modelling stereopsis**

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A global computational model of stereopsis and computer simulations are presented. A new constraint has been developed to avoid false targets and to indicate half-occluded regions. The conventional approach starts with the matching of a stereo image pair and employs some constraints (ordering, smoothness, uniqueness, primitive similarity, etc) to avoid false targets. But all of these constraints do not create a computational solution that can indicate whether the correct 3-D surface has been found. Furthermore, a really effective criterion identifying the half-occluded regions is not known.

My goal is a direct search for the 3-D object that is in the best correspondence with the left and right images. This correspondence is tested and measured by the surface constraint: with a given stereo image pair and known camera parameters, if the left and right images are projected on the surface of the original 3-D object in its original position, the projected images will perfectly overlap with the regions of the surface that are visible from the positions of both cameras. The computational goal is to find the 3-D surface that provides the best fit to the surface constraint. The surface constraint gives exact criteria for testing the solution in stereopsis: if, and only if, the true 3-D surface is found, then the correlation between the two images projected on the surface is 100%. For avoiding false targets and indicating half-occluded regions, a surface constraint is sufficient: conventional constraints are unnecessary.

◆ **Combining retinal images to form a spatial reference frame II: practice**

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Glennerster and Hansard (1998 *Perception* 27 Supplement, this issue) propose a representation of the location of objects which avoids the use of 3-D coordinates and instead stores only information about the relative position (relative visual direction) of points in the scene.

We describe an implementation of the model applied to natural images. Using a calibrated camera, we recover the spherical angles between pairs and triples of image features. These angles define relative positions which are mapped onto a representation of the viewing sphere (or optic array) as the camera rotates and translates. This is accomplished without any knowledge of the location or orientation of the camera itself.

In order to organise the information without computing the relative position of every possible feature-pair, image primitives are grouped in a scale-based hierarchy (Watt, 1987 *Journal of the Optical Society of America A* 4 2006–2021). We show how images taken from one location can be related to each other by describing the relative positions of image features (or the eye movements that would be required to foveate them). Once relative orientation has been established in this way, the direction of camera translation is defined by the objects that are approached. We illustrate how navigation within a room can be decomposed into a number of such 'orient' and 'approach' sequences. For smaller camera translations, parallax is measured in relation to a framework of distant points.

Our goal in working with natural images is to determine just how useful a representation based only on relative position could be in controlling a variety of visually guided behaviours.

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◆ **Temporal integration in the processing of binocular disparity**

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Although a disparity can be detected within 50 ms (Uttal et al, 1975 *Vision Research* 15 705–712) detection thresholds decrease with longer presentations up to 180 ms [Tyler, 1991, in *Binocular Vision* vol. 9 of *Vision and Visual Dysfunction* Ed. J R Cronly-Dillon (London: Macmillan) pp 38–74]. We investigated the nature of this integration process. For both detection and discrimination tasks we determined (i) the minimum number of signal frames necessary to perceive depth presented within a sequence of noise frames, and (ii) the degree to which the presentation of these signal frames can be separated in time.

Sequences of binocularly uncorrelated dynamic random dots were presented at 67 Hz in a Wheatstone stereoscope. A 2AFC procedure with two 67-frame sequences was used to determine thresholds. In the first experiment, signal frames (binocularly correlated) depicting a horizontal sine wave were inserted within one of the sequences. The minimum number of consecutive frames

and the maximum interval between successive frames for which the signal could be detected were determined. Observers were unable to detect sequences of signal frames with a duration of less than 50 ms. Moreover, sequences could only be detected if the interval between successive signal frames was less than 50 ms. In the second experiment, observers judged the magnitude of depth perceived in sequences for which the interval between successive signal frames differed. As this interval decreased, the amount of depth perceived increased. These results demonstrate that disparity information is integrated over time, and that this integration occurs only for inter-stimulus intervals of less than 50 ms.

◆ **Disparity interpolation in the blind spot**

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A monocular 2-D figural filling-in in the blind spot was demonstrated by Ramachandran (1992 *Scientific American* 266 86–91). We tried a 3-D extension to examine if disparity interpolation can be induced into the blind spots by the spreading of surrounding stimuli. An anaglyph was presented to five experienced subjects wearing red–green glasses. Four planes were created on the anaglyph. A fixation plane was assigned with zero disparity ( $d = 0$ ). A 1-deg patch, which is small relative to the real size of the blind spot, was designed to be at  $d = 0$ ,  $d = -2$ , or  $d = +2$  for the viewing with both eyes. It was now seen by one eye only since the corresponding patch falls into the blind spot of the opposite eye. A binocular rivalry pattern with ambiguous disparity was arranged 5 deg above the whole blind-spot region. The fourth plane was a background plane which comprised a whole frame minus the above three arrangements. The disparity of the background plane was set at  $d = -2$  or  $d = +2$ . We found that depth identification of the patch involving the blind-spot region coincided with the depth level of the background plane, no matter whether the original disparity of the patch was same as or different from that of the background plane. A similar result was also observed for the binocular rivalry patterns. These 3-D findings are compatible with the 2-D demonstration of Ramachandran. The depth representation in blind spots as well as in binocular rivalry seems to be strongly regulated and filled-in by the surroundings.

◆ **Ghost on random-dot stereogram?**

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It is believed that a binocularly-unpaired region of a stereogram should be perceived at the same depth as the background or at a farther depth than a paired region [Julesz, 1971 *Foundation of Cyclopean Perception* (Chicago: University of Chicago Press); Nakayama, Shimijo, and Silverman 1989 *Perception* 18 55–68]. We reported earlier that binocularly unpaired regions on an object with a curved surface play an essential role in the volume perception (Idesawa, 1991 *Japanese Journal of Applied Physics* 30-4B L751–754).

We investigated a partially unpaired region in a random-dot stereogram (RDS). There was no depth difference between the paired areas. Two disks with the same radius overlapped slightly eccentric to the horizontal direction; two crescent regions were formed by an 'Exclusive OR' operation. These crescent regions were filled with independently generated random dots, so that binocularly unpaired regions were in the opposite crescents. According to conventional thinking, this RDS should be perceived as concave valleys with the crescents lying inside of them. However, we observed entirely different stable percepts: two convex ridges or a transparent cylindrical object. In addition, the percept was the same when the half-images were reversed.

Surprisingly, the binocularly unpaired regions could be perceived at a nearer depth than the paired regions. In further work, we showed that this percept corresponds to a physically valid object.

◆ **Influence of the frame in stereoscopic images on vergence eye movement**

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When a scene is represented in a stereoscopic display, depth distortions are perceived at the edge of the image. From our previous research (Ohtsuka et al, 1996 *SID '96 Digest* pp 893–896),

we concluded that the depth distortions are due to the interocularly unpaired region produced by a frame having zero disparity. We proposed that adding a virtual frame with a crossed disparity relative to the objects in stereoscopic images would get rid of this distortion.

In the present study, we tested this hypothesis. Specifically, we investigated how the binocular disparity of a frame affects vergence eye movements. Observers were required to fixate an object having a crossed disparity. The vergence eye movements were measured. The results show that when the virtual frame has zero disparity, the eyes converge at a point between the disparity of the screen and that of the object. When the virtual frame has a crossed disparity, convergence is located at the position indicated by the object. These results are consistent with the perceived depth. They show that presenting a stereoscopic image accompanied by a virtual frame with a crossed disparity protects against an undesired shift in convergence, as well as against depth distortion.

◆ **Fixation disparity and nonius bias**

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Fixation disparity, ie the vergence error of a few minutes of arc within Panum's area, can be measured psychophysically with two nonius (Vernier) lines that are presented dichoptically, ie one to each eye. The observer adjusts these nonius lines to subjective alignment; the resulting physical nonius offset indicates the amount of fixation disparity.

We investigated the relation between fixation disparity and the nonius bias, which is the physical offset of the nonius lines (up to 2 min of arc in the present conditions) that is adjusted by the observer in order to perceive them as aligned when both nonius lines are presented to both eyes (binocular nonius bias) or both to the left or both to the right eye (monocular nonius bias). It was found (i) that the fixation disparity is correlated with the binocular nonius bias in the horizontal ( $r = 0.49$ ,  $p = 0.036$ ) and the vertical ( $r = 0.83$ ,  $p < 0.001$ ) meridian; and (ii) that the binocular nonius bias can be predicted from the average of the right-eye and left-eye monocular nonius biases ( $r = 0.90$ ,  $p < 0.001$ ). To remove the influence of the nonius bias on measured fixation disparity it is possible to calculate the fixation disparity relative to the individual binocular nonius bias, rather than to the physical coincidence of the nonius lines. This procedure tends to increase the correlation between fixation disparity and the tonic resting position of vergence. We discuss the clinical relevance of the dichoptic nonius method for measuring fixation disparity and its limitations as compared to physical recordings of eye position.

◆ **A comparison of first-order and second-order transparency thresholds in stereopsis**

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When presented with a product of a vertical square-wave grating (the contrast envelope) and a horizontal sinusoidal grating (the carrier), the envelope and carrier may be perceived transparently at different depths. The percept of transparency is, however, asymmetric. We find that it only occurs when the envelope disparities are crossed. When the same two signals were added rather than multiplied, the percept of transparency was symmetrical: either signal could be seen in front of or behind the other. It is explained how the depth asymmetry found for contrast envelopes may be explained by two constraints placed on monocular transparency as proposed by Metelli [1974 *Scientific American* 230(4) 91–98].

Differences between additive/multiplicative signal combinations are examined in two experiments. In one, disparity thresholds for transparency as a function of the frequency of the vertical square-wave grating were measured. In the other, disparity discrimination thresholds were measured for vertical square-wave gratings combined with sinusoidal gratings that differed in their interocular spatial frequencies and appeared in binocular rivalry. In both experiments, thresholds for the multiplicative condition were minimum when the spatial frequency of the contrast envelope was close to  $0.4 \text{ cycle deg}^{-1}$ : at about two octaves lower than the frequency of the carrier grating. For additive signal combinations no peak sensitivities were found at these spatial frequencies. Instead, thresholds declined as a function of increasing spatial frequency. The different sensitivity curves found for multiplicative and additive combinations of a common pair of signals suggest that different processes mediated the disparity signal. The data are consistent with a two-channel model of binocular matching and idea that the visual system may represent multiple depth cues at common retinal locations.

◆ **A Gestalt bubble model reconstructs a 3-D percept from a 2-D image in an isomorphic volumetric representation by emergence from local field forces**

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Gestalt theory observes that the subjective experience of a 2-D line drawing of a cube is of a solid 3-D percept complete with filled-in white surfaces mapped continuously in depth, as well as amodally perceived hidden rear surfaces. The Gestalt principle of isomorphism suggests that the information apparent in this solid spatial percept must be explicitly encoded in the corresponding neural representation. In reversible figures this kind of solid percept is observed to invert spontaneously, changing the perceived location in depth of every point on every surface.

A perceptual modeling approach is proposed to capture the dynamics of perceptual organisation seen in such spatial percepts in a fully isomorphic volumetric representation, ie where the depth information of every surface is explicitly encoded in the perceptual model exactly as it is experienced. The 2-D input is inverse-projected into this volumetric matrix where dynamic local field-like interactions lead to the formation of the final perceptual state by emergence, ie the parallel action of a multitude of local forces in 3-D, stimulated by the individual edges in the 2-D input. This general approach to modeling perception accounts for many of the most troublesome aspects of perception, such as perspective cues, the Müller-Lyer illusion, the interaction between perceived illumination and 3-D form, attached shadows, cast shadows, specular reflection, transparency, multiple depth planes, complex and fragmented surfaces, etc in a manner consistent with Gestalt theory.

◆ **Does the computation of lightness precede stereopsis?**

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Based on his original ingenious experiment, Gilchrist [1979 *Scientific American* 240(3) 88-97] proposed a hypothesis on lightness constancy termed the coplanar ratio principle. Frisby [1979 *Seeing* (Oxford: Oxford University Press) p.154, also figures 216 and 217 on p.88] designed a stereogram that simulated Gilchrist's original situation. Since binocular observation of that stereogram elicited the same perceived contrast as in the monocular test, Frisby questioned Gilchrist's hypothesis. For this report, five experimental conditions have been prepared to investigate this issue: (1) Gilchrist's original real 3-D stimulus pattern; (2) a simple 2-D plan of the pattern; (3) a stereogram of the pattern; (3') monocular observation of the stereogram; (4) observation of the pattern with motion parallax, with the use of a stroboscopic presentation of two patterns. Under these five conditions, the task of an observer was to compare the perceived lightness of two small grey insert flaps (left, L, and right, R) in the pattern. The results of these five conditions are summarised as follows. In condition (1) and (4) L seems darker than R, and therefore the constancy effect is affirmed. But in (2), (3), and (3') L seems lighter than R, in which case the contrast effect is recognised. First, the results of (1) confirm the findings of Gilchrist. Second, the results of (4) support Gilchrist's hypothesis. Third, it seems that the results of (3) support Frisby's findings, although the fact that the contrast effect in (3) is smaller than that of (3'), provides further support for Gilchrist's hypothesis.

◆ **A two-stage model for binocular summation**

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In our recent studies on binocular summation (1997 *Perception* 26 1334; 1998, ARVO) we demonstrated that binocular contrast summation at threshold reflects both a higher sampling efficiency and a lower equivalent internal noise for binocular targets. In those studies we presented target Gabor patches to one or both eyes in the presence of various levels of binocular two-dimensional static random noise that was visible only during the 200 ms 2AFC intervals. The pattern of changes in equivalent internal noise and sampling efficiency was found to differ, depending on whether the masking noise was correlated or uncorrelated between the eyes during each block of trials.

Our results, and others in the literature, can be explained by a new, two-stage model. The first stage consists of a matrix of channels that are selective for all possible pairings of ocular dominance and stereoscopic depth preferences. The second stage is one of selective readout from the matrix. By analogy with a mechanism of selective attention, the 'ideal observer' should monitor only the channels where the target will occur. In our experiments, all targets were presented on the horopter but binocular and monocular (left or right eye) targets were randomly intermixed. Correlated binocular noise thus impaired detection by injecting noise into the attended channels (zero disparity and all ocular dominances). However, uncorrelated noise onset

acted mainly by broadening attention: because the noise energy was distributed across all depth and ocular dominance channels, its onset automatically drew attention away from the horopter to monitor all channels.

◆ **Monocular stimulation conditions and stereoacuity**

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Earlier experiments have shown that a global figure in a random-dot stereogram is recognised when the anaglyphs are monocularly presented with a frequency down to 2.5 Hz alternately to the right and the left eye (Pieper, 1997 *Perception* 26 Supplement, 46).

In the present experiments we examined (i) the influence of the alternating frequency, and (ii) the influence of interocular delay on stereoacuity. LCD shutter glasses were used to control the viewing conditions. Measurement of minimal disparity (stereoacuity) was performed psychophysically with the three-rod method (according to Helmholtz). The distance of the rods was 1.4 deg. The background luminance was 100 cd m<sup>-2</sup>. Transmittance of the open LCD shutter was 30%. Subjects were eight male and seven female students with normal binocular depth vision.

In experiment 1 we measured the stereoacuity with six alternating frequencies (1, 2, 4, 8, 16, and 32 Hz). The minimal disparity at 1 Hz alternating frequency was 120 s of arc. Stereoacuity increased linearly (against log frequency) up to 40 s of arc at 16 Hz and kept this value at 32 Hz. In experiment 2 monocular exposure time was 25 ms separated by interocular delays of 0 ms, 25 ms, and 50 ms. Stereoacuity decreased from 60 s of arc (0 ms delay) to 70 s of arc (25 ms delay) and to 80 s of arc at 50 ms delay. Under optimal binocular visual conditions minimal disparities of 6 s of arc were found. The monocular conditions reduced the spatial acuity to 40 s of arc minimal disparity at alternating frequencies of 16 Hz or more. Some rivalry was apparent in stimuli alternating at 4 Hz. Below this frequency (at 2 Hz and at 1 Hz) both stimuli were seen in alternation, often with apparent motion from one to the other. Part of the stereoacuity loss at low frequencies of monocular stimulation may therefore be due to diplopia and asymmetries in vergence eye movements.

◆ **Modelling vertical-disparity pooling by the human visual system by an ideal-observer analysis**

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A frontoparallel plane appears slanted around a vertical axis if one eye's image is magnified in the vertical dimension. This induced effect can be explained in terms of the visual system using vertical disparities to recover viewing geometry parameters. We have exploited this effect to study pooling of vertical-disparity information. Observers saw a plane made of many dots, half of which had one magnification applied to their vertical image coordinates, the remaining half another. When the difference between the two intermingled magnifications was below a critical value, the mixture generated an induced effect whose size was determined by the mean magnification. When this value was exceeded, a bifurcation appeared in which the size of the effect was captured by one or other magnification value. We demonstrate that an ideal observer for this task, which is robust given the presence of incorrect stereo matches, shows a similar bifurcation at a critical value determined by the acuity limit for vertical disparity. In fact the human observer performs close to the ideal-observer limit given a reasonable estimate of vertical acuity. As far as we are aware ideal-observer analysis of human performance has not previously been based on a critical phenomenon (in this case a bifurcation onset) rather than a performance threshold. The implementation of the ideal observer suggests a biologically plausible pooling algorithm which generates optimal estimates of viewing parameters even when the stereo correspondence problem is not solved.

◆ **Broad-band disparity masking in stereopsis with Gabor stimuli**

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The disparity range for depth discrimination in localised bandpass patches at contrast threshold extends to phase disparities of much greater than half a cycle (Prince and Eagle, 1998, ARVO). However, large disparities cannot be perceived in bandpass noise stimuli. In order to examine this discrepancy the effect of disparity noise on depth discrimination in Gabor patches was measured as a function of signal disparity.

On each trial a signal Gabor patch was presented on every other frame. Subjects fixated a cross and judged whether the patch had a crossed or uncrossed disparity. In the baseline condition, the

intervening frames were set to mid-grey. In the masking condition, the intervening frames consisted of Gabors in the same location as the signal. The disparity of each of these masking Gabors was randomly selected from the measured working range for this task. Threshold contrast for disparity discrimination was measured as a function of signal disparity. Mask and signal frequency were varied together over 3 octaves.

In the absence of the mask, the contrast threshold for depth discrimination was constant over a large range of disparities (to 1000° phase or more). In the presence of disparity, noise thresholds were relatively unaffected at disparities of 180° phase or less, rose markedly at 270°, and fell again at 360°. At disparities greater than 360°, performance became gradually more impaired until it reached chance levels. Results were qualitatively similar at all frequencies. We conclude that below 360° phase, masking results can be predicted from the cross-correlation function. However, the decline in performance at phase disparities greater than 360° suggests the involvement of a different mechanism at large disparities which is more sensitive to this noise.

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◆ **Binocular integration: combining unpaired fragments of left and right visual images**

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In natural viewing conditions, left and right images of visual scenes usually differ significantly not only because of somewhat different points of observation but also for some anatomical and physiological reasons (blind spots, angioscotomas, afterimages, etc). Since most of these 'defective' zones of the two retinas correspond to different areas in the visual field, left and right images usually contain a number of unpaired fragments whose 'partners' have fallen on blind zones in the other eye. Our aim was to develop an experimental paradigm for studying characteristics of the integrative processes underlying combination of unpaired fragments into a single percept. For this purpose we created test software which allowed us to generate independent left and right stimuli (containing main and masking parts) and to vary their duration as well as stimulus onset asynchrony (SOA) in steps of 50 ms. Preliminary experiments with this software were performed on five subjects with fragments of letters used as stimuli. Initial results are as follows: (i) in the case of synchronous presentation of left and right stimuli (SOA = 0), different subjects needed substantially different exposure intervals ranging from 50 to 200 ms; (ii) control presentation of both fragments to one and the same eye could be more effective than synchronous dichoptic presentation but only stimulus durations up to 50–100 ms; (iii) sequential presentation of left and right stimuli without overlap did not ensure reliable letter recognition even in the absence of masking; (iv) monocular front part of stimulus sequence could exert both positive and negative effects on letter recognition, depending on the time parameters of stimulation.

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◆ **Disparity detection in reversed-contrast stereograms**

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Stereograms with opposite contrast signs in the two eyes elicit disparity-selective responses from neurons in V1 which are the reverse of responses to correlated stimuli [Cumming and Parker, 1997 *Nature (London)* 389 280–283]. Previous psychophysical investigations revealed no corresponding reversals of depth sensation. However, the stimuli used in psychophysical studies differed from those used physiologically. We therefore re-examined the psychophysical effects of reversed-contrast stereograms.

With reversed-contrast bar stimuli, subjects were able to detect depth, but with poor stereoacuity. There was no tendency to report depth in the direction opposite to that specified geometrically by the disparity, contrary to explanations based on local contour matching and existing data from cat V1 cortical neurons measured with reversed-contrast bars (Ohzawa et al, 1990 *Science* 249 1037–1041).

When subjects were presented with anticorrelated random-dot stereograms, psychophysical performance depended on dot size and density. At low dot densities, subjects were able to perform a forced-choice depth-detection task, but only after extensive training with feedback. Again there was no tendency to report reversed depth. At higher dot densities subjects were unable to perform better than chance, even though such stimuli support robust disparity-selectivity in V1 neurons. This was despite extensive training and continual feedback, in human observers and two monkeys (from whom the V1 neurons were recorded). Variations in the disparity of anticorrelated random-dot stereograms produce substantial changes in the pattern of neural activation in V1, yet these changes are psychophysically undetectable.

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◆ **Modeling the 'Venetian blind' effect**

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Cibis and Haber (1951 *Journal of the Optical Society of America* **41** 676–683) discovered that a pair of dichoptically presented square-wave spatial gratings that are geometrically identical but have differing average luminances may appear (once fused) to have bars that are individually oriented out of the frontoparallel plane about their vertical axes, much like a set of vertically oriented, partially-open Venetian blinds. They proposed that the optics of the eyes smear the two images thereby creating a geometric disparity at the points where the intensity of each image rises above threshold.

Using a model for the modulation transfer function of the human eye, we show that the Cibis–Haber model cannot work. The function defining the difference of intensity between the two eyes at each corresponding retinal location is developed for the Venetian-blind stimulus and a stimulus that has a physical geometry matching the geometry perceived for the Venetian blind stimulus. The Venetian-blind function is monotonic at a stimulus edge while the function for the matching stimulus is roughly symmetric. Further, the point of maximum slope for the Venetian-blind function is roughly the same as one of the two maximum-slope points for the matching function, though the slopes themselves differ markedly, with the matching function slope being considerably greater than the Venetian-blind function slope. Any computational model of stereo must not be able to discriminate these two cases. We consider several classes of models in an attempt to characterise what qualities of the Venetian-blind stimulus and the matching stimulus are equivalent.

◆ **Fusional area in Panum's limiting case**

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The fusion in Panum's limiting case is not completely clear. In this case one eye sees two stimuli, but the other sees only one, ie one of the stimuli is hidden by another. Investigating fusion for Panum's limiting case we used Polaroids for dichoptic presentation of stimuli. Two bars B1l and B2l (30 min × 3 min) horizontally shifted by 30 min and an X-shaped stimulus Xl (10 min × 10 min) 20 min above bars were shown to the left eye. A bar Br (30 min × 3 min) flickering at the rate of 4 Hz and an X-shaped stimulus Xr were presented to the right eye. After fusion the subject sees the X fixation cross, and two bars below it, one of which was perceived as flickering. We think that flickering could show which monocularly seen bar, right or left, was fused. When the Xl stimulus is slowly shifted from left to right, the subject first sees the left bar as flickering. On shifting Xl further he/she perceives three bars—two stable bars and a flickering one somewhere between them. Next, he/she sees two bars again but now the right bar is flickering. Finally, the subject perceives three stimuli again—the flickering bar is now at the extreme right. We determined the region within which the stable left bars are fused with the right flickering one. This region coincides with Panum's regions determined for our subjects, which range from 4 to 8 min.

◆ **Cyclopean and frontoparallel plane equidistance horopters measured with the sequential stereopsis paradigm**

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Participants set the positions of two laterally displayed targets so that they appeared at the same distance from the cyclopean eye as a central target fixed in position in the median plane. The lateral targets were arranged on each trial to be either 20° or 30° either side of the fixed target. In other conditions participants set the targets to be in the frontoparallel plane. In each case, required settings for the most peripheral targets were far from the isovergence circle. Each target was a high-spatial-frequency-filtered random texture mounted on a carriage whose position in depth was adjustable. Each was seen behind its own small viewing port in an apparatus based on that of Enright (1996 *Vision Research* **36** 307–312). The apertures were set in black curtains that obscured all parts of the apparatus other than the visible regions of the targets. The high spatial-frequency textures ensured that when one target was fixated, the textures of the other two could not be resolved. Thus the task cannot be performed on the basis of simultaneously available disparities, but has to be done with gaze shifts (head position fixed by a bite bar), hence Enright's term sequential stereopsis. Several experiments were run under a range of conditions, including three different distances of the central fixed target (715, 905, and 1120 mm). The main

result was that sequential stereopsis yielded deviations in settings from frontoparallel qualitatively similar to the HeringHillebrand deviation, whereas cyclopean equidistance settings showed errors in the opposite direction.

◆ **Neural and psychophysical responses to binocular compound gratings**

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The stereo disparity of a binocularly viewed sinusoidal grating is inherently ambiguous owing to its periodic nature. Combining information across different spatial frequencies in more complex stimuli can resolve this ambiguity. We used compound gratings composed of two spatial frequencies to investigate this process, both psychophysically and in single V1 neurons recorded from two alert monkeys.

Human and monkey observers were presented with sinusoidal gratings whose contrast was modulated with a broad Gaussian envelope. The gratings consisted either of a single sinusoid or the sum of two sinusoids with spatial frequencies in the ratio 3 : 4. Subjects indicated in a forced-choice task whether the stimulus was behind or in front of the fixation marker. With single sinusoids at disparities corresponding to phase angles greater than  $\pi/2$ , front/back judgments were inconsistent from trial to trial. The same subjects at the same angular disparities consistently judged depth correctly with compound gratings.

We examined the responses of V1 neurons to the disparity of compound gratings like those used for psychophysics. The spatial frequencies were chosen to ensure that each component alone produced strong responses. The disparity tuning functions for compound gratings showed multiple peaks. The location and magnitude of these peaks were well described by the linear combination of responses to each component alone. The responses of V1 neurons differ from psychophysical judgments in that they appear not to exploit the phase relationships between the two grating components to disambiguate stereo matches. Subsequent combination of V1 outputs could produce neuronal signals consistent with the psychophysics.

◆ **Optimal slant estimation and binocular depth contrast**

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Werner described binocular depth contrast. A horizontal test pattern with no disparity is presented with a large inducing pattern that contains disparities specifying slant about a vertical axis. The inducer's perceived slant is less than specified and that of the test is opposite to the inducer. Current theory states that depth contrast is caused by 'normalisation' toward frontoparallelism of slants specified by first-order disparities and by preservation of second-order disparities like those between the inducer and test. This theory does not explain why normalisation occurs, nor why first-order disparities are not preserved. Depth contrast can be understood by analysing the available signals and their noises. A stereoscopic estimator uses disparities and a perspective estimator uses monocular cues like texture gradients. Depth contrast is predicted when the stereoscopic and perspective estimators specify different inducer slants. Therefore, we measured depth contrast when the correlation between stereoscopic and perspective information in the inducer was varied.

We presented a large inducing pattern above and below a test pattern. The inducer's regular texture provided strong perspective, and the test provided weak perspective. The inducer had disparities specifying vertical-axis slant. The inducer's texture specified either frontoparallelism or the same slant as the disparities. The test's perceived slant was measured by slant-nulling and slant-estimation procedures. We also presented these conditions to an optimal slant estimator.

Depth contrast was consistently smaller when perspective-based slant was consistent with stereoscopically specified slant. The optimal estimator behaved similarly. Thus, depth contrast is a byproduct of conflicts between stereoscopic and perspective slant cues.

◆ **Distance perception from stereoscopic information**

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We are studying the development of absolute distance perception in real and virtual environments when the amount of stereoscopic information is changed.

Twelve children and the same number of adults participated in the experiment. Subjects had two mobile objects, B and C, in front of them, progressing approximatively along the line of sight.

They had to assume that their own position, **A**, corresponded to the observation point of a virtual camera. Stereoscopic glasses were available in some predetermined conditions. As the distance between **B** and **C** varied in time, the task was to push a button every time the distance **AB** was perceived to be equivalent to **BC** (absolute bisection).

Results confirm that distance judgments are generally more precise with stereoscopic glasses than without them and that children underestimate distance **AB**, which is the opposite of what the adults do. However, the performance of the adults in the real conditions was poorly correlated with the bisections produced in virtual conditions, whereas the judgments of children wearing stereoscopic glasses were highly correlated with their performance in real space.

In conclusion, these data demonstrate experimentally the tendency known otherwise that children consider themselves as perceptually deeply immersed in simulated environments.

◆ **The effects of local depth context on stereo thresholds**

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To assess the role of **VI** in contour integration Kapadia et al (1995 *Neuron* **15** 843–856) examined contrast thresholds for detection of simple bar targets in different local contexts. By varying the position of a flanking bar they observed up to a 40% improvement in sensitivity for a target bar. Here we examine the effects of flanking bars in the cyclopean domain through the use of 50% random-dot stereograms.

We measured subjects' disparity detection thresholds for target cyclopean bars (7 min × 28 min in size) when flanking bars were presented at varying distances from them. Target bars were centred 54 min away from a fixation cross. Flanking bars were located below the targets and had a depth which ensured that they were clearly visible (disparity = 6 min). The target to flank separation was varied between 0 and 60 min. For these conditions, enhancement effects were not observed. However, a slight inhibitory effect of the flanking bar was observed; this was greatest when the flank and target were abutting.

Since the conditions approximate those used in the Kapadia et al luminance study, the results suggest that the effects of local context (as determined by flanking bar stimuli) in the cyclopean domain differ from those for simple luminance targets. This is consistent with other work on the cyclopean domain which indicates that the coding of depth information does not necessarily mirror the coding of luminance. Long-range interactions may be organised differently in the two domains.

◆ **Vergence eye movements and stereopsis with brief-duration stimuli**

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Are reports of stereoscopic depth perception with large-disparity stimuli due to subjects monitoring vergence direction rather than responding to depth per se? Whilst sub-160-ms presentations preclude the initiation of a vergence eye movement before stimulus offset, there is ample evidence that post-presentation eye movements are evoked (eg Mitchell, 1970 *Vision Research* **10** 145–162). In this study the direction (convergent/divergent) of vergence response was measured by infrared oculography during a depth identification task. The stimulus was a 0.5 cycle deg<sup>-1</sup> Gabor patch presented for 150 or 200 ms. Stimulus contrast was 25% and the disparity was 150 min of arc (crossed or uncrossed) relative to fixation. Nonius lines were presented before and after stimulus presentation; a fixation circle was present throughout. Subjects were instructed to maintain fixation, but respond to the perceived depth (front/back). This manual response was correlated with any movements of the eyes during and immediately after stimulus presentation. Manual responses were 90% correct, and vergence eye movements were appropriate 78% of the time. There was also a 78% correlation between the direction of the manual responses and the vergence eye movement. The average peak magnitude of the vergence eye-movement response was 0.4 deg. The relatively high correlation between vergence direction and subjective report suggests some sort of shared pathway for disparity vergence and stereopsis. The less than 100% correlation suggests that a vergence eye movement in the correct direction is not a necessary condition for a particular subjective depth report. These results suggest that reports of subjective depth with these large-disparity brief-duration stimuli are genuine and not artifactual.

◆ **Can the stereoscopic anisotropy be predicted by monocular sensitivity to orientation and spatial-frequency differences?**

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For most observers there is a pronounced orientational anisotropy in the perception of 3-D surfaces (Rogers and Graham, 1983 *Science* 221 1409–1411). Inclined surfaces (rotated about the  $x$  axis) are typically seen faster and with more depth than their slanted counterparts (rotated about the  $y$  axis) although there are significant individual differences in the magnitude of this effect. The pattern of disparities created by inclination and slant differs: the former creates larger differences in orientation, whereas the latter creates larger differences in spatial frequency. Therefore we investigated whether the magnitude of the stereoscopic anisotropy was associated with differences in monocular sensitivity to orientation and/or spatial-frequency changes. We tested this possibility by determining relative 2-D (orientation and spatial frequency) and 3-D (inclination and slant) thresholds in a large group of subjects ( $N = 20$ ). The stimuli comprised a luminance sine wave (2 cycles  $\text{deg}^{-1}$ ) oriented vertically and presented within a 3 deg circular window. In each condition a reference surface was displayed for 2 s followed by a surface which differed in orientation, spatial frequency, inclination, or slant. The method of constant stimuli was used to determine thresholds. There were large individual differences in the magnitude of the stereoscopic anisotropy, the ratio of inclination to slant sensitivity varied from 0.8 to 2.1. However, this was not related systematically to orientation or spatial-frequency sensitivity. We conclude, therefore, that the stereoscopic anisotropy cannot be predicted by monocular sensitivity to orientation and spatial-frequency differences.

◆ **Factors that determine the maximum disparity for stereoscopic shape perception**

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The maximum disparity supporting stereopsis for single-element or double-element stimuli has been shown to depend on several factors, including luminance spatial frequency, element size, and disparity gradient. Do these findings apply to shape perception from multi-element stimuli? Our task required observers to discriminate two oblique orientations of a 3-D corrugation defined by disparity modulation of 1200 micropatterns.

We measured  $D_{\max}$  for combinations of carrier luminance spatial frequency (0.42 to 3.36 cycles  $\text{deg}^{-1}$ ) and Gabor size ( $\sigma = 0.18$  to 0.72 deg). The value of neither parameter alone was found to predict shape  $D_{\max}$ . Instead,  $D_{\max}$  consistently rose as their product decreased (a pattern of results distinct from that reported for single-element stimuli). Was this because a smaller number of features (bars, edges) appeared in each Gabor micropattern, or was it due to a larger luminance-spatial-frequency bandwidth? We addressed this directly with 'edgels'—micropatterns with a single luminance edge but having very different Fourier components. One type of edgel was a Gaussian-windowed step-edge. Another was identical except its fundamental was subtracted. Both edgel types, however, provided the same  $D_{\max}$ .

Furthermore,  $D_{\max}$  decreased with the frequency of the sinusoidal disparity-modulation. Was this due to a disparity-gradient limit (one  $G_{\max}$ )? With triangular and trapezoidal modulations,  $G_{\max}$  was found to be relatively constant (1.1–1.7). It increased sharply, however, as the shape approached a square wave (1.7–4.4). For a square wave,  $D_{\max}$  was constant over a range of modulation periods. The implications of these findings are discussed regarding possible models for stereo shape perception.

**SURFACE AND DEPTH PERCEPTION**

◆ **Dynamic distortions in rotating radial figures**

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A white sector on a rotating black disk appears narrower than its actual width for observers fixating the centre of the disk. Using a matching technique, we examined this compression for sectors ranging from 30° to 150°. For a rotation velocity of 1.25  $\text{rev s}^{-1}$  and a disk diameter of 8 deg, we found a mean shrinkage of the sector between 8° and 16°. However, a black sector on a rotating white disk always showed less compression than a white sector, especially for sectors wider than 100°. The amount of compression increased with increasing rotation velocity producing

values between  $7^\circ$  and  $30^\circ$  for velocities between  $0.8 \text{ rev s}^{-1}$  and  $2 \text{ rev s}^{-1}$ . To determine the location within the rotating sector where apparent compression occurs, we presented a black radial line at various positions within a  $90^\circ$  white sector. Observers matched the position of this line using a static hand-held disk. In this case both the leading and trailing portions of the rotating sector were equally compressed, whereas expansion occurred in the middle region. Consistent with these findings, we found that two black lines 20 mm apart extending from the centre to the edge of the rotating disk appeared to converge at the edge when they were actually parallel but were seen as parallel when they physically diverged by  $6^\circ$ . Our findings suggest a foreshortening process which ensures that the shapes of moving stimuli are perceived approximately correctly, irrespective of whether they are actually sharp or blurred.

◆ **Perceptual segmentation in structure-from-motion**

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In four experiments we investigated the ability to discriminate structure-from-motion displays depicting either two rigidly rotating objects or one rigidly rotating object embedded in visual noise (non-rigid rotation). The motivation of these experiments was to compare human performance with the outcomes of a model based on the deformation (def) component of the first-order optic flow. The def-based model predicts that observers should be able to segment two objects when two peaks can be identified in the frequency distribution of the def magnitudes computed for each triplet of points in the display, and that one object should be perceived when only one peak can be identified. Each simulated object was composed of a set of points randomly chosen from either a sinusoidally corrugated surface, a plane, or a perturbed plane. Detection decreased with the increase of the amount of random perturbation of the depicted planar surfaces (experiment 1). Detection decreased with the increase of the amplitude of the sinusoidally corrugated surfaces (experiment 2). Detection was not facilitated when the dots were placed on sinusoidally corrugated surfaces instead of on randomly perturbed planar surfaces equated for amount of perturbation magnitude. Detection increased with more points on each surface (experiment 3). Detection decreased as more noise points were added to the displays depicting either one or two planar surfaces (experiment 4). The results of experiments 1–3 are in agreement with the outcomes of the model. The results of experiment 4 reveal, however, that the model is more robust to noise than human performance.

◆ **Segmentation in structure-from-motion: a computational approach**

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Much work has been done on how the human visual system extracts three-dimensional (3-D) structure and motion from 2-D motion information. Most of it is concentrated on the case where the optic-flow field arose from a single object. Less work has been done on the case where multiple objects are present, where the problem is further aggravated by the need to solve the segmentation problem (which point belongs to which object).

We propose an approach that is perceptually plausible, because it relies on first-order temporal calculations and does not require arbitrary divisions of the motion signals into two groups. For each triplet of points, compute a quantity which is known to be shared by points that belong to the same object, and different for different objects. The number of segregated objects will then emerge as the number of clusters, or peaks in the distribution of the quantity used. At least two such quantities are available: (i) The affine families of motion and relative-depth solutions, under a rigidity assumption. There are two possible solutions for each triplet, but one of them will be spurious (ie, not belong to a cluster). (ii) The def component of the optic flow. The def of each triplet is constant only for planar surfaces, and therefore for curved surfaces the computation needs to be restricted to local neighbourhoods of points.

The def approach has the advantage that it is more plausible for the human visual system. In a series of experiments, reported in a related abstract, we show that this latter model gives accurate predictions about human performance in segmentation-from-motion tasks.

◆ **Investigation of visual space with an exocentric pointing task**

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Although the curvature of visual space has been an issue in the literature for a long time, it is still unclear whether visual space has a metric and, if so, if it is constantly curved. In daily life

people are capable of judging the direction of gaze of others. This competence was used in an exocentric pointing task where subjects were asked to direct a pointer at some location such that it pointed straight to a target at another location. Both target and pointer were situated in a horizontal plane at eye height. The pointer was operated by remote control from a prescribed vantage point. The subject was seated in a 6 m × 6 m room with normal room lighting and was allowed to turn both head and eyes freely. The floor, ceiling, and the edges and corners of the walls were hidden from view. The apparent separation between pointer and target with respect to the vantage point ranged from 15° to 210° whereas the distance ranged from 1.47 m to 4.31 m. The pointer and target sizes were scaled with distance such that they covered a constant visual angle. The measurements were conducted both monocularly and binocularly. Monocularly the subjects tend to point too much towards themselves; this effect disappears binocularly. Also the relative distance is distorted very differently for these conditions. Allowing subjects to turn their heads does not imply that visual space is isotropic. Currently an attempt is being made to describe the data in terms of a single distance function.

◆ **Mutual dependence of luminance, size, and disparity in depth, size, and luminance discrimination tasks**

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It is known that depth influences perceived size and vice versa. It is also known that luminance influences both perceived size and perceived depth. However, these relations have thus far been established in separate experiments. In the experiment reported here we measured the combined effects by threshold measurements in a 2AFC paradigm. Theoretically, the resulting thresholds of size difference, luminance difference, and binocular disparity difference form three planes in three-dimensional space. The orientations of these planes give us information about the interactions of two fixed parameters in the determination of the thresholds. Two disks were presented on a computer screen and relative thresholds for size, luminance, and binocular depth were measured for a range of luminance–disparity, size–disparity, and luminance–size pairs, respectively. Pilot experiments clearly show interdependences among the three variables. Changes in size or depth did not affect luminance. Greater luminance led to larger perceived size and the object perceived as being closer. The closer was the object the smaller was its perceived size, and the larger was the object the closer it appeared. Clearly, the interactions are not necessarily symmetric.

◆ **The combined influence of stereo and shading on shape perception**

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Depth and shape judgments are based on various cues, such as binocular disparities, texture gradients, shading, and perspective. In this project the combined influence of binocular disparity and shading was studied.

Measurements were performed on several pairs of stereo photographs of plastic human torsos. Between pairs of pictures the stereo baseline was varied over three distances (0, 7, and 14 cm), while the direction of the illumination source was varied over three positions (from the viewpoint, perpendicular to the line of sight, and a position in between these two), so in total nine different combinations were studied. Subjects had to perform local settings of the surface normal on about 300 positions on the torso. The gauge figure task as described by Koenderink et al (1992 *Perception & Psychophysics* 52 487–496) was used for this purpose. From the settings, depth maps were calculated on which a principal components analysis was performed. It was found that only three components were needed to account for up to 97.5 % of the variance in the data. The effects of the two cues could be isolated within these three components. Surprisingly, no interactions were found between the effects of the disparity and the shading cue variation.

◆ **Distance miscalibration under reduced-cue viewing conditions can explain metric errors in judging surface normals**

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Errors in judging metric properties of the world have been used as evidence that visually perceived space is represented in terms of non-Euclidean geometries. An alternative interpretation is that

visually perceived space has a Euclidean representational framework but that errors can arise owing to poor calibration, for example misestimating distance to fixation. We report two experiments in which observers made surface-normal judgments using a remotely operated stick probe positioned on a randomly textured and binocularly viewed real plane surface. The stimulus was presented over a range of viewing distances (65–165 cm) and angles of slant ( $\pm 50^\circ$  around the horizontal axis). In the first experiment, the plane was viewed through a reduction tunnel to occlude the edges of the surface and visibility of the experimental room. Systematic patterns of error were found which could be accurately modelled by means of an incorrect (too-close) registered viewing distance. This supports the interpretation that internal space is Euclidean with errors arising from poor calibration in reduced-cue conditions. The second experiment, with different participants, compared surface-normal judgments made with and without the viewing tunnel. It was predicted that performance should improve without the tunnel as then more cues were available for distance calibration. The prediction was confirmed, supporting the poorly-calibrated-Euclidean-space interpretation of metric errors in perceptual judgments. We also report that the fit of the model could be improved by supposing that some observers exhibit a constant offset error in perceived gravitational vertical.

◆ **Combining binocular and dynamic information to recover 3-D shape**

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The information provided by a single binocular view of an object, or two monocular views of an object undergoing 3-D rotation is compatible with a one-parameter family of 3-D shapes. Because these families are different, with both cues present there is an intersection of constraints from which 3-D metric shape can be recovered. Here, we determine the extent to which the visual system exploits these different sources of information.

Subjects were tested in four conditions, each of which involved presentation of a 3-D vertically hinged plane (open book): (i) stereo and motion; (ii) static stereo; (iii) monocular motion; (iv) dynamic stereo with one-frame lifetime dots. The conditions were run at three viewing distances and with three rotation angles, in which both vergence and rotation angles were set to  $3^\circ$ ,  $6^\circ$ , or  $12^\circ$ . The perspectively viewed stimuli subtended  $6 \text{ deg} \times 6 \text{ deg}$  and consisted of low-density patterns of random dots. The screen was moved for different simulated viewing distance so that accommodation was in concordance with vergence. Subjects moved a mouse to set the perceived shape of the hinge to a right-angle. In (i) performance was close to veridical in all conditions. In (ii) shape was misestimated, with larger viewing distance causing depth to be increasingly underestimated. In (iii) larger rotation angles led to an increase in perceived depth, but with no dependence on viewing distance. In (iv) performance was little improved over (ii). We conclude that the visual system is able to combine stereo and motion information to recover shape in a non-trivial fashion (ie not an averaging). The presence of monocular motion is vital in this, and the judgments are not exclusively based on multiple stereo views.

◆ **Perceptual assumptions and projective distortions in a three-dimensional shape illusion**

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Three-dimensional shape identification is an under-determined task. We have explored how suitable heuristics and prior assumptions constrain possible solutions. We studied an illusion in which the physically horizontal balconies of a building appear tilted up or down, depending on viewpoint. This illusion persists despite repeated viewing and cognitive implausibility.

A set of 21 parallelogram stimuli (7 shapes  $\times$  3 physical tilts) were presented monocularly to observers at an elevation of  $30^\circ$ , in four different viewing angles. Observers estimated the tilts and shapes of the stimuli. In most cases, perceived shapes and tilts were significantly different from physical shapes and tilts. Furthermore, perceived tilt was not reliably predicted by angles in the projected image, but was found to be a function of stimulus shape and orientation. Perceived tilts were successfully predicted by a model in which all ambiguously projected 2-D angles are initially assumed to correspond to  $90^\circ$  angles in the 3-D stimulus. Since these local assumptions lead to conflicting interpretations of the projected image, in the model they are selectively revised in order to reach a consistent interpretation. The degree of revision of shape-related versus tilt-related assumptions was found to be a function of the visibility of the stimulus shape.

We conclude that perceived shape is influenced by perceptual assumptions about local angles. The compromises between local-shape and tilt assumptions lead to a final percept that is not an example of 'good form'.

◆ **Evidence for independent channels in the perception of motion-parallax-defined surfaces**

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Sensitivity to spatial modulations in luminance, disparity, and parallax differs as a function of spatial frequency. In both the luminance and disparity domains these sensitivity functions have been found to comprise a range of independent spatial-frequency-tuned channels. However, as yet there are no data which address whether this is also true for motion parallax.

In the present experiments we determined whether such channels exist in the parallax domain, and estimated their bandwidth. Stimuli were 14 deg by 23 deg in diameter and were presented on a Radius 21-inch monochrome monitor, with a linearised look-up table, connected to a Macintosh PowerPC. The observer moved to-and-fro  $\pm 6.5$  cm at 1 Hz and horizontal corrugations were created by linking the display with the head position. Detection thresholds were determined in a 2AFC task for three corrugation frequencies (0.2, 0.4, 0.8 cycle deg<sup>-1</sup>) in the presence of two 0.5-octave noise masks positioned symmetrically around the signal (notched noise). The size of the notch was varied from 0.5 to 2 octaves in 0.5-octave steps. Threshold-elevation functions were calculated by comparing these results to baseline data. Baseline thresholds were established for corrugation frequencies between 0.05 and 3.2 cycles deg<sup>-1</sup> in 0.5-octave steps. Thresholds were found to increase linearly with increases in the magnitude of the noise. Threshold elevation increased as notch size was decreased for each of the frequencies tested. This is consistent with the fact that the parallax-sensitivity function is comprised of a series of independent channels which is in accord with findings in other domains.

◆ **Parallactic depth, concomitant motion, and motion without head movement for different viewing times**

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How does viewing time affect perception of depth from motion parallax and motion perception? To answer this question we measured thresholds, expressed in retinal-image velocities, for parallactic depth, concomitant motion, and motion without head movement while the stimulus was presented for various durations. The stimulus (5.5 deg  $\times$  8.5 deg), which consisted of four horizontal bands of 0.92 cycle deg<sup>-1</sup> sinusoidal gratings, was presented on a computer display, 116 cm from the observer. Adjacent gratings moved in opposite directions. During the parallactic-depth and the concomitant-motion trials, motion of the grating was yoked to the observers' head movements which followed a computer-controlled guide under the chin. The stimulus was presented while the guide moved with a constant velocity of 20 mm s<sup>-1</sup>. During the motion without head movement trials, the moving grating was viewed while the head was stationary. The viewing time ranged from 45 to 3885 ms. The thresholds were measured by the method of adjustment. The thresholds for parallactic depth, concomitant motion, and motion without head movement decreased up to approximately 330 ms but remained constant after that. Moreover, the thresholds of concomitant motion were higher than the other two thresholds for all the viewing times. These results suggest that (a) the 'front-end' for parallactic-depth and motion perception is the same, and (b) the visual system interprets the residual-motion signal, which cannot be converted into depth, as concomitant motion when retinal-image velocity becomes too high.

◆ **When is the detection of structure-from-motion in noise facilitated by colour/luminance segregation?**

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In natural visual scenes a moving object often differs from its background in ways besides motion, eg colour, luminance, scale, etc. We have examined whether detecting structure-from-motion (SFM) in noise can exploit colour and/or luminance-polarity differences. The SFM target was a rotating 'V-shape' 3-D structure, constructed from an array of moving limited-lifetime Gaussian micro-patterns (dark red, bright red, dark green, and bright green). Subjects were required to discriminate the V-shape from a flat-plane as a function of the angle of the V-shape, under two main conditions: with and without static form cues to the target. The static form cue was controlled by

manipulating the relative numbers of micropatterns with different colours or luminance polarities. When the target micropatterns were less than 50% of the total, a difference in colour between target and noise introduced a static form cue to the target, whereas when target and noise micropatterns were equal in number, no static form cue was present. In the presence of static form cues, SFM detection was facilitated when target and noise were segregated by colour/luminance polarity. However, in the absence of static form cues, segregation did not facilitate SFM detection, even when subjects knew the colour/luminance polarity of the target and were thus able to selectively attend to it. This implies that while we are able to use colour/luminance differences to reveal otherwise camouflaged objects, and then select them for motion processing, motion mechanisms do not automatically group features with similar colour/luminance.  
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◆ **Exploring binocular rivalry in transparency situations**

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Two eyes presented with conflicting images show binocular rivalry. An interesting situation is created when one of the eyes is presented with a transparent image that conflicts with a background image presented to both eyes. Results from pilot studies indicated that the ability to discriminate between a transparent and a background image depends on the amount of transparency as well as the mutual spatial frequency. We examined the discriminability of binocularly and monocularly presented transparent stimuli from a background stimulus. Gaussian blurred, black-and-white block patterns were used as the distracting image. A group of Landolt-C 92s with various orientations comprised the test image. Test and distracting image were presented as transparent foregrounds and backgrounds, respectively, or vice versa. Spatial frequency and the amount of transparency were made variable. Both images were fixed in their overlay position. Each trial took 2 s. The subjects' task was to recognise a closed-gapped Landolt-C as the odd figure in the test image. Results showed that transparent images restrained discriminability when both foreground and background had equivalent spatial frequency. However, discriminability for monocular transparent images appeared to be restrained by a difference in spatial frequency for low transparency. The results suggest that binocular rivalry can be influenced by varying the transparency of the monocular image.

◆ **Surface texture enhances the recovery of shape from disparity and motion information under quasi-natural viewing**

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We previously reported that systematic distortions in the perception of depth can occur for physical stimuli under quasi-natural viewing conditions (Bradshaw et al. 1997 *Perception* 26 Supplement, 48). The stimuli comprised three points of light viewed in darkness. However, surfaces viewed in well-illuminated environments, which provide perspective information and higher-order motion and/or disparity cues, can support near-veridical performance (Durgin et al. 1995 *Journal of Experimental Psychology: Human Perception and Performance* 21 679–699). Here we investigate the role of surface-texture information within our quasi-natural viewing paradigm.

Observers set the angle between two adjustable lines, on a computer display, to match the angle between two planar surfaces hinged around a vertical axis. The surfaces comprised twenty-five LEDs which either formed (i) a regular pattern, with LEDs equally spaced within a 25 cm square grid, or (ii) an irregular pattern, with LEDs randomly arranged within the same area. Five test-surface angles (60°, 80°, 90°, 100°, and 120°) were presented at three viewing distances (150, 212, and 300 cm). Surface texture enhances the recovery of shape from disparity and motion information under quasi-natural viewing conditions and under three viewing conditions (monocular static, monocular moving, and binocular static). There was a significant effect of texture in the binocular condition. Both bias (RMS) and sensitivity (SD) were 50% lower for the regular textures. However, in the monocular motion conditions the pattern of texture had little effect—RMS and SD were approximately 13.5% and 12%, respectively. Judgments were not significantly affected by changes in viewing distance. We conclude that, although the addition of explicit surface information improves performance, systematic biases persist; regular surface texture further enhances the veridical perception of binocularly viewed surfaces only.

◆ **Using active manipulation to facilitate visual discrimination: How subjects judge a view is good enough to support a decision**

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Provisual actions are movements used to facilitate vision. They have been studied with computer-generated images of two objects presented side by side. Subjects judged which had a target property, with or without the opportunity to adjust the orientation of the objects in depth. The objects were plane quadrilaterals, with or without shading, texture, and/or legs attached at the corners (giving a table-like, 3-D structure). Cowie, Graham, and Gielen (1996 *Perception* 25 Supplement, 63) showed that allowing provisual action improves discrimination between rectangles and squares much more than enriching traditional cues. New experiments show that subjects' strategies do not reduce to a simple prescription ("rotate the object to maximise the horizontal and vertical extent of the image"). Even with provisual action, the rectangle/square discrimination is performed much better than a matched discrimination between rectangular and non-rectangular parallelograms, suggesting that the visual processing which controls manipulation relies on assumptions about form. Also, although objects are generally moved towards the frontoparallel position in active conditions, judgments are made well before it is reached. This suggests that subjects balance multiple indications to establish when they have achieved a good enough view to make a judgment. Decision times and subjective reports clarify the movements used.

◆ **Depth reversal of a random-dot hollow face on a display with a self-produced motion parallax**

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Although depth reversal of the hollow-face illusion is robust, the random-dot cyclopean hollow face is not reversible if all the monocular pictorial-depth information is eliminated (Georgeson, 1979 *Perception* 8 585–588). We investigated whether the depth reversal occurs to a random-dot hollow face on a self-produced motion-parallax display which has no pictorial-depth information. We simulated four surfaces: a human face relief, a hollow face, a circular bump, and a circular dent. Subjects monocularly viewed the patterns while moving their heads laterally back and forth, and reported whether the centre of the pattern looks closer or farther than the periphery, that is, whether it is convex or concave. All surfaces except the face mould were perceived correctly in accordance with their simulated convexity or concavity. There were significantly fewer correct responses to the hollow face than for any other surface. The random-dot hollow face is reversible when it is simulated with a motion-parallax display yoked to lateral head movements.

◆ **Perceived depth of a target in oscillatory motion**

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In a study on stereoscopic depth combined with periodic motion (Cumming and Parker, 1994 *Vision Research* 34 483–495) a minimum threshold was found at 2 Hz. Analysing the data of Regan and Beverley (1973 *Vision Research* 13 2369–2379, 2403–2415) we found a similar minimum and also a possible change of the exponent in the vicinity of 1 Hz in the empirical threshold-frequency dependence. The purpose of our investigation was to find more direct evidence of processes within the brain occurring at similar frequencies. We expected sinusoidally modulated light signals emanating from stationary stimuli to be an effective probe. Random-dot stereograms formed by pairs of spots of polarised light were viewed through an ocular polariser. A 90° difference existed for the polarisation vectors within each dot pair as well as for the polarisation vectors in the left and right field of the ocular polariser. Rotation of the ocular polarisation vectors relative to those of the dots provided continuous alternation of the crossed and uncrossed disparity views. The perceived depth oscillations were studied over a 0–2.2 Hz frequency range. Most of the fifty-six observers reported a strong reduction of the amplitude for the perceived oscillations at 0.8 Hz. At higher frequencies the target failed to appear in the uncrossed-disparity view. The depth of this rectified motion demonstrated another minimum at 1.6 Hz. These findings offer compelling evidence that low-frequency cyclic processes exist within the brain, revealing themselves through interaction with external sinusoidal signals in a resonance-like manner.

◆ **A ratio model of perceived transparency for stimuli with no contour intersections**

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The perception of the degree of transparency of a surface depends on the chromatic differences between stimulus areas. This experiment was designed to test the hypothesis that the degree of transparency of a transparent surface M seen on another surface N and on a background L depends on the comparison between lightness contrasts. M, N, and L were concentric and their contours did not intersect. The luminances of M, N, and L were  $m$ ,  $n$ , and  $l$ , respectively. There were three stimuli for each luminance order: (i)  $m < n < l$ , (ii)  $n < m < l$ , and (iii)  $n < l < m$ . Eighteen observers participated in the experiment. They rated the lightness contrasts between M and N ( $C_{MN}$ ), L and M ( $C_{LM}$ ), and L and N ( $C_{LN}$ ), and the degrees of transparency of M, T, using integers from 0 (no contrast or opacity) to 100 (black vs white or perfect transparency). The results confirm that the ratio between  $C_{MN}$  and the sum of  $C_{MN}$  and  $C_{LM}$ , which expresses an integration of these perceived contrasts, gives valid predictions of T for stimuli with orders (i) and (ii). For stimuli with order (iii), the rated degrees of transparency differ from the predicted ones, and this is probably due to the observers' tendency to base their ratings of T more on  $C_{MN}$  rather than on  $C_{LM}$ .

◆ **Similarity and interaction of shadow and disparity cues of depth**

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Shadow and disparity are quite different depth cues. For example, shadow may need a recognition of image pattern to be processed for perceiving depth, whereas disparity (both motion and binocular disparities) does not. However, these cues have some features in common: the existence of a limit of perceived depth extent from the individual cue alone and a limit of temporal frequency of perceived depth change.

We tried to examine the similarities and interaction of these cues to explore the process of depth perception. The stimulus was a two-dimensional pattern consisting of a rectangular object and a checkerboard background. In the first experiment we examined the temporal-frequency limit of depth changing. The rectangular object was made to simulate a motion-in-depth with several frequencies either by shadow movement or by motion disparity. The results showed that the extent of motion-in-depth decreased above 2 Hz and totally disappeared above 5 Hz, as shown both by shadow and by disparity cues. In the next experiment we examined the interaction of cues using cue-conflict paradigm. The results showed that the perceived depth from cue combination exceeds that from either cue alone when the depth produced by either cue was more than 1 cm. This can be interpreted as implying that the disparity cue corrected the assumed light direction for the shadow cue, which indicates that the interaction is not confined to the estimation of the depth extent. The results of these experiments showed the nature of the depth-perception process after individual cue processing.

◆ **Subjective expansion and contraction of acute angles**

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It has been shown that the apparent orientation of a single straight line changes in the presence of nearby lines of somewhat different orientations: acute angles are perceptually expanded while obtuse angles apparently contract (Carpenter and Blakemore, 1973 *Experimental Brain Research* 18 287–303). Lateral inhibition in the orientation domain is thought to underlie this phenomenon. It is not yet known what happens when the acute angles are smaller than  $10^\circ$ . In our experiment, as in above-mentioned paper, the subject saw three lines. The subject was always required to set the angle of the comparison line (M) so that it appeared to be parallel to the base line (T) which forms an angle ( $a$ ) with the induction line (I). The stimuli on the monitor screen were generated under conditions of 1 pixel = 40 s of arc. We have done the experiment under two conditions: (i) the induction line was continuous, (ii) a segment of this line was removed (truncated or line with a gap). By comparing the dependence  $D(a)$  for the induction line without and with a gap we could estimate the influence of the removed segment on the perception of the orientation of the base line (T) [ $D$ ] as the angle of (M) with respect to (T)]. The obtained results show that the apparent angles between lines (T) and (I) contract when  $a < 10^\circ$  to  $15^\circ$ . In other cases the obtained relation coincides with the data described in the above-mentioned paper. These data are explained by a model proposed by Vaitkevičius et al (1983 *Biological Cybernetics* 48 139–147). The paradoxical Poggendorff illusion (Restle, 1969 *Perception & Psychophysics* 5 273–274) could also be explained by taking into account the obtained data.

◆ **Effects of changing context on shape perception**

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The appearance of an object depends on the geometrical and physical properties of its surface. Moreover, an object is situated in an environment and the setting influences the perception of its shape. In this study the effects of the environment on shape perception are investigated by changing the setting and the viewing conditions in a systematic way.

The stimuli in these experiments were real 3-D scenes, or pictures of real 3-D scenes. The objects in the scenes were triaxial ellipsoids. Their shape was measured by probing local surface attitude via a gauge figure that had to appear as a circle painted upon the surface of the objects (Koenderink, van Doorn, and Kappers, 1992 *Perception & Psychophysics* 52 487–496; Koenderink, van Doorn, and Kappers, 1995 *Perception* 24 115–126).

The effects of scene geometry were investigated by systematically changing size, distance, and orientation of the objects relative to the observer. The effects of contour information were investigated by varying dark–light contrasts of objects and their surrounding in a systematic way. The effects of limiting the field of view were investigated by changing size, form, and position of frames with respect to observer and scene (Eby and Braunstein, 1995 *Perception* 24 981–993).

◆ **The effect of surface orientation on the perception of parallax-defined corrugations**

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Rogers and Graham (1982 *Vision Research* 22 261–270) noted similarities between the parallax-sensitivity and disparity-sensitivity functions. Both produced inverted-U shapes with peak sensitivity around 0.2 to 0.4 cycle deg<sup>-1</sup>. At a previous ECVF we replicated and extended part of these results by determining disparity-sensitivity functions for a range of surface orientations (Parton et al, 1996 *Perception* 25 Supplement, 67–68). A monotonic increase in thresholds between horizontal and vertical surfaces was found. In addition, in a suprathreshold depth-matching task a non-monotonic trend in perceived depth was found as surface orientation was varied between horizontal and vertical.

The present experiments follow our previous design but use parallax-defined surfaces. Surface orientation was varied from horizontal to vertical in 22.5° increments to investigate its effect on (i) discrimination thresholds and (ii) perceived depth. Stimuli were 10 deg in diameter and were presented on a Radius 21-inch monochrome monitor with a linearised look-up table. The surfaces were modulated in depth at four different corrugation frequencies (from 0.1 cycle deg<sup>-1</sup> to 0.8 cycle deg<sup>-1</sup> in octave steps). Thresholds were found to increase monotonically with increasing surface orientation. This increase was less marked at higher corrugation frequencies. Although perceived depth in vertically oriented corrugations was significantly smaller than in horizontal corrugations, the largest amount of perceived depth was found for surfaces oriented at 45°. This effect is much smaller than we previously found with disparity-defined surfaces. The results from both experiments add to the evidence for operational similarities between the two cues.

◆ **Nonhomogeneous compression of space in aperture viewing**

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Previous studies of aperture viewing (also known as slit viewing or anorthoscopic perception) have shown that objects appear horizontally compressed when seen translating horizontally behind an occluder with a slit. This horizontal compression occurs even when the observer maintains fixation, ruling out explanations based on retinal painting. Computationally, the recovery of velocity based upon local information is necessary to recover the shape. The perceived velocity determines the degree of the perceived compression.

We present three experiments exploring the role of tilt upon perceived compression. In the first experiment, three observers estimated the magnitude of a single line segment. Results showed that the perceived length of the line segment depended upon tilt, with greater compression for the segments that were more tilted from vertical. In the second experiment, the same observers judged the disparity between the tilt of a line segment when seen translating through an aperture and the tilt of the same segment when stationary and fully visible. Observers all perceived the translating line as being more tilted from vertical than the stationary standard. In the third experiment, observers discriminated the relative lengths of two line segments that were horizontally aligned and embedded within a circular frame. Preliminary results suggest that the line segment that passed

behind the slit second was perceived as less compressed than the segment that passed behind the slit first. Results suggest that the recovered velocity is not homogeneous across the object.

◆ **Measuring pictorial shape**

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'Pictorial shape' does not exist in the physical world and can only be defined operationally. The result will depend on the particular operationalisation. Hence it becomes of interest to compare various types of operationalisation. Since the issue of veridicality is a moot one (after all we don't even know how to enumerate the—possibly infinite number of—scenes that would yield the fiducial picture given a certain method of rendering), we studied systematic differences between, and reproducibility of, three methods: gauge figure adjustment (Koenderink, van Doorn, and Kappers, 1992 *Perception & Psychophysics* 52 487–496), pairwise depth comparison (Koenderink, van Doorn, and Kappers, 1996 *Perception & Psychophysics* 58 163–174), and (a perversion of) the method described by Frisby et al (Frisby, Buckley, Baylis, and Freeman, 1995 *Perception* 24 Supplement, 136). We used several photographs of sculptures by Brancusi (loosely speaking: 'generic egg shapes with appendages'). We find that the least scatter occurs with estimations of local surface orientation, whereas the global depth map is more uncertain. We stumbled on an interesting feature of the Frisby task: Our subjects cleanly divide into two camps with clear-cut preferences regarding certain (apparently minor) variations of the task. When preferences are followed, results between these groups are quite different; when either method is enforced, results are similar but different for each variation. We conclude that such a study over task variations yields a powerful handle on the human 'shape from picture' mechanisms.

**OBJECTS AND SYMMETRY**

◆ **Object perception and object categorisation**

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Theories of object recognition explain the preferred usage of an object dimension (eg shape, colour, or texture) in terms of its usefulness (ie its diagnosticity) for the task at hand. For example, 'orange peel', the texture, is used to recognise orange, the fruit. However, the perception of the object dimensions has generally been neglected in object recognition. There is an important asymmetry between the perception and the usage of dimensional information. The perception of, eg, textural cues is a prerequisite to their eventual diagnostic use in recognition, but textural cues that were not diagnostic could still be perceived without being used. This asymmetry points to the necessity of assessing the perception of object information with tasks (eg same/different) which bypass recognition.

In three experiments we tested whether the diagnosticity of a dimension in a categorisation task changed its perception. Stimuli were 3-D computer-synthesised fruits and abstract objects. Same/different judgments between objects that varied along one or more dimensions assessed the baseline perception of shape, colour, and texture information following 30, 120, and 1000 ms exposures. In a second experiment, the same/different judgments followed the acquisition of perceptual expertise with different object dimensions in three experimental groups. In a third experiment we tested whether the perceptual expertise acquired with a subset of dimensional values generalised to the entire dimension. We also tested perceptual expertise with a dimension-improved subsequent recognition performance. Together, results suggest that categorisation experience changes the perceived information in objects.

◆ **Visual segmentation and the model of Siddiqi, Tresness, and Kimia**

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A common view about object recognition is that the first visual representation is split up into parts. In order to achieve recognition, these parts and their spatial orientations are encoded.

One of the most recent models which tries to find the same parts in shapes as the visual system is the model of Siddiqi et al (Siddiqi, Tresness, and Kimia, 1995 *IEEE Transactions on Pattern Analysis and Machine Intelligence* 17 239–251). It computes two types of lines which divide shapes into parts: limbs and necks. Limbs mark protrusions in a shape and necks local narrowings. Siddiqi et al asked participants to divide a shape into parts by drawing lines. The

resulting lines were compared to the lines computed by the model. The results supported the model. However, the shapes which formed the stimuli of the experiments were chosen rather arbitrarily. Furthermore, on practical grounds, the participants were restricted in the kind of lines they could draw.

We investigated the influence of these factors. With a systematic set of stimuli and without the restrictions mentioned above, it appeared that only limbs were well predicted. This means that the model cannot predict as well as Siddiqi et al claim.

◆ **Predicting individual differences in performance of an object-recognition task**

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Observers were asked to recognise a set of rotating dot-covered rigid objects from a series of distractor objects displayed on a computer monitor in a dimly lit room. The stimuli were viewed binocularly but with the main cue to object shape provided by the differential motion of the dots and with the stereo cue being consistent with the flat screen. These stimuli therefore contained cue conflicts. Prior to performing this task the observers were given a set of orthoptic measures: heterophoria, visual acuity, and stereo acuity. We also measured each observer's resting state of accommodation in the dark (DA) with a Canon R1 Auto-refractor. Owens (1984 *American Scientist* 72 378–387) has suggested that an individual's DA can be used to predict which observers will experience visual difficulties under reduced-cue situations. We would therefore predict that those observers who had a DA close to 57 cm would find our object-recognition task more easy than those with DA more distant than the screen. Performance on the object-recognition task was assessed by  $d'$  measures, reaction times, and learning rates.

We found marked individual differences in these performance measures and DA was related to these measures in line with predictions. These results have implications for many psychophysical experiments that rely on monitor displays where individual differences are often both mysterious and ignored. They are also relevant to virtual reality and remote-sensing applications that rely on monitor displays and where the observer is required to recognise objects in the scene.

◆ **Why we placed the paper clip in the living room**

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Previous studies have found that visual recognition of novel 3-D objects is influenced by the degree of deviation from familiarised viewing direction. This suggests that recognition involves bringing both stimulus and representation into correspondence and this can be facilitated by knowing the observer's current viewpoint. The absence of such information in previous studies could have caused the observed view-dependence.

We addressed this issue by constructing a highly realistic virtual living room, rich in visual depth information, which served as an implicit specification of the observer's viewpoint. On a pedestal in the middle of the room, we placed various 'paper-clip' objects (Bülthoff and Edelman, 1992 *Proceedings of the National Academy of Sciences of the USA* 89 60–64). After an initial exploratory period in which subjects familiarised themselves with the room, training and recognition tests were conducted.

We compared performance in object-identification and same-different tasks (with and without the room). In the former, eight subjects learned to differentiate between objects by interactively changing their view about a fixed direction. They were then tested for generalisation to novel views. Error rates and response latencies were a function of distance from the familiar direction. The room helped reduce error rates but did not eliminate view-dependence. Results of controls in which subjects gauged their change in orientation after a deviation in viewpoint revealed similar errors as the recognition experiments; this suggests that making view deviations more explicit may reduce view-dependence even further. In the same-different tasks, five subjects had to decide whether two sequentially presented objects were the same, given an intervening shift in viewpoint. Performance was similar to the identification task. Results indicate that observers can use implicit vantage-point information to improve object recognition performance.

- ◆ **Modelling of the effect of pattern symmetry, similarity, and complexity on recognition time**  
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At the 14th, 16th, and 17th ECVF (1991 *Perception* 20 Supplement, 124; 1993 *Perception* 22 Supplement, 50–51; 1994 *Perception* 23 Supplement, 44), we reported on the influence of pattern (figure composed of horizontal and vertical line segments) symmetry, similarity, and complexity on its recognition probability in psychophysical tachistoscopic experiments on human subjects. To determine the mechanism underlying this influence, a model of an active recognition system of such simple formalised patterns is introduced. Recognition in the model is regarded as a process of creation and verification of hypotheses by matching the features (line segments) of presented and hypothetical patterns. If the line segment in the presented pattern is absent, all hypothetical patterns that possess this line segment are rejected and vice versa. The recognition time is defined by the number of verified hypotheses and that depends on the efficiency of features used for pattern description. The most effective features are those which allow a reduction in the number of hypotheses by one half. A computer simulation was carried out with the same patterns as those used in the psychophysical experiments. In most cases the obtained results correlated with the psychophysical data. This allows us to propose that similarity, symmetry, and complexity define the efficiency of features used for pattern description in the human visual system, and how these influence recognition time.

- ◆ **Anisotropies in perceiving whether an object is lying on a surface: superiority for the ground plane**

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An important problem in visual object recognition is that of recovering object pose as well as object identity. An object in a void has six degrees of freedom: it is free to rotate and translate in each of the three dimensions of space. In the world, however, the pose of many objects (such as vehicles) is constrained by the surface of the Earth (the ground plane), which reduces the number of degrees of freedom of pose to three (two translations and one rotation). The notion that the ground plane may be an important reference in human vision is supported by the enhanced stereoscopic sensitivity for the lower half of the visual field (Manning et al, 1992 *Documenta Ophthalmologica* 79 161–175). To test this idea further, twelve subjects were required to detect whether an array of items (such as cubes) all lay in a single flat plane, defined by the perspective of the cubes and their relationship. Subjects were significantly faster, more accurate, and more confident in their judgments when the plane was horizontal than when it was vertical, suggesting that the ground plane has an importance in human vision which is not shared by vertical surfaces. The data may reflect an important computational heuristic in early human vision.

- ◆ **Recognition of depth-rotated objects among qualitatively similar and dissimilar distractors**

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In some object-recognition experiments, rotation of an object between a study phase and a test phase produces an increase in reaction times and error rates. In other experiments, subjects recognise a rotated object as quickly and as accurately as they recognise an object shown from a repeated viewpoint. Many theories (eg Biederman, 1987 *Psychological Review* 94 115–147; Tarr, 1995 *Psychonomic Bulletin and Review* 2 55–82) explain this difference as being due to the context within which recognition takes place; as objects share more qualitative features with each other, recognition costs associated with a change in viewpoint are predicted to increase.

We tested this hypothesis by requiring subjects to recognise objects in one of two conditions: either the distractor objects were qualitatively similar to the target, or they were qualitatively dissimilar. In addition, we tested one subset of objects with straight axes of elongation and another subset with curved axes. We found that performance was affected by both the context of the distractor objects (recognition costs were greater when the target object was qualitatively similar to the distractor objects) and the specific shape features present in the target object (objects with straight axes showed smaller recognition costs than objects with curved axes).

◆ **Task-dependent effects on memory for contour information**

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Viewpoint-invariant properties (VIPs) have been implicated by Biederman and others (Biederman, 1985 *Computer Vision Graphics and Image Processing* 32 29–73) as the fundamental encodings in human visual object recognition. These encodings, such as curved vs straight, and parallel vs nonparallel are robust across modest changes in viewpoint or image degradation. According to Biederman, information carried by viewpoint-dependent properties (VDPs) such as degree of curvature is not utilised for entry-level object recognition. If object recognition does indeed rely on VIPs then changes from straight to curved should affect object-recognition performance.

Following either object naming or prototypicality-rating study tasks, viewers were given a two-alternative forced-choice recognition test with the previously studied items as recognition targets. In both cases, the recognition distractors varied from the target items in terms of either viewpoint-invariant (eg change from curved to straight) or viewpoint-dependent (eg change in curvature) properties. The results indicated that observers registered VIP encodings only when actively rating an object prototypicality but not when simply naming the item. The positive results with prototypicality suggest that VIP encodings can be extracted, but only when the task demands very close attention to the object shape. The lack of positive findings following the object-naming study task argue that, although available, VIP encodings are not registered by the act of simply naming the object, as characterises real-world object recognition. Thus viewpoint-invariant encodings of image edges are unlikely to be the sole or primary route to everyday object recognition.

◆ **Selectivity of macaque inferior temporal neurons to coloured photographs, line drawings, silhouettes, and subjective contours of the same shapes**

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Human object recognition is substantially resistant to the changes in images caused by changes in retinal position, viewing distance, angle, illumination, defining cue, and partial occlusion. Cells in the anterior part of the inferotemporal cortex (IT) of macaque monkeys seem to match these characteristics of our visual capacities, showing relative invariance to the above changes in stimulus parameters.

We tested how the responses of IT neurons change if we present the same set of stimuli with different contour and surface information to an actively fixating monkey. We used colour pictures (COL, with the most visual detail, including colour, occluding contours, internal contours, luminance gradients, and textures), line drawings (LD, by removing all the contrast of the images, except for the outer edges and internal parts), and silhouettes (SIL, the occluding contours only), as well as subjective contours (SC, generated by abutting gratings). We recorded 101 neurons and found that IT neurons are selective for shapes defined by all four rendering conditions. The absolute firing rate of the neurons, however, depended on the stimulus type, being the highest with COL (17 Hz) and lower with LD and SIL (10 Hz), and SC (5 Hz). Shape-selectivity of the tested neurons did not change significantly in LD and SIL, when compared to COL, but was significantly different in SC. This confirms that IT contributes to the invariant recognition of shapes independently of colour, internal-contour, and surface information.

◆ **'Left-right' and 'right-left' observers: Two different styles of picture viewing**

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Is it possible to measure the ability of an observer to perceive the correct composition in paintings? To answer this question we selected twenty-three copies of landscape paintings by some famous painters, combined them with their inverted (mirror) versions and presented them to fifty-three subjects. The task of each subject was to choose the version with the 'correct' composition. As 'correct' we considered compositions with a large important object in the foreground shifted to the left from the centre and less important and smaller objects in the background (sometimes with a fragment of the horizon) and shifted to the right. The reason for the left shift of a large visual mass is the 'left-right' (L-R) direction of eye movement in viewing [R Arnheim, 1974 *Art and Visual Perception* (Berkeley, CA: University of California Press)]. Among our subjects were forty-four students of fine arts and nine students of computer science. Six subjects were left-handed. The results we obtained show that the average scores of the fine-arts students were

higher. In addition the results enabled us to identify two extreme groups of subjects: nine 'experts' with the highest scores (more than 80% of correct responses) and six 'anti-experts' with the lowest scores (less than 20% of correct responses). All in this last group were fine-arts students! But an additional analysis showed that the latter ones consistently chose inverted (mirror) versions of original pictures and that half of all the left-handed subjects were in this group. The results suggest that some people have a strong tendency to view a picture in the 'R-L' direction. We can call them 'R-L observers' in contrast to ordinary 'L-R observers'. The obtained results may shed light on the mechanisms of dyslexia (difficulties in L-R reading in children), especially since among dyslexics there are many left-handed children.

◆ **Mental rotation of dot-defined objects**

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Object recognition is based on extracting 3-D shape from 2-D pictures. Previous studies have used perspective line drawings of ten solid cubes, attached face-to-face to form an extended structure. Observers' speed of reaction in judging identity between pairs of objects depends on the angular difference in viewing position between the objects (mental rotation). We investigated whether this ability is preserved when objects are represented only by isolated points at the vertices of the cubes (dot-objects). Both opaque and transparent representations of 2-D (monocular) and 3-D (stereo) views were tested. Each dot-object consisted of forty-four vertices defining a ten-cube shape. In some presentations the objects differed in terms of rotation in the picture plane; in other presentations the objects differed in terms of rotation in depth. Reaction time (RT) increased monotonically with the angular difference between views for all stimuli except one, consistent with mental rotation. Results suggest that 3-D shape can be extracted even from transparent displays containing only vertex information. The exceptional condition involved 2-D presentations of objects that differed in terms of a rotation in depth. Here RTs were longest for 90° rotations.

◆ **Basic-level and subordinate-level object categorisations affect induced change blindness (ICB)**

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In induced change blindness, ICB (Rensink et al, 1997 *Psychological Science* 8 368-373), one change between two successively presented pictures of the same scene separated by a flicker is difficult to perceive. We used ICB to examine the visual encodings of objects in complex scenes—an office cluttered with many objects. Between two successive frames, a mug could change or disappear, a computer could change or disappear, or other office objects could disappear.

Prior to the task, two subject groups received a differential category training on the same set of mug and computer pictures. One group was trained to name the mugs at their precise, subordinate level, but name the computers at their more abstract, basic level. The other group learned to assign opposite categorisation levels to the same objects (basic mugs and subordinate computers). This ensured that both groups saw all mugs and computers that changed between the two frames of a sequence, but differed on the categorisation level applied to the same objects.

Subjects did not immediately perceive a change in their respective basic-level objects (mugs or computers), but did so for their subordinate-level objects (computers or mugs)—as measured by the repetitions of the two-picture sequence needed to notice the change. This is not simply a problem of subjects not attending their basic-level objects (object disappearance was immediately detected). Instead, their visual encodings included categorisation-level-specific properties which either facilitated or hindered detection of identical changes by subjects.

◆ **A model of visual segmentation for images with T-junctions**

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Occlusion cues such as T-junctions in an image are useful to perceive a 3-D world from 2-D retinal images. However, typical algorithmic methods for computer vision have difficulty in analysing the images with occlusion in the way human vision does. We propose a model for detecting the depth relationship between overlapping surfaces based on T-junctions. Our model contains four stages. In the first stage, edges of different orientations are detected separately to make an orientation map by spatial filtering and calculation of local energies with filters similar to cortical

simple and complex cells (Gabor filters with twelve different orientations). In the second stage, T-junctions are detected from the orientation map by finding the regions where two perpendicular (or close to perpendicular) edges form the shape of a T. In the third stage, the two orientation components at each T-junction are separated in different depth planes on the basis of the occlusion relationships between the two (the leg of a T is assumed to be behind the crossbar of the T). In the fourth stage, the occluded edges are interpolated by interpolation filters. The interpolation filters are also a set of Gabor filters with a larger space constant. They operate on each of the orientation maps with a weight that depends on the difference between the preferred orientation of the filter and the orientation of the map. This operation generates responses at a point where there is no edge information but there are edges directed to the point in the neighbourhood. The model has been successfully applied to monochromatic images.

◆ **Perception of a camouflaged point-light walker: differential priming effect**

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Recently, we showed that recovery of a priori known structure from biological motion leveled off with changing display orientation (eg Pavlova and Sokolov, 1997 *Perception* 26 Supplement, 92). How does image-plane rotation of a prime affect detection of a camouflaged point-light walker? At each of five randomly presented display orientations between upright and inverted (0°, 45°, 90°, 135°, and 180°), viewers saw a sequence of displays (each display for 1 s). Half of them comprised a camouflaged point-light walker, and half a 'scrambled-walker' mask. In a confidence-rating procedure, observers judged whether a walker was present. Prior to each experimental sequence, they were primed (for 10 s) either with an upright-, 45°-, 90°-, or 180°-oriented sample of one walker. Pronounced priming effects were found only with an upright-oriented prime: it improved detectability for the same-oriented displays, and to a lesser extent for 45°. With 45°-prime, sensitivity for 0°-, 45°-, and 90°-oriented displays was higher than for 135° and 180°. However, with 90°- and 180°-primes ROC curves for all orientations were situated close to one another. These findings indicate that the priming effect in biological motion is partly independent of the relative orientation of priming and primed displays. Moreover, it occurs only if a prime corresponds to a limited range of deviations from upright orientation within which display is spontaneously recognisable despite a discrepancy between event kinematics and dynamics (Pavlova, 1996 *Perception* 25 Supplement, 6). The primacy of dynamic constraints in the perception of structure from biological motion is discussed.

◆ **Are silhouettes easier to recognise than outlines?**

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Snodgrass and Vanderwart (1980 *Journal of Experimental Psychology: Human Learning and Memory* 6 174–215) have developed a standard set of line drawings of 260 everyday objects, which has been used widely in research on object identification, picture naming, etc. We have produced two variants. In the silhouette version, the surface inside the boundary of the original drawings was blackened so that interior features were no longer visible. In the outline version, an edge-detection algorithm was used to extract the contour and a spline-fitting technique was used to obtain perfectly closed figures with smoothly varying curvature. Three hundred and fifty six subjects were asked to identify the pictures. Silhouettes were identified better than outlines, both when a strict criterion of correct name was used (53% vs 51%) and when responses were more liberally taken to reflect the correct concept (65% vs 62%). However, exactly the same information about an object's contour is present in both versions. What could be the nature of this difference? The largest silhouette advantage occurred for objects with a dark surface (eg, ant, barrel) while an outline advantage occurred for objects with a light surface (eg, glass, ironing board). Significant correlations between the silhouette–outline differences and the surface-colour ratings from an independent set of observers supported the idea that memory for natural surface colour may have affected identification. To test this hypothesis further (and to rule out edge quality as a lower-level explanation), we will repeat the study with polarity-reversed silhouettes (with white interiors against a black background).

◆ **The typicality and base levels for 'yes' and 'no' judgments**

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In previous research, it was shown that judgments about similarity and dissimilarity were not symmetric. We proposed that yes–no judgments in a discrimination task are based on different visual characteristics of both target and items. The experiments were carried out with meaning-less geometrical figures presented simultaneously in pairs on a computer screen. In the first experiment, the subjects had to discriminate (by means of a 'yes–no' technique) between the original target and one of seven similar figures. These figures were different from the target in some perceived features. In the second experiment, the subjects had to judge whether geometric fragments were a part of the target ('yes'-response) or a part of the other figures ('no'-response). The 28 fragments were different, in a graded way, either from the target or from one of the other items. All the fragments were presented in two orientations (vertical and horizontal) and in three strings interpreted as three levels of experience. The response times and types of judgments (yes–no) were recorded.

The most typical fragments named the 'target invariants' and the 'non-target invariants' were extracted across both 'yes' and 'no' judgments by means of configuration-frequency analysis. Base levels were calculated for both the 'target invariants' and for the 'non-target invariants'. It was found that the index of typicality was higher for the 'target invariants' and the base level was more abstract for 'non-target invariants'. The orientation of fragments had no influence on either 'yes' or 'no' judgments; but levels of experience did affect 'no' judgments only.

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◆ **Recognition of rigid Johansson objects mediated by spatiotemporal signatures**

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Recognition of human Johansson figures is thought to be mediated by spatiotemporal characteristics, and not via shape-from-motion cues (Mather and Murdoch, 1994 *Proceedings of the Royal Society B* 258 273–279). Evidence is presented that recognition of dot-covered rigid objects, which are analogous to Johansson figures, is mediated by spatiotemporal cues.

Subjects learned to recognise the same set of twelve novel, smooth, pebble-like, rotating objects from image sequences presented as part of a continuous recognition task. Each object was textured uniformly with white dots. Both its surface and the background were coloured black so that the surface and occluding contour were invisible. During learning, the temporal order of images of a given object was the same every time that the object was presented. During testing, half of the learned objects acted as controls, and the order of each control sequence was the same during testing as it was during learning. In contrast, the temporal order of the remaining sequence was reversed relative to its order during learning (ie the image sequence was played 'backwards').

This image sequence reversal produced significant reaction-time increases and recognition-rate decreases. For the control objects, no corresponding significant differences were found. Results are interpreted in terms of object-specific spatiotemporal signatures. These results cannot be interpreted in terms of shape-from-texture/motion cues because these imply exactly the same shape irrespective of the temporal ordering of images in a sequence. This, and a previous experiment with fully rendered objects (Stone, 1998 *Vision Research* 38 in press), suggest that spatiotemporal cues may be involved in recognition of rigid objects.

◆ **Performance on object decision priming is task-dependent**

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Task dependence of performance on object decision priming was demonstrated in two experiments. In the first, subjects studied a series of line drawings of possible and impossible objects under left–right (structural) encoding instructions, and then judged whether briefly presented depictions of objects were possible or impossible with respect to 3-D structure. Priming was measured as greater accuracy for studied, compared to nonstudied, objects. Significant priming was observed for possible, but not for impossible, objects. Moreover, within the set of possible objects, the level of priming was equal for objects with symmetric and asymmetric structures. In the second experiment, the same set of possible objects was used. Subjects completed the same left–right encoding task but they made judgments concerning each object's symmetric or asymmetric structure in the decision task. Significant priming was observed only for symmetric

objects. This result contrasts sharply with that of the first experiment in which both symmetric and asymmetric objects exhibited priming when the test decision concerned an object's possible or impossible structure.

We argue that such task dependence arises from an interaction between the processes involved in a particular task and the information coded in a structural description system. Specifically, the structural description system codes global information and salient structural features of an object, such as symmetry. Asymmetric possible objects showed task-dependent priming because, while their global structures are coherent, they nonetheless fail to possess the property of overall symmetry.

◆ **Rotating simple two-dimensional figures through space along the shortest path**

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Perceiving that the shape of an object does not change when it is viewed from different angles, is called 'form constancy'. According to mental transformation theory the visual system corrects for differences in size and/or orientation by 'mentally undoing' the geometric transformation. An alternative theory assumes that form constancy is based on the detection or computation of properties that remain invariant under a well-defined group of transformations.

Wagemans, Van Gool, De Troy, Foster, and Wood (1993 *Perception* 22 Supplement, 107) have attempted to differentiate between the two approaches. Simple 2-D dot patterns were rotated, slanted, and in some conditions also tilted. The fact that the addition of a tilt component did not cause an increase in the response times was taken as evidence against mental transformations and in favour of invariants. However, one can undo a rotation, slant, and tilt in one single rotation along the shortest path in 3-D space. Parsons (1987 *Perception & Psychophysics* 42 49–59) showed for 3-D objects that humans somehow can detect and use such an axis and angle in space. Although a posteriori analyses of the previous data did not provide strong evidence for the use of this 3-D mental rotation procedure, new experiments were designed to further investigate this issue.

In a same-different task, simple 2-D pentagons were rotated in space and distractors now consisted of mirror-reflected targets instead of new random shapes. Results showed a typical linear effect of the orientation difference on the response times, which is classically taken as evidence for mental transformations.

◆ **Objects can guide attention**

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Egley et al (1994 *Journal of Experimental Psychology* 123 161) argued that shifting attention between objects is slower than shifting attention within objects, because disengaging the object provides an additional cost. However, in this study we argue this shifting attention between objects is slower, because attention is not guided by an object between the cue and target.

As in the study of Egley et al, a cueing task was used. The stimulus consisted of a fixation point with a vertical rectangle on the left and right of it. The cue could appear at each end of the rectangles. The target was presented at the same position (valid condition) or on the opposite side (invalid condition). In the first experiment the two rectangles were connected by a horizontal bar at the top, at the bottom, or not at all. In the second experiment the bar was at the top or at the bottom and was either connecting the rectangles or not.

The results show an effect of validity. Furthermore, shifting attention was faster when the connecting bar was closer to the cue/target. The second experiment showed no significant effect of connectivity. These results indicate that the presence of an object can facilitate the attentional shift. Absence of this attentional guidance could explain the additional cost of shifting attention between objects, as found by Egley et al.

- ◆ **Viewpoint-dependent recognition of 3-D objects need not imply mental rotation in space**  
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Novel 3-D objects were created by attaching four small components ('geons') to different parts of one large component (middle-left, middle-right, top, and bottom). For each object, three distractors were created by exchanging the positions of the small components. Subjects were asked to determine whether a test image belonged to a target object or a distractor object. In three experiments, target objects were presented as an apparent-motion sequence of twelve views (30 deg apart). The axis of rotation was either aligned with an axis of the environment, with the main axis of the object, with both of these reference axes, or with none of these. Response times for correct-match trials were shorter when the test views were views shown in the apparent-motion sequence than when they were in-between them (by only 15 deg) on the same path, or when they were on a path orthogonal to that of the motion sequence. However, the orientation of the axis did not matter, contrary to what could be expected if mental rotation were used (eg Pani, 1993 *Perception* 22 785-808). In two additional experiments, only one target view was presented and angular disparity between test and target view was varied from 0 to 90 deg. Linear effects were obtained on both response times and error rates but axis orientation yielded no effect. We conclude that viewpoint-dependence need not imply that observers undo the viewpoint change by mentally rotating objects in 3-D space. These results are consistent with the multiple-views approach (eg Bülthoff et al, 1995 *Cerebral Cortex* 5 247-260).

#### FACES

- ◆ **A disproportionate effect of inversion in cross-category morphs of familiar faces**  
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Last year (Angeli and Gerbino, 1997 *Perception* 26 Supplement, 35) we reported evidence that the identity of a morphed face is perceived categorically by observers who are familiar with faces defining the extremes of the morph continuum. This finding is supported by the comparison of familiar and unfamiliar observers. Within-category and cross-category morph pairs were used in discrimination and classification tasks. Discrimination was operationally defined by sensitivity in simultaneous matching (AB task), and classification by sensitivity in sequential classification involving short-term memory (ABX task). We computed  $d'$  as a common measure of sensitivity and compared the amount of the inversion effect.

In the AB discrimination task, morph-pair type and observer's familiarity with original faces did not affect the amount of the inversion effect. Such a result is consistent with the assumption that perceptual discrimination of faces does not involve specific knowledge of person identity and with the assumption that the morph continuum is linear. In the ABX classification of cross-category morph pairs, a disproportionate effect of inversion was obtained with familiar observers, but not with unfamiliar observers.

Taking into account the linearity of the morph continuum, we suggest that such a disproportionate effect of inversion depends on two components: (a) improved classification of familiar upright faces based on the effective use of global differences available in cross-category morphs, and not in within-category morphs, and (b) impaired classification of familiar inverted faces due to the specific loss of local differences in cross-category morphs, possibly dependent on the smoothing effect of the morphing algorithm.

- ◆ **An effective model for classification of facial expression**  
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To date, classification of facial expressions of emotion by statistical models has been less than perfect. One hundred and twenty photographs of male and female posers were examined for their six universally recognised expressions produced in accordance with FACS. A hybrid coding of each image was employed. Thirteen real-valued spatial attributes and thirteen binary attributes (signifying presence or absence of facial features) were used. Spatial measures described the relationship between features and feature size. Binary terms represented low-dimensional, low-spatial-frequency attributes such as those derived from template-based machine-vision systems. A degree of redundancy was built into the model to compensate for those measures which could not be made but for which a binary decision could be made.

Bayesian classification was implemented so as to provide automatic inductive inferences about the distributions of facial attributes; statistical inference was built around information theory. The solution yielded 100% correct classification. A minimum of fifteen (two real, thirteen binary) attributes were required to generate >98% accuracy. Conjunctions of binary decisions regarding facial displays could arguably contribute to the most accurate decisions about emotional states. The statistical influence of the attribute of each class was used to assess the relative importance of individual features in signalling each emotion. Since FACS was used to score the purity of the originating materials, the new model is particularly sensitive to blended emotions and has high explanatory and predictive power. Application of the model in categorical perception and clinical assessment is discussed.

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◆ **Gender perception of 3-D head laser scans**

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We investigated whether the judgment of face gender shows the typical characteristics of categorical perception. As stimuli we used images of morphs created between pairs of male/female 3-D head laser scans. In experiment 1, texture and shape were morphed between both faces. In experiment 2, either the average texture of all faces was mapped onto the shape continuum between the two faces or we mapped the texture continuum between each face pair onto an average shape face. Thus, either the shape or the texture remained constant in any one condition. The subjects viewed these morphs first in a discrimination task (XAB) and then in a categorisation task which was used to locate the subjective gender boundary between each male/female face pair. Although we found that subjects could categorise the face images by their gender in the categorisation task and that texture alone is a better gender indicator than shape alone, the subjects did not discriminate more easily between face images situated at the category boundary in any of our discrimination experiments. We argue that we do not perceive the gender of a face categorically and that more cues are needed to decide the gender of a person than those provided by the faces only.

◆ **Manipulation of visual cues to perceived health in faces**

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Our study aimed to capture and manipulate visual cues related to perceived health. Factor analysis of the ratings of six skin-appearance experts on nine descriptors of facial health for sixty two female faces (age 18–59 years) revealed three factors. The factors correlated with three descriptors related to the prevalence of 'skin inflammation' (associated with blocked skin pores), 'lines-wrinkles' (skin aging), and 'a healthy glow in colour'. Multiple linear regression of RGB pixel colour and ratings revealed different topographic distributions of colour cues related to the three perceived health qualities. The fifteen face images rated highest and lowest on each quality were averaged to make three high and three low blends. Eleven subjects were asked to make the faces of twenty seven individuals (three rated low, average, and high on each quality) look as healthy as possible by moving a computer mouse from left to right. Mouse movement produced a real-time transformation of the facial image adding or subtracting the colour difference between the high and low blend for one facial dimension. To optimise healthy appearance, subjects applied transforms, which corresponded to reducing inflammation and lines-wrinkles, and increasing healthy glow; the amount of transformation applied depended on the original ratings of faces. When subsequently presented with one label (skin inflammation, lines-wrinkles, or healthy glow), subjects recognised the high blend as exhibiting more of the quality than the low blend. Thus, visual qualities related to perceived health can be captured from faces and this information used to manipulate perception of health of other faces.

◆ **Faces projected on hollow and convex masks**

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It is well known that a hollow mask, when viewed from a distance, gives the illusory perception of a normal, convex face.

Experiments are reported with faces projected on hollow and convex masks. Results indicate that when faces are projected on the convex mask, there is interference between the face

features—rendering the projected face difficult to recognise. When faces are projected on the hollow mask, the features do not interfere as much: the projected features win out over the hollow-face features.

◆ **The pigeon paradigm: complex categorisation with simple perceptual tools**

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Studies based on anthropocentric cognitive models of categorisation and computer simulations have failed to explain the ways in which animals analyse and group natural stimuli. Among animal researchers, it is commonly agreed that stimuli that may appear complex to the experimenter might be classified by the subjects using very simple image properties. Furthermore, a fundamental problem posed by natural categorisation is how organisms such as the pigeon, which are devoid of language and presumably also of further high-level capacities, can rapidly extract abstract invariances from stimulus classes containing instances so variable that neither the class rule nor the exemplar can be physically described.

An example of such a class is the human face. Despite innumerable attempts, it remains to be determined how humans sort faces into psychologically relevant classes. However, it is possible that birds categorise this class of stimuli in much simpler, though still successful ways. Our pigeons rapidly sorted two hundred photo-realistic frontal views of human faces according to sex. Using a correspondence-based representation of faces, we dissociated the information about an item into two parts; one coding for the spatial configuration of its features, and the other for its particular appearance. The results of the original discrimination training clearly indicated that pigeons preferred to exploit the surface properties of faces to their spatial properties. Furthermore, subsequent transfer tests revealed that within the surface domain they used overall brightness, colour, brightness gradients (ratio between the top and bottom half of the face), and shading.

◆ **Analyses of delays in recognising facial expressions resulting from adaptation to faces**

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We investigated subsystems underlying the recognition of facial expressions by an adaptation method. In a preliminary experiment, pictures of female faces were presented with the following six expressions: 'happiness', 'sadness', 'surprise', 'anger', 'disgust', and 'neutral'. The subjects were asked to rate the magnitude of each expression. Principal-component analysis (PCA) performed on the mean ratings revealed that the first component corresponded to 'pleasantness' ('happiness'–'disgust'), while the second component corresponded to 'arousal' ('surprise'–'sadness'). In experiment 1, the subjects orally judged as quickly as possible the expressions on test faces (expressing one of all categories) following either 1-s (control condition) or 25-s (adaptation) viewing of an adaptation face (expressing one of five expression categories excluding 'neutral'). The delays produced by the adaptation condition were calculated by comparing the reaction times under both conditions. Significant delays occurred when the adaptation face had high absolute values on the first component of PCA. For example, the adaptation face showing 'happiness' produced significant delays in the recognition of 'happiness' and 'neutral' in the test faces. In contrast, adaptation to faces having high absolute values only on the second component (for example 'sadness') produced no effect. In experiment 2, inverted faces were used as the adaptation stimuli. As a result, there were no delay effects resulting from prolonged viewing of 'happiness' faces. This suggests that there are at least two subsystems involved in recognising expressions on upright faces and that each system has different temporal characteristics.

◆ **Cross-modal contextual effects on facial-expression judgment**

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Two experiments were conducted to investigate whether or not facial-expression judgment might be affected by concurrent, 'emotional' information presented in another, nonvisual modality.

Ambiguous facial expressions were generated by using pairs of facial expressions (eg an angry face and a sad face were averaged by a morphing technique) and were presented to subjects along with pieces of background music (experiment 1) or written sentences (experiment 2). In experiment 1, ambiguous facial expressions affected by contextual music were all judged to contain more of the emotion expressed in the music. In experiment 2 memories of ambiguous facial expressions were found to be generally distorted towards the direction opposite to the emotion expressed in the sentence. The latter finding is analogous to a 'relativity effect' (eg Russell and Fehr, 1987 *Journal of Experimental Psychology: General* **116** 223–237) that shows that when two facial expressions are judged in succession, the second facial expression is perceived to contain more of the emotion opposite to that of the first facial expression (eg a sad face is perceived sadder after seeing a happy face). Taken together, it seems that the discrepancy between the results of experiments 1 and 2 may not be due to the difference in the experimental tasks required of the subjects (ie perceptual vs memory) but to the difference in the modality characteristics (ie auditory vs visual) and/or the perceived location (ie the observer's vs expresser's) of the contextual emotion.

◆ **Gender, faces, and asymmetries**

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In a gender-categorisation task, Khurana and Prince (1997, ARVO) reported that the perceptual salience of male faces allows them to be processed more efficiently compared to female faces. It has also been shown that women are faster at gender perception (Khurana et al, 1998 *Cognitive Neuroscience Society Abstracts*). To further understand the basis of these differences in face processing we investigated the lateralisation of the perception of gender.

We presented unfamiliar faces bearing neutral expressions with either the left or the right half of the face (from the viewer's perspective) visible. Observers were instructed to categorise the gender of the face. Reaction times and error rates were recorded.

As in past studies, we found that both women and men were faster at categorising the gender of male faces on the basis of the left side. However, we failed to find this left-side-of-face advantage for female faces. While women showed no advantage for the left or the right half of the female face, men were in fact slower at categorising the gender of a female face given its left half. Male faces were categorised faster regardless of the half presented and women were faster on halves of both female and male faces.

Thus, lateralisation of perception of gender is a function of the gender of the face and the gender of the observer. Furthermore, even when presented half faces, women are more efficient than men at gender perception and male face 'marking' is operative.

◆ **Can perceived facial attractiveness be represented by a linear scale?**

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A Darwinian model relates attractiveness to reproductive fitness. If such a model is true, a linear scale of attractiveness is expected. Indeed, the experimental design of some previous studies of facial attractiveness presupposes such a linear scale. Here we examine that hypothesis. All 190 possible pairs of photographs of twenty young adult Japanese female faces were presented sequentially to subjects who were asked to select the more attractive face of each pair. A graph structure derived from the responses compactly displays attractiveness relationships (eg  $A > B$  means A is more attractive than B) as well as intransitivities ( $A > B$ ,  $B > C$ ,  $C > A$ ). We calculated an objective function to quantitate the number and degree of intransitivities. A purely linear graph has no loops and the intransitivity is zero. Pilot experiments showed significant nonlinearity in graphs and non-zero intransitivity. Studies with twenty four Japanese male and female paid subjects supported these findings. However, averaged responses of the subjects tended towards linearity and low intransitivity. Monte-Carlo simulations showed that response averaging alone does not yield a linear scale. In conclusion, while individual responses cannot be represented by a linear attractiveness scale, the population response does provide evidence for a linear, universal scale of facial attractiveness. We suggest that the nonlinearity in individual responses could be due to contextual effects.

◆ **Positional uncertainty of faces prevents size-scaling from equalising contrast sensitivity across eccentricities in a detection task**

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Size-scaling of visual stimuli has successfully equated peripheral performance with that of the fovea for many visual tasks. However, tasks dependent on accurate positional encoding (for example face recognition or phase discrimination) have been less successfully size-scaled. The residual deficit (ie lower contrast sensitivity following size-scaling) found in some studies has been associated with an increase in photoreceptor disorder leading to inaccuracies in positional information, and also changing proportions of X and Y cells, which have both been implicated in phase processing.

In a 2AFC detection task, a face and a blank field were presented at a range of retinal sizes (0.625 – 10 deg) and eccentricities (0 – 10 deg). In each exposure the face appeared in one of three poses (front on, or 45° to the left or right). RMS sensitivities found for a detection task (which can be successfully scaled with a single stimulus) showed a residual decrease in sensitivity with increasing eccentricity despite size scaling. Detection tasks with a single stimulus are evidently simpler because, as the image is the same each time, the visual system 'remembers' where to expect certain details. Use of three different poses removes this cue and thus makes detection harder. It appears from these results that peripheral performance suffers proportionately more than foveal from this increase in positional uncertainty. This could be because (a) the already disrupted positional encoding is more affected, or (b) the superior processing power of the fovea is more able to cope with positional uncertainty of a face.

◆ **Involvement of posterior temporal and frontal cortical zones in recognition of facial emotions**  
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The aim of the present study was to analyse the role of cortical zones in different stages of facial-emotion processing. Twenty two right-handed subjects were asked to identify the emotional expression of sad, neutral, or laughing faces presented for 80 ms on a computer screen and push the key under the right hand or to watch the same stimulus without its identification. The visual evoked potentials (VEPs) were recorded from occipital, parietal, central, frontal, and posterior temporal symmetrical zones. During passive watching, the peak latencies of VEPs in posterior temporal zones were found to be significantly shorter at negative expression than those at other facial stimuli. The same tendency was found for VEPs in occipital and parietal cortical zones. The performance of facial-emotion identification was shown to require the involvement of both posterior temporal and frontal cortical zones. Importantly, correct answers were characterised by close interhemispheric correlation of peak latencies of P150 wave in posterior temporal and N180 wave in frontal zones. The possibility of the primary pattern recognition in posterior temporal zones and the role of frontal zones in making the correct decision about the type of facial expression are discussed. [Supported by Russian Foundation for Basic Research and Russian Foundation for the Humanities.]

◆ **Exploring the interaction between face processing and attention**

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In recent years, a wide range of techniques has been employed to explore the ways in which humans visually process faces. However, to date surprisingly little work has been devoted to the relationship between face processing and attentional factors. We examined this issue by using a technique employed recently by Oliva and Schyns (1997 *Cognitive Psychology* 34 72–107). Stimuli were hybrids, consisting of one source of visual information presented at restricted spatial scales, superimposed with information from another image at other spatial scales. Oliva and Schyns demonstrated that the use of scales in scene categorisation was best considered as flexible and driven by the diagnosticity (ie usefulness for the task at hand) of the cues at the scales. We examined whether this was also the case when stimuli were the faces of celebrities. We found that attention could select facial information present at specific spatial scales even when meaningful information was present at other scales. Participants were unable to identify the face present at the unattended scale, though they were often aware that two faces appeared in the displays. This technique of using hybrid stimuli also allows us to explore the mechanisms that enable us to select information existing in restricted scales when competing information is present at other scales, and how different information (eg. face vs nonface) present at restricted spatial scales captures attention.

◆ **Identification of human heads from a variety of viewpoints**

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Psychological studies of the recognition of human heads suggest that recognition performances depend on the viewpoints (eg Harries et al, 1991 *Perception* **20** 669–680). Neurophysiological studies on the monkeys also found that different classes of cells in STS were activated by different views of the head and that most of the cells depended on viewer-centred descriptions (eg Perrett et al, 1991 *Experimental Brain Research* **86** 159–173). Our aim was to investigate the information used to recognise the human head at a variety of viewpoints. Subjects' task was to identify three familiar people from five different viewpoints. Stimuli were images of the heads viewed from 0° (frontal face) to 180° (back of the head) in steps of 45° and were pixelised at four levels of spatial frequency between 2.7 and 8.4 cycles deg<sup>-1</sup>. The mean response times depended on the viewpoints of the images. Observers identified significantly faster the heads viewed from 0°, 45°, and 90° than those viewed from 135°, and 180°. Moreover, the mean response times significantly increased with blurring of the images which were viewed from 0°, 45°, 135° and 180°, while there was no effect of blurring on the recognition of the images viewed from 90°. These results suggest that different view-specific information is used at different viewpoints for identification. Face recognition depends more on internal features of the face such as eyes, mouth, and nose. Also, the recognition of the back of the head depends more on internal features such as hair colour or hair quality. In contrast, profile recognition might depend just upon external features such as contour or shadow.

◆ **Spatial-frequency bandwidth of face recognition**

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The relative sensitivity of human-face recognition to different object spatial frequencies was estimated by using a noise masking technique. Signal-to-noise ratio thresholds were measured as a function of the centre spatial frequency of narrow-band additive spatial noise. The relative sensitivity function derived from these results peaked at 11 cycles per face width. At half-height the bandwidth was slightly less than two octaves. The band-pass nature of face recognition was confirmed by the results of two further experiments. Contrast energy thresholds were measured as a function of the centre spatial frequency of a narrow spatial-frequency band within which the Fourier phase information was destroyed by confounding the phase spectrum. With increasing object spatial frequency the energy thresholds first increased and then decreased. The largest increase was found at 8 cycles per face width. Further, contrast energy thresholds were measured as a function of the centre spatial frequency of band-pass-filtered facial images. As a function of object spatial frequency, energy thresholds first decreased and then increased. The lowest energy thresholds, which were found around 10 cycles per face width, were clearly lower than the energy threshold for unfiltered images. This is what one would expect if face recognition is narrow-band, since band-pass-filtered images of optimal spatial frequency do not contain redundant contrast energy at low and high spatial frequencies. In conclusion, the present results suggest that face recognition is tuned to a relatively narrow, less than two octaves, band of mid object spatial frequencies.

◆ **Factors for the asymmetry in similarity judgments**

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The asymmetry in similarity judgments is well known and has been investigated, although not fully.

Two experiments involving similarity judgments were conducted by using a pair of stimuli where the similarity distance between them was controlled. The similarity of the first presented stimulus to the second one was evaluated by subjects on a five-point scale. The same pair of stimuli was used twice by changing the presentation order. 'Familiarity' and 'information quantity' were the variables in the experiments. Each variable had two levels, ie face-like stimulus and non-face-like stimulus as the former variable, line-drawn parts and photographic parts of faces as the latter. The non-face-like stimulus had the same parts as the face-like stimulus but the configuration of the parts was different.

The statistical significance test revealed that the similarity judgment decreased with increase in the similarity distance. Between the face-like and non-face-like conditions, the mean values of similarity judgment were different under the photographic condition, but not under the line-drawn condition. An asymmetric similarity judgment was found under the photographic condition, but not under the line-drawn condition. The non-face-like stimulus had a stronger asymmetry than the

face-like stimulus under the photographic condition. Moreover, the factor of 'similarity distance' had no effect on the asymmetric similarity judgments.

These results imply that the factors 'familiarity' and 'information quantity' of stimuli influence the asymmetry in similarity judgments, but that the 'similarity distance' does not.

◆ **Facial topology mediates decoding of emotional expression**

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Facial muscle actions are meaningful components in decoding emotion expressions. We asked whether topological measures between facial features could mediate interpretation of expressions.

Photographs of facial displays of the six basic emotions (two of each plus two neutral expressions) were produced in accordance with FACS [Ekman and Friesen, 1978 *Facial Action Coding System Manual* (Palo Alto, CA: Consulting Psychologists Press)]. Each pattern was quantified by twelve measures between facial features in line with FACEM (Katsikitis and Pilowsky, 1991 *Journal of Nervous and Mental Disease* 179 683–688). Twenty subjects judged the dissimilarity of stimulus pairs. The averaged matrix was submitted to multidimensional scaling (MDS) which resulted in a 3-D solution: D1 characterised hedonistic tone, D2 personal agency (active vs reactive), and D3 intensity of expressed emotion. The MDS solution and FACEM measures were then submitted to multiple-regression analysis. Four measures were required to explain the spatial representation (mouth width, inner eyebrow separation, and top and lower lip elevations). D1 highly correlated with mouth width, suggesting a global distinction can be made between positive and negative emotions on the basis of this measure. D2 was significantly correlated with five measures between eyes, eyebrows, and mouth, suggesting the displayed action tendency is conveyed by their configural relationships. No correlations were found with D3.

The findings provide arguments consistent with the topology of facial features being responsible for read-out of emotion expression.

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◆ **Primate first? How expertise affects the ability to identify individuals within and across species**

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Face recognition is disproportionately impaired by stimulus inversion (Yin, 1969 *Journal of Experimental Psychology* 81 141–145) in adults. The configural relations between face features may be the aspect of the face that is sensitive to vertical orientation. Inversion effects can extend to other 'objects of expert identification' such as dogs, whose shape, when recognised by dog-experts (Diamond and Carey, 1986 *Journal of Experimental Psychology* 115 107–117), may be processed in this way. We compared upright-face and inverted-face recognition for human (HF), monkey (MF), and sheep faces (SF) in a group of primatologists, presumed to be expert at identifying individual monkeys and monkey species, and in a non-expert group. A forced-choice matching task was used. It was predicted that primatologists would show similar inversion effects for HF and MF, while for non-monkey-experts HF faces would show significantly greater inversion effects. However, this was not found. Instead, both HF and MF showed inversion effects when viewed by non-experts, while experts showed no inversion effect for MF and a greater inversion effect for HF than the non-experts. It appears that a general 'primate-template', sensitive to inversion may underly non-expert performance (Campbell et al. 1997 *Proceedings of the Royal Society of London* 264 1429–1434), while monkey-experts have differentiated templates for the different species. For the primatologists we tested, the 'monkey' template may not utilise orientation-specific configural information.

◆ **Developmental prosopagnosia: should it be taken at face value?**

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This study presents the third ever reported case of developmental prosopagnosia. This syndrome is defined as the inability to recognise familiar faces from birth, which, unlike its better known acquired equivalent, occurs in the absence of an established neurological disease. By employing magnetic resonance imaging to rule out overt brain damage, this study supplies the strongest evidence so far for a developmental form of this disorder. The subject was tested on basic visual perception, face perception, and face recognition. Neuropsychological investigations indicated that this case presents a 'pure' (ie specific to faces) manifestation of the syndrome. By designing

novel tests of face recognition and memory for unfamiliar faces, coping mechanisms employed by prosopagnosics, such as the often-reported reliance on external facial features, have been empirically demonstrated for the first time. Furthermore, an excessive reliance on feature-based (presumably left hemispheric) face processing strategies is revealed which, following from the widely held tenet that face recognition is most effectively achieved by right hemispheric configural processing, is considered to contribute to the face-recognition problems in some cases, and indeed in this case, of prosopagnosia.

◆ **Perceiving images reconstructed from face space**

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Current computational theories of face representation are based on principal-component analysis of digitised images. This method identifies dimensions of a face space (called eigenfaces) which explain different amounts of variance in the data. As a consequence, relatively low-dimensional face spaces suffice to reconstruct recognisable images. For technical applications and for modelling purposes the effect of reconstruction quality on human perception of the images is of interest.

A set of digitised portraits of male subjects was projected into a face space computed by principal-component analysis and reconstructed with different numbers of eigenfaces. These images vary in quality and 'closeness to the original' depending on the number of eigenfaces used in the reconstruction. In experiment 1 subjects had to decide whether two images (original and reconstruction) presented successively depicted the same or different persons. Errors and reaction times could be closely predicted by the amount of variance left unexplained at different levels of reconstruction. In experiment 2 a recognition task was used: subjects studied twenty (unaltered) faces and had to identify them later in a 2AFC task. The quality of reconstruction of the test stimuli was varied systematically. Again, errors and reaction times could be predicted by the amount of variance not explained at the level of reconstruction.

These results suggest that humans are sensitive to the information which is coded in eigenfaces. The appropriateness of the eigenface approach as a model of human-face perception is discussed. [Supported by DFG Zi 378/6-2.]

◆ **The relationship between visual information and affective meanings from facial expressions of emotion**

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Our previous studies (Yamada, 1993 *Applied Cognitive Psychology* 7 257–270; Yamada et al, 1993 *Japanese Psychological Research* 35 172–181) indicated that at least two kinds of structural variables of the face, which could be named as 'slantedness' and 'curvedness/openness', might be the physical variables or visual information for the recognition of emotion from the face.

The present study addresses the issue of how those physical variables are related with the dimensions of affective meanings, which have been found repeatedly in the traditional dimensional studies on the recognition of facial expressions of emotion. We run three experiments of a semantic differential ratings. The first experiment had six schematic faces of typical expressions judged by 20 participants on 52 bipolar scales. The second experiment had the same stimuli judged by 50 participants on 20 bipolar scales, which were selected from the previous set. The third experiment had the same six schematic faces and another fifteen schematic faces of intermediate expressions judged by 42 participants on the same 20 bipolar scales. Throughout these experiments, factor analysis on their ratings yielded the same two factors, interpreted as 'pleasantness' and 'activity', as past research. Furthermore the constellation of stimuli on factor space seemed very similar to the one on the space constructed with the physical variables mentioned above. The correlational analysis showed that each of the factor scores correlated independently and significantly with one of the scores of the two physical variables, such as 'pleasantness' with 'slantedness', and 'activity' with 'curvedness/openness'.

**THURSDAY and FRIDAY****POSTERS B****CROSS-MODAL INTERACTIONS**◆ **Facilitation of visual conjunctive search by auditory spatial information**

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Task-irrelevant auditory stimuli facilitate visual search within the central 15 deg of the visual field (Perrott et al, 1991 *Human Factors* 33 389–400).

We examined whether spatial coincidence of auditory and visual stimuli is necessary for such facilitation. Speakers were aligned with a central fixation point and a circular array of six potential target locations. The display, projected onto an acoustically transparent screen, consisted of a target accompanied by zero, one, three, or five non-targets. Target and non-target shapes were identical in appearance but possessed different combinations of features; eg a green horizontal target or a red vertical target could be presented with red horizontal and/or green vertical non-targets. All elements had a white dot on the left or right side and participants made a 2AFC response as to the location of this dot on the target.

The visual display was presented alone or accompanied by a 150 ms burst of white noise at the target location or at the fixation point; trials from these conditions were blocked (experiment 1) or interleaved (experiment 2). Stimuli were presented for 150 ms to preclude target-directed eye movements. In both experiments discrimination response time and errors were reduced when a task-uninformative sound was presented at the target location, but not when the sound was located centrally. These results indicated that sound source location was critical and the auditory spatial information may have guided attention to the target, engendering enhanced visual processing at this location.

◆ **Effect of auditory cues on visual attentional and non-attentional tasks**

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It is known that sensory cues in one modality affect perception in another. For instance, recent findings have shown strong audiovisual links in covert spatial attention. Using simple 'feature' and 'feature conjunction' discrimination tasks, we tried to establish whether audiovisual interactions occur only at an attentional level of processing or take place at lower levels.

In the first experiment, subjects had to report the orientation ( $0^\circ$ ,  $90^\circ$ ,  $180^\circ$ ,  $270^\circ$ ) of a T ('conjunction stimulus') centred among distractors (four Ts of different orientations). The display randomly appeared either on the left or the right side of a monitor ( $\pm 4.36$  deg eccentricity with respect to a central fixation point). The visual display was preceded (30 ms) by a sound (bandpass noise, 400 Hz, 75 dB) which was either spatially coincident with the target or at its contralateral location. The same audiovisual conditions were used in the second experiment. The target was a line segment ('feature stimulus') whose orientation ( $\pm 45^\circ$ ) had to be reported. The distractors were line segments each of which was randomly tilted at  $+45^\circ$  or  $-45^\circ$ . In both experiments the short presentation duration (150 ms) did not allow eye movements. In the 'conjunction' experiment (which is assumed to require focused attention to be achieved), an ipsilateral sound increased performance whereas a contralateral sound decreased performance with respect to the neutral condition. In the 'feature' experiment (which is assumed to be achieved without focused attention), the sound had no effect on performance. Although more data are required, these results suggest that audiovisual interactions take place only at an attentional stage of processing.

◆ **Signal detection analysis on cross-modal interaction of sub-threshold sound and bistable motion**

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Two circular discs moving steadily towards each other are innately ambiguous and can be perceived as either passing each other (streaming) or colliding and bouncing back. A loud sound added at the time of coincidence can significantly bias perception towards bouncing [R Sekuler, A B Sekuler, and R Lau, 1997 *Nature (London)* 285 308]. We manipulated the level of sound, and quantitatively analysed the audio-visual interaction in the framework of the signal-detection theory.

We provided a continuous background noise throughout the whole trial session. Trials with a signal (duration 62 ms) whose loudness varied randomly from  $-12$  dB to  $10$  dB above sensation level (SL) were interleaved with trials of no signals. The discs of  $0.3$  deg diameter moved at a speed of  $1.84$  deg  $s^{-1}$ . Observers had to report both the perception of motion and the detection of the sound signal. Five naive subjects participated.

We found objective effects of presence/absence of sound: the probability of bouncing was higher in misses (M) than in correct rejections (CR), and higher in hits (H) than in false alarms (FA). We also found subjective effects: the probability of bouncing was higher in H than in M, and in FA than in CR. By comparing the conditional probabilities of detection as a function of loudness with bouncing and passing judgments, we found that sound reporting increased when bouncing was observed, and decreased when streaming was observed. Cognitive inference could not account fully for the data for two reasons. First, minor temporal offsets (< 200 ms) from the exact timing of coincidence significantly decreased the probability of bouncing. Second, there is no difference in the conditional probability of sound reporting between the case of bouncing report and that of streaming report when there was no sound. Not only the objective presence of sound affects the solution of motion ambiguity, but the solution to visual ambiguity is also correlated with subjective sound detection.

◆ **Visual and haptic recognition of unfamiliar three-dimensional objects: effects of transfer**

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We investigated whether the representation of objects is modality-independent or modality-specific for visual and haptic memory. Recent studies have shown that the representation of verbal material is modality-independent (Easton, Srinivas, and Green, 1997 *Journal of Experimental Psychology: Learning, Memory, and Cognition* 23 153–163). Other studies have reported modality-specific representations for familiar objects (Easton, Green, and Srinivas, 1997 *Psychonomic Bulletin and Review* 4 403–410). However, we argue that verbal material may be coded in a lexicon which is shared by the visual and haptic systems and therefore the results are equivocal. Also, property differences between common objects may promote better recognition performance within modalities suggesting differences in strategy not representation.

In our experiments objects were constructed from six parts (Lego-1®, standard bricks) arranged randomly in stacks. All objects were made of the same material with the same overall size and aspect ratio. We used a recognition memory paradigm to test subjects' ability to recognise objects that were studied either haptically or visually. At test, the objects were presented either within or transferred across modalities. A cost of transfer was expected if vision and haptics did not share the same representation. In experiment 1, subjects studied each target object, visually or haptically, for 30 s. We found a cost in transfer on recognition performance. However, this cost was mainly due to the high number of correct responses within the visual modality. In experiment 2, the study time for haptic recognition was increased so that haptic performance was equivalent to visual performance. Again, we found a cost of transfer. We conclude that the visual system and the haptic system do not share the same representations.

◆ **Monotonic percepts from periodic stimuli—yet another analogy between vision and audition**

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Despite obvious differences between vision and audition, there are interesting analogies between the two modalities both in the early processing stages and at higher levels. An earlier analogue of Shepard's (1964 *Journal of the Acoustical Society of America* 36 2346–2353) auditory paradox in stereopsis (Papatomas and Julesz, 1989 *Perception* 18 589–594) is based on the proximity principle that obtains in both modalities. According to the proximity principle, the percept of an ambiguous stimulus, resulting from the presence of two competing values of an attribute, is biased toward the value that is more proximal to that of an unambiguous stimulus which is present in temporal or spatial proximity.

Shepard (1964) produced an ever-ascending sequence of tones from a periodically changing sequence, using the proximity principle in auditory frequency. In this report, a visual analogue is explored, with spatial frequencies in place of auditory frequencies. It works in two ways: (i) as a one-dimensional (1-D) motion stimulus, producing an ever-receding pattern, based on the proximity principle in spacetime; or (ii) as a 2-D stimulus, periodic in the vertical dimension, producing a seemingly aperiodic pattern, based on the proximity principle in 2-D space. It is argued that, even though there seems to be a one-to-one correspondence between the two cases in stimulus space, the visual and auditory paradoxes are nevertheless based on very different underlying principles: The former is based on proximity of zero-crossings on the retina; the latter is based on the mapping of frequency onto locations along the basilar membrane.

◆ **The effect of different sounds on visual apparent movement**

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According to Werner's hypothesis (Zietz and Werner, 1928 *Zeitschrift für Psychologie* 105 226–249), the phenomenal concomitance of two dynamic events (visual and auditory) gives rise to an intermodal unitary event. Zietz and Werner showed that a hardly noticeable apparent movement of a visual stimulus became more evident when a sound event was presented simultaneously. Other authors, for example Staal and Donderi (1983 *American Journal of Psychology* 1 95–105), did not always obtain the same results.

The purpose of the present work was to investigate the effect of different sounds on a visual bistable event: two different apparent movements can be seen inside a black frame: a 'phi' movement, ie a small square moving from left to the right, or a 'gamma' polarised movement, ie an expansion of the small square toward the centre of the frame from both sides in succession. I used (i) continuous, (ii) increasing and (iii) decreasing in frequency sounds, and (iv) two short sounds in succession. 'Gamma' polarised movement was seen only in the latter condition. On the other hand, the degree of visibility of the 'phi' movement increased by adding sound with dynamic qualities (increasing and decreasing in frequency).

These results are in accord with Werner's hypothesis; a greater probability of one perceptual solution compared to the other was observed when the auditory and the visual events were phenomenally congruent.

◆ **Audiovisual tunnel effect**

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Recent researches demonstrate how auditory information can influence visual perception of events, for example how a simple sound affects visual event discriminations [Gerbino, 1997, in *Human and Machine Perception* Eds Cantoni et al (New York: Plenum Press) pp 147–154].

Here we present a case of a tunnel effect accompanied by a sound. We used the same values—length of trajectory for the moving object and length and width for the tunnel—as in Burke (1952 *Quarterly Journal of Experimental Psychology* 4 121–138) but we added a sound (220 Hz) accompanying the visual movement and a different speed— $25 \text{ mm s}^{-1}$ . The aim of our experiment was to demonstrate that a particular sound can influence the perceptual duration of the entrance–exit interval (EEI)—the duration for which the object is totally hidden by the screen. For this purpose we used five different between-subjects conditions: (i) a continuous sound (220 Hz) during the whole event; (ii) no sound under the tunnel; (iii) sound shifting up in frequency under the tunnel; (iv) sound shifting down in frequency under the tunnel; (v) no sound throughout.

Results show the longest EEI for condition (iii), indicating that a particular kind of sound can influence the movement, although this is not a simple interference effect: EEI in (iv) is shorter than in (v). EEI is significantly shorter in condition (ii) than in conditions (i) and (v): this suggests that the absence of sound during EEI speeds up the amodal visual movement.

**EYE MOVEMENTS AND MECHANISMS; WAYFINDING; PROPRIOCEPTION**

◆ **Programming of saccadic eye movement direction and amplitude**

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We studied how amplitude and direction of saccadic eye movement are programmed, by a novel method in which the information about amplitude and direction of the required movement became available at different time moments. Observers were instructed to move their eyes as fast as possible to one of four equally probable new locations in two possible directions (left and right) at two different distances (4.6 and 9.2 deg of visual angle) from the initial fixation point. Instructions specifying the required saccadic movement were presented immediately under the central fixation point in the form of an arrow pointing to the left or right, and a numeral, 1 or 2, denoting the amplitude of the designated saccadic movement. Both instructions, the arrow and the numeral, were presented on the display screen simultaneously or in succession with 42, 85, 128, and 399 ms intervals between them. Eye movements were recorded by a contact-wire-free electromagnetic recording method (Allik, Rauk, and Luuk, 1981 *Perception* 10 39–51) warranting about 1 min of arc precision and 1 ms time resolution. The saccadic reaction time (SRT) was measured from the onset of the second of any two instructions, that is the final event completely eliminated uncertainty about parameters of the forthcoming movement.

The results suggest that (i) a considerable fraction of SRT embodies premotor processing of parameters of the forthcoming saccade; (ii) the direction and amplitude are two parameters which can be programmed separately and independently from each other; (iii) the programming of direction is about twice more time-consuming than the programming of the saccade amplitude.

◆ **Cyclovergence with isoluminant stimuli**

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We studied the effects of isoluminant stimuli on the cyclovergence mechanism. Some previous studies report that stereo depth perception is compromised at isoluminance. Other studies report that rotation disparities affect ocular torsion, which affects perceived inclination of stereo images. We measured the effects of presentation duration and luminance contrast, across the isoluminance point, of a red, zero-disparity pattern (R0) against a dim green background, on the perceived inclination of a superimposed high-luminance-contrast, green, 4° rotation-disparity pattern (G4). Each stereo image included two arrays (R0 and G4) of randomly distributed texture elements (crosses, squares, etc) subtending 53 deg height × 43 deg width visual angle, which yielded two depth planes. The luminance of the red, R0-plane was randomly varied. Presentation duration varied between 2 s and 12 s and the perceived inclination of the G4 pattern was measured. At 2-s duration, the inclination function was almost level at about 16°, across all red luminance levels. At 7-s duration, a gradual change in inclination indicated a decreasing effect of R0 as it approached isoluminance, with a sharp compromise directly at the isoluminance point. At 12-s duration, the area of gradual inclination-change widened and also deepened to near the maximum level at 7 s. Isoluminance clearly affected relative inclination of R0 and G4, from which we infer reduced stimulation to the cyclovergence system. The widening and deepening of the para-isoluminance area indicate a strong temporal integration component to isoluminant stimulus effects in the visual system. Apparently, the magnocellular channel is dominant in cyclovergence control.

◆ **Saccades to peripheral targets on a bright background with steady and intermittent illumination**

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We investigated the effect of several intermittent light stimuli on saccadic control. Fifteen subjects followed a red laser point of light that induced a series of saccades from central fixation to eccentric positions at 1, 2, 3, 4, or 5 deg (right or left) and back to central fixation. During one run, each of the ten eccentric targets were presented eight times (for 500 ms) in random order, separated by presentations of the central fixation point (1000 ms). These stimuli were presented at 63 cm viewing distance on a circular milk-glass screen (18 cm diameter), that was back-illuminated ( $50 \text{ cd m}^{-2}$ ) by fluorescent lamps operated to produce either intermittent light at repetition rates of 50, 75, 100, and 125 Hz (with light pulses of about 4 ms duration), or steady light as a reference condition of natural viewing. Separate runs were made for each lighting condition. While saccade latency and duration were unaffected, the mean saccade amplitude was about 9% larger ( $p = 0.01$ ) at 50 Hz than in the other conditions which did not differ significantly between them (including steady light and repetition rates of 75, 100, and 125 Hz). Since we included the control condition with steady light, we conclude that saccades were most adversely affected by repetition rates around 50 Hz, which induced visible flicker in all subjects. The eccentricity condition was also significant ( $p < 0.001$ ), the saccade overshoot increased with the area of intermittent illumination that was crossed by the saccade. A posteriori analyses on the number of light pulses occurring during the saccade showed no evidence that saccadic control was modulated by intra-saccadic visual stimuli. However, a clustering analysis on subjects showed very different pattern of saccades as function of individual sensitivity to intermittent lights. These individual oculomotor differences are discussed according to reading models on VDU.

◆ **Perception of locomotor paths during virtual displacements**

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Previous research with simulated pursuit-fixation displays shows that we use the vector field resulting from observer's movement to achieve considerable accuracy in way-finding (Cutting,

1995 *Psychological Review* **102** 627–651). Using the same kind of computer-generated cluttered environments we investigated how children and adults represent locomotor paths perceived during virtual displacements. Stimulus trials simulated locomotion across a tree-filled plane while the subject looked at a particular tree. We varied the angle between the line of gaze (directed towards a fixation point) and the simulated direction of movement (GMA) between 0° and 20°. Subjects were divided into four groups including 6–10-year-old children and adults.

Results show that as GMA increases, so does the systematic shift in the drawn paths. We found also a direct relationship between the perceived end position of the path and the line of gaze. The convergence of the drawn trajectories towards the fixed trees suggests that subjects may have some difficulties in decomposing the vector field into its translational and rotational components. Moreover, this effect tends to increase with age. A possible explanation of these facts is that with age we may have the tendency to assimilate the direction in which we move to the looking point. In conclusion, the relation between GMA and the reproduced paths, even if discrepant with the true paths, is coherent enough to provide evidence of the kind of spatial reference systems used by children and adults.

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◆ **Emmert's law in the dark: differential effects on body parts and objects**

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Retinal afterimages are normally scaled in size proportionally to the distance of the surface they are projected upon. It has been known for some time that nonretinal information such as oculomotor cues or the incorporation of parts of the body in the afterimage can produce quantitative and qualitative effects on the afterimage when it is viewed in the dark. In the present study, positive afterimages of observers' hands were used as targets, as well as objects held by that hand, to investigate the effects of moving the hand to and fro along the line of sight for different distances in the dark on size-constancy scaling. The most intriguing result consists of the finding that moving the hand, while resulting in changes of size—here due to proprioceptive cues—has a limit to the decrease in hand size that falls short of predicted changes. When observers focus on a held object, however, the decrease in size predicted by Emmert's law occurs. It appears that the visual system 'refuses' to size scale the hand below a limit it accepts as representative or acceptable of 'its' hand. The implications of these results are discussed in the context of the amodal nature of space perception and the role of the observer's body image in the construction of space.

◆ **Locomotor pointing with different rate of optical expansion pattern**

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An observer walking towards an obstacle needs to modulate his/her pace to control efficiently an upcoming contact. So far, the role of visual information in this task is derived only from indirect evidence (studies of perceptual judgments). The aim of the present study was to determine to what extent active braking behaviour depends on the change in the optical expansion rate of texture surrounding the target (local visual information). We used a device that allowed us dynamically to link texture size to unconstrained linear displacement of subjects (walking). Subjects walked toward a target (two luminous diodes that were switched off at the initiation of locomotion) and were instructed to stop when they believed they were at the target position. We varied the dynamic size of texture elements (circular patterns) surrounding the target, and measured subjects' braking behaviour. The results showed a linear relationship between braking behaviour and increases in texture expansion rate. The distance walked decreased proportionally to increases in texture expansion rate. In addition, we found that the time-to-contact values were constant across expansion-rate conditions. We conclude that braking before an obstacle is linked to the subject's ability to use the optical expansion of the surrounding texture, with adoption of a tau-constant strategy probably used to initiate braking.

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◆ **Quantitative analysis of similarity of dynamic scanpaths**

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An eye-movement sequence, or scanpath, during viewing of a stationary stimulus has been described as a set of fixations onto regions of interest, ROIs, and the saccades or transitions

between them. Such scanpaths have high similarity for the same subject and stimulus both in the spatial loci of the ROIs and their sequence; scanpaths also take place during recollection of a previously viewed stimulus, suggesting that they play some role in visual memory and recall (Brandt et al, 1989 *Proceedings of the Annual International Conference of the IEEE EMBS* pp 278–279). In a dynamic scenario the features corresponding to ROIs change their absolute and relative positions in time.

We introduce a concept of dynamic scanpath, which utilises feature-based ROIs, so that a smooth-pursuit tracking can be treated as equivalent to a fixation. Quantitative comparisons with string analysis are thus applicable to the dynamic as well as static scanpaths. We compared dynamic scanpaths for three subjects (four trials per subject) on six stimuli, lasting 10 s each. The same three-dimensional road scene was presented with three different-viewpoint motions (stationary, panning, and zooming) and two world models—with and without the cognitive structure. In the later case, road and grass are replaced by a uniform background and cars by spherical blobs, so that the sequence loses its resemblance to a road scene. We found significant correlation in viewing different dynamic versions of the same scene by the same subject in both the abstracted and the non-abstracted scenes. For different subjects there is correlation in viewing the same dynamic version of the road scene, while for the abstracted version there is none. The repetitive correlation (same-subject/same-view) was the highest in all cases in accordance with the scanpath theory.

◆ **A model for perceived speed of self-motion after treadmill walking**

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Several authors, including Reiser et al, and Pelah and Barlow have shown that the sense of perceived speed of self motion adapts after a mismatch between motor activity and its optical consequences. In Pelah and Barlow's experiment, subjects ran on a treadmill for 20 min and then were asked to walk at a constant visual speed. Initially subjects walked about 25% too fast and after several minutes walked at the specified speed. Though the task was different, Reiser et al reported similar results.

I captured the adaptation of speed of self-motion after treadmill walking in a dynamic system. The dynamic variable is goal velocity, ie the target speed of the locomotor system. Goal velocity is subject to a first-order dynamics (leaky integrator) since a simple relaxation is enough to capture the data. To model Pelah and Barlow's finding I assume that the goal dynamics has an attractor at the specified velocity. The goal dynamics is coupled additively to the expansion rate of the visual surround corrected for the optical consequences of locomotion. Since during normal locomotion this correction is adequate, the goal dynamics relaxes to the specified velocity. During treadmill walking, the expansion rate is zero and thus the 'correction' remains, effectively changing the specified velocity. Since the correction is based on an estimate of where the visual surround is, a prediction of the model is that the size of the aftereffect changes with visual distance but that the time course does not.

◆ **The perception of absolute speed during self-motion**

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Perceived velocity and smooth-pursuit eye movements for drifting gratings were shown to involve different combinations of signals (Gegenfurtner and Hawken, 1995, ARVO). We considered whether the estimation of absolute speeds of optic flow might also be different for a speed-matching task done by walking compared with a perceptual rating task. In the motor task, subjects were required to walk on a non-motorised, manually driven treadmill at their chosen pace while being presented with optic flow in the form of bright rectangles expanding against a dark background. In each trial an optic flow pattern was displayed for 10 s on a large rear-projected screen, and subjects were asked to adjust their walking speed to match the optic flow. Thirteen levels of optic flow ranging from 1 to 7 km h<sup>-1</sup> were tested. In the rating task, standing subjects were required to make verbal judgments of speed (in km h<sup>-1</sup>) for the same optic flow presentations. We ran a third condition in which subjects rated as well as matched the flow by walking in each trial. The results for all subjects and conditions showed walking and rating speeds linearly related to the speed of the optic flow ( $R^2 \geq 0.91$ ). However, the slopes of the regression lines were consistently lower for matched walking compared with the rating condition. Results from the third condition showed no direct effect of walking on the rating task. We conclude that visual velocity while walking relies on different mechanisms than those used for speed judgments based on visual signals alone.

◆ **Layout perception when moving in virtual scenes**

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Our purpose is to show how the modification of visual information available to moving observers can change the perception of the environments they pass through. Subjects were presented with short motion sequences showing a fixed line of three simplified trees (FT) and two additional trees (AT) with nearby variable locations. The path of the camera was parallel to FT, but the axis of view was constantly oriented toward the middle tree of FT. Subjects were young children aged from 6 to 10 years and adults. In this experiment we used inward projective displacement (ID) of some objects (moving towards the fovea), as opposed to centrifugal flow patterns. After each trial, participants drew the position of a particular tree on a schematic map of the environment. Both children and adults show a similar and important error in the accuracy of depth representation for objects in the visual field when ID is present. Therefore, opposite motions in the same region of the visual field (as encountered with ID patterns), may modify significantly the information used to integrate spatial relationships in the environment. The perceived positions of AT with the other flow patterns show notable and systematic errors displacing them proportionally farther away from FT. However, from a developmental point of view, localisation errors decrease globally with age. In conclusion, the relation between the optical displacements and the reproduced positions suggests that the perceived positions in the real world are based on a different maplike representation in children and adults.

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◆ **Size-contrast illusions deceive grasping as well as perception**

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Size-contrast illusions are assumed to exert a smaller effect on human motor behaviour than on perception, indicating different cortical pathways for perception and action (eg Aglioti, DeSouze, and Goodale, 1995 *Current Biology* 5 679-685). We tried to replicate these findings for the Ebbinghaus illusion. Special effort was taken to minimise the effects of motor learning and to assess the size of the perceptual illusion.

An aluminium disc (28, 31, 34, or 37 mm in diameter; 5 mm in height) was positioned as target on a board. Around the target were drawn either small or large context discs (10 or 58 mm in diameter). Close to the board a monitor was mounted on which a comparison disc was displayed. In a visual task, twelve subjects adjusted the size of the comparison disc to match the size of the target. In a grasping task, subjects grasped the target. Subjects wore shutter glasses and could not see their hand during grasping (open-loop condition). The grasp trajectory was recorded and the maximum pre-shape aperture was calculated.

Pre-shape aperture and adjusted size showed strong and similar linear relationships to the size of the target. The mean perceptual effect of the illusion was 1.4 mm (SE = 0.1 mm) while the effect of the illusion on pre-shape aperture was 1.5 mm (SE = 0.4 mm). Thus, grasping was just as much influenced by the illusion as perception. Possible reasons for this discrepancy with respect to previous studies are discussed.

◆ **The perception of simulated trajectories by drivers and passengers**

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An observer moving through a cluttered environment needs an accurate estimation of the direction of his trajectory in order to avoid obstacles. We simulated observer's displacements with a camera motion through a small group of simplified winter trees. This scenery was generated by a Silicon Graphics Workstation while the subjects kept their gaze fixated on a central tree. The participants had either to drive the camera (drivers) or to watch to the scenery available during a pre-established trajectory (passengers). Their accuracy was measured with two different psychophysical methods. An adjustment technique was used for drivers and a constant-stimuli technique for passengers. Our assumption is that the direction of a divergent trajectory set (DS) is easier than that of a convergent one (CS). However, the results do not show any differences between the results collected with the constant-stimuli method, and no differences appeared also between DS and CS. In conclusion, the adjustment method, because of its ease of use, could efficiently replace the

constant-stimuli method in way-finding tasks, and the gaze-movement angle (GMA) is confirmed to be a good means of studying way-finding, whereas the distance of the fixated point does not need to be considered.

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◆ **Estimating time-to-contact from retinal flow: the roles of changing position and changing size of texture elements**

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Human judgments of time-to-contact (TTC) are based on the expansion of the image that accompanies movements about the world. Such an expansion has two potentially useful components: individual texture elements change their relative position while simultaneously changing in size. Conventional random-dot kinematograms, in which individual dots typically remain fixed in size, demonstrate that the changing-position cue alone is sufficient for judgments of TTC.

In the present study we systematically investigated the effects of both cues by varying them independently using computer-generated displays. We found that, under appropriate conditions, the changing-size cue alone is also sufficient for judgments of TTC. However, when the two cues are placed in conflict, judgments are based almost entirely on the changing-position cue and the changing-size cue is largely ignored. These results indicate that TTC judgments are dominated by the smooth changes in the relationships between elements, rather than by smooth transformations of the elements themselves.

◆ **Spatial control of saccadic eye movements: Stimulus-driven and expectancy-driven processes**

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In a series of experiments we attempted to separate the perceptual effect of stimulus properties from the cognitive effect of expectancy and instruction on visual attention. The visual display (EIZO Flex Scan F7801 monitor driven by a CRS visual stimulus generator) comprised 8 circular stimuli with a diameter of 5.2 deg, arranged in equal distance of 7.7 deg from fixation. The 8 stimuli consisted of gray-level images of natural objects and were created by a  $2 \times 2 \times 2$  factorial combination of spatial-frequency content (low-pass filtering,  $>2.5$  cycles  $\text{deg}^{-1}$  vs high-pass filtering,  $<2.5$  cycles  $\text{deg}^{-1}$ ), contrast (high vs low), and brightness (bright vs dark), randomising their positions.

On each trial, first a target was presented for either 500, 1000, or 2000 ms, followed by the 8-stimulus display which was presented for 1500 ms. On half of the trials the target was present among the 8 stimuli. The task of the observer was to decide whether the target had been present or not. The saccadic responses on the 8-stimulus display were recorded by a Double Purkinje Image eye tracker. Stimulus-driven processing was assessed by the relative preference of salient stimulus properties independent of the target. Expectancy-driven processing was assumed to occur if in the target-present condition the first saccade was aimed towards that stimulus which matched the target.

Significant stimulus effects were found for spatial frequency and for contrast; but no evidence for expectancy-driven processing could be found, even under the condition of long target presentation. Apparently, it is impossible for the observers, within a time span of up to 2000 ms, to prepare a saccade towards a specific target among 8 distractors.

◆ **Time-to-contact and heading direction from sparse non-evolving optic flow: data and models**

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Previous work has established that human estimates of time-to-contact (TTC) and heading direction remain accurate with very sparse random-dot flow patterns, suggesting that the processes underpinning these tasks require only a few, discrete flow points. However, conventional displays provide additional information in the way that the flow evolves over time. Here I demonstrate that performance with sparse flow patterns remains remarkably good even when the additional temporal information is eliminated from the stimulus.

Human performance under these conditions is also compared with that of two computer models. The first, which has been previously described, decomposes the flow into translational and rotational components using directional templates with 'receptive fields' similar to those found in area MST. The second model is a simple variant of Bruss and Horn's general approach,

requiring flow at only 3 discrete points rather than 6. Like human observers, both models function well with stimuli that contain only a few points and that do not evolve over time.

◆ **Mislocalisation of stimuli flashed near the time of a saccade of different amplitude**

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When a brief visual target is flashed near the time of a saccade, it is perceived at a position different from its real position. From the time course of mislocalisation, this phenomenon has been usually interpreted as showing that target position is calculated by adding the retinal image position and eye position, but that the velocity of the eye is underestimated (Honda, 1993 *Vision Research* 33 709–716). Though it is unknown why eye velocity is underestimated, it is possibly because the eye position signal is passed through a low-pass filter before the addition process. If this explanation is correct, the amount of mislocalisation should increase approximately in proportion to the amplitude of the saccade. To examine this prediction, I measured the amount of mislocalisation when subjects made saccades of 4 deg and 8 deg amplitude. A brief (8 ms) visual target was flashed in the dark at a random time near the time of saccades, and subjects were required to respond to the target location. The result was contrary to the prediction. The difference in the magnitude of mislocalisation between the two conditions was small, and there was no consistent trend for larger saccades to cause larger mislocalisation. This result tells us that the process of calculating target position is not a simple addition of retinal-image-position and filtered-eye-position signals. Other cues, such as an exocentric cue must also be involved in this process.

◆ **A method for rehabilitation of eye movements**

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Various kinds of neurological and endocrinological disorders can cause disturbances in eye movements. Oculomotor anomalies related to head trauma and thyroid optic neuropathy were examined and rectified by means of transcutaneous electrostimulation (TES). Correlations were determined between eye-motility disorders before and after TES. In thirty-two persons with oculomotor disorders caused by head trauma there were signs of brain injury, increased intracranial pressure, or fracture of the skull. Ten persons with thyroid optic neuropathy showed eye-movement disorders as a result of infiltration and swelling in or near the extraocular muscles. A total of forty-two persons with oculomotor impairment were tested by determining thresholds for the onset of electrically induced visual phosphenes. Thresholds of stimulation were selected individually. The amplitude of current was 50–200  $\mu$ A. After 10–20 applications of TES, eye-motility functions showed improvement both in cases of disorders caused by head trauma (70.2% of cases) and those caused by thyroid optic neuropathy (70% of cases). The results suggest that TES can improve eye motility in persons suffering from thyroid optic neuropathy and head trauma.

◆ **Stimulus factors in the preparation of visually guided saccades**

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The purpose of these experiments was to investigate to what extent stimulus factors, ie spatial-frequency filtering (low-pass,  $<2.5$  cycles  $\text{deg}^{-1}$ , versus high-pass,  $>2.5$  cycles  $\text{deg}^{-1}$ ), contrast (low versus high), and the content of the images (human faces versus buildings) elicit saccadic eye movements. A set of eight stimuli in the size of 5.2 deg of visual angle was created by a  $2 \times 2 \times 2$  factorial combination of the three stimulus variables, and presented in a circular arrangement around the fixation cross for 1500 ms. On each trial, first a target was presented for 500 ms. On half of the trials, the target was identical with one of the eight stimuli. The task of the observer was to decide whether the target was present in the stimulus set. Eye movements were recorded during the presentation of the eight-stimulus display with a Double Purkinje Image Eye Tracker. The first saccade was aimed significantly towards the content of the stimulus. Additionally, however, in the data we found consistent effects of the high-pass filtering and the high-contrast stimuli. Evidence for expectancy-driven processing is reported in this experiment: in the target-present condition the relative preference of the stimulus matching the target was significantly higher. When attempting to describe the total patterns of these eye movements (1st, 2nd, etc) individual's fixation strategies seem to be aimed at covering all necessary information.

◆ **Stationary distractors and the gap effect on smooth pursuit**

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Smooth pursuit (SP) is classically regarded as a visuomotor reflex in which the eyes track a target with eye velocity matching target velocity. However, SP is modified by nonvisual factors and SP latency is reduced in gap trials (Knox, 1998 *Neuroreport* 9 809–812). Normally, after the gap only one (moving) target appears. The effect of adding a stationary distractor has now been investigated.

All tasks were performed monocularly. A fixation target, presented for a variable period (0.5–1.5 s) in the middle of the display, was replaced by the pursuit target (speed: 14 deg s<sup>-1</sup>) which moved from 5 deg to the left/right of fixation, through the centre of the display, continuing laterally until disappearing off the edge. In sets of four interleaved tasks (always two leftward, two rightward) one task had no gap, the other three had gaps of 100, 200, or 400 ms. In 50% of trials a stationary distractor appeared in the mirror image position to and simultaneously with the moving target. Subjects were instructed to track the moving target. Eye position was recorded with infrared oculography. SP latency was measured off-line from velocity traces for each trial in which pursuit was preceded by a period of steady fixation.

The distractor increased SP latency in both gap and non-gap trials. However, the effect was particularly marked, at least in some subjects, at longer gap durations. These results provide further evidence that the 'visuomotor reflex' view of SP is inadequate, and suggest an important role for other factors, such as attention, in SP initiation.

◆ **Compensatory eye movements induced by active and passive head movement modify motion perception**

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Estimating the velocity of moving objects is important for orientation in a dynamic visual world. An object moving at constant speed produces different perceptions of velocity dependent on the state of eye movement (fixation or smooth pursuit). Koga and Groner (1990, in *From Eye to Mind* pp 59–68) studied the modulating effects of pursuit eye movement on the perception of motion. The present experiment is an attempt to compare the modifying effects of motion perception under both active and passive head-movement conditions. When a moving target is shown on a head-mounted display to an observer who is instructed to move the head laterally in the same direction, an unstable (nonveridical) target movement is reported. Active head movement produces compensatory eye movements (=VOR). When the slow phase of compensatory eye movement is synchronised with the motion of the target, the perceived velocity of the target becomes slower (Koga and Groner, 1997, paper presented at the 9th European Conference on Eye Movements). Passive head rotation was introduced by horizontal/vertical rotation of a chair to eliminate afferent signals from the neck muscles. The same results were observed as in the active head-rotation condition. This means that the compensatory eye movements driven by both active and passive head movements modify the target-motion perception directly. These findings indicate that the retinal displacement of the target during body rotation leads to the impression of an unstable external world.

◆ **Spatial localisation during smooth-pursuit eye movements**

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It is well known that, when a moving target is tracked in the dark by pursuit eye movements, the target's trajectory is judged to be shorter than the actual trajectory. This misjudgment seems to indicate that visual space is distorted during pursuits. Here, we measured the perceptual location of probe stimuli presented briefly when a moving target is tracked by pursuit eye movements.

The target moved 20 deg from the left position toward the right position at a velocity of 18 deg s<sup>-1</sup> in a black background of 0.13 cd m<sup>-2</sup>. A stationary probe was presented for 15 ms in the vicinity of the target or at the same position as the target when the target was moving. The observer tracked the moving target with pursuit eye movements. The observer's task was to localise the apparent position of the probe after the target reached the final target position. Our results show that the probe stimuli presented on the right side of the target at the beginning of pursuits

are mislocalised in the same direction as pursuit, but that the probe stimuli presented in the same position as the target are localised approximately at the actual position. We also found that the probe stimuli presented during pursuits were mislocalised in the vertical direction and converged slightly on the viewing point. These results suggest that the visual space is extended in the same direction as pursuit at the beginning of pursuit and is compressed in the vertical direction during pursuit.

◆ **Illusory motion in the direction opposite to smooth pursuit in an unadapted static region after adaptation to dynamic random noise**

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We previously reported that when dynamic random noise (DRN) is replaced by static random noise (SRN) after a period of adaptation, SRN in an adjacent unadapted region appears to 'jitter' coherently in random directions for some time. This illusion led us to propose a model of visual compensation of retinal slip (1998, ARVO). Here we report what happens when smooth pursuit is made during the test. During adaptation, SRN was presented in a circular patch, 6.7 deg in diameter, surrounded by a 13.3 deg outer-diameter annulus of DRN. A fixation spot was provided at the centre. SRN was presented in both regions at test, during which the central spot moved horizontally with a sinusoidal velocity profile. Tracking the spot, the subject reported in which direction the unadapted central region appeared to move with respect to the surround. The major finding is that the central region always appeared to move smoothly in the direction opposite to the spot, while the adapted surround appeared to be stationary. We suggest that the attenuated motion responses in the adapted region give this area the lowest motion field so that it is taken as the baseline and subtracted from the rest of the motions in the visual field. This retinally based compensation for eye movements accommodates a wide range of data, and indicates that our model applies not only to small fixational eye movements, but also to smooth pursuit.

◆ **Gravitational influence on representational momentum**

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The memory for the final position of a moving stimulus is shifted forward in the direction of its motion. This forward shift is termed representational momentum (RM). Hubbard and Bharucha (1988 *Perception & Psychophysics* 44 211–221) reported that when an observer sat in an upright position, physically downward motion of a stimulus along the gravitational axis produced larger RM than did physically upward motion of a stimulus (downward effect). However, there was a possibility that egocentrically downward motion of a stimulus along the head/body axis produced larger RM than did egocentrically upward motion of a stimulus, because, in the upright position, a stimulus moved along both the gravitational and the head/body axes.

We examined whether downward effect in RM occurred along the gravitational axis or the head/body axis. Participants, in both upright and prone positions, were asked to judge whether the final positions of moving stimuli were the same as the positions of stationary probes presented subsequently. In experiment 1, a stimulus moved egocentrically upward and downward in both positions. Downward effect was observed only in the upright position. In experiment 2, approaching and receding motions of a stimulus along the line of sight were used in both positions. Downward effect was obtained only in the prone position. Thus, downward effect occurred along the gravitational axis. These results imply that the gravitational attraction affected RM and that the representational system could utilise the information about the direction of gravity even when observers were not in the upright position.

◆ **A comparison of the gap effect on saccade and pursuit latencies in dyslexic and nondyslexic subjects**

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Saccade latency is modified differently in dyslexic subjects compared to normals in gap saccade tasks. It is now known that smooth-pursuit latency is altered in gap tasks. We have compared the gap effect on pursuit latency in dyslexic and nondyslexic subjects.

Subjects viewed a visual display at 57 cm with their left eye. Sets of four saccadic or pursuit tasks were interleaved in runs of 52 or 96 trials. In saccade runs, normal (gap: 0 ms) and gap (200 ms) trials to left and right were presented pseudorandomly. In pursuit runs, the target stepped 5 deg either to the left or right of a fixation target and then moved at 14 deg s<sup>-1</sup> back

through the centre of the display (gaps: 0, 100, 200, 400 ms). Left-eye position was recorded by infrared oculography, digitised and stored on disc for analysis. Eye-movement latencies were measured off-line from velocity traces. Two dyslexic subjects exhibited a gap effect for saccades in one direction only. In one dyslexic subject, pursuit latency was significantly longer than in normals for both leftward and rightward pursuit, and the gap effect was absent for rightward pursuit. In others, the absolute latency values for pursuit and the gap effect on pursuit latency were similar to those in normals.

These results suggest that the alteration in gap effect for saccades that is present in a subset of dyslexic subjects may also extend to other classes of eye movement, in particular smooth pursuit.

◆ **Contrast modification of smooth-pursuit latency**

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It has recently been confirmed that smooth-pursuit (SP) eye-movement latency is reduced in gap pursuit tasks (Knox, 1998 *Neuroreport* 9 809–812). Usually high-contrast targets are used in these experiments. We wished to investigate whether low-contrast targets would alter either SP latency or modify the gap effect on SP latency.

All tasks were performed monocularly. A fixation target (a dark square, 0.3 deg), presented for a variable period (0.5–1.5 s) in the middle of the display, was replaced by the pursuit target (also a dark square, 0.3 deg; speed: 14 deg s<sup>-1</sup>) which moved from 5 deg to the left or right of fixation, through the middle of the display, continuing laterally until it disappeared. In sets of four interleaved tasks (always two leftward and two rightward) one task had no gap, the other three had gaps of 100, 200, or 400 ms. Each set of tasks consisted of either high-contrast (92%) or low-contrast targets (25%, still well above threshold). Subjects were instructed to track the moving target. Eye position was recorded by infrared oculography, digitised and stored on disc. SP latency was measured off-line from velocity traces for each trial in which pursuit was preceded by a period of steady fixation.

SP latency was clearly reduced in low-contrast (25%) tasks by, on average, 36 ms from the high-contrast value for all subjects in all tasks. There was little consistent difference in the gap effect between low-contrast and high-contrast conditions. Thus the visual parameters of a task appear to have little influence on the gap effect.

◆ **Some relations between eye fixation points and landscape preferences**

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Elements in a landscape upon which subjects fix their eyes have been investigated. Ten undergraduate students participated in a task that required them to decide which of two different landscapes they preferred.

Stimuli consisted of pairs of photographed natural scenery mounted on slides. Eye trajectories and fixation points were recorded with an NAC EMR 600 while each subject looked at the slides. Preference for the left or right landscape was recorded manually. Results show that there is a relation between landscape preference and the elements in a landscape on which the subjects fix their eyes. For example, it is important to note that when the choice is between a landscape with 'sharp and straight vertical' forms and a landscape with 'diffuse and round' forms, subjects who fix their eyes on the luminous parts of the landscape with diffuse and round forms prefer this landscape while those who focus on the dark or shaded parts choose the other landscape in the pair. We also found that, for each pair of landscapes, the number of fixation points on the preferred landscape is higher than for the other, for all subjects involved.

◆ **Influence of context on exocentric pointing**

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We examined the influence of context on exocentric pointing. In a virtual 3-D setup we asked our subjects to aim a pointer towards a target in two conditions: only target and pointer visible; or target, pointer, a plane through the pointer, and a plane through the target visible. The planes consisted of a grid of horizontal and vertical lines. The presence of the planes shifted the indicated direction systematically. These shifts in indicated direction depended upon the orientation of the planes relative to the subject and the angle between the planes. When the orientation of the (perpendicular) planes varied from asymmetrical to symmetrical to the frontoparallel plane,

the indicated direction varied over a range of 15°: from a slightly larger slant to a smaller slant as compared to the condition without the contextual planes. When the dihedral angle between the two planes varied from 90° to 40°, the indicated direction varied over a range of 5%: a smaller angle leads to a slightly larger slant. The standard deviations in the indicated directions (about 3%) did not change systematically.

The additional structure provided by the planes does not lead to more consistent pointing. The systematic shifts in indicated direction contradict all theories which assume the perceived distance between any two given points to be independent of what else is present in the visual field, ie they contradict all theories of visual space which assume its geometry to be independent of the contents [eg R K Luneburg, 1947 *Mathematical Analysis of Binocular Vision* (Princeton, NJ: Princeton University Press); M Wagner, 1985 *Perception & Psychophysics* **38** 483–495].

◆ **Transfer of spatial knowledge from real to virtual environments**

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We are investigating the nature and quality of mental spatial representations by studying spatial behaviour in real and virtual environments. Last year we presented data on bearing estimations in a real environment. New bearing data obtained in a corresponding virtual environment have allowed us to study knowledge transfer between real and virtual environments.

From each of eleven familiar locations in the centre of Tübingen, subjects had to estimate the direction of the ten other occluded locations. Whereas the subjects in the outdoor experiment had walked to each subsequent location, in the laboratory the same ten subjects were seated in front of a half-cylindrical projection screen (7 m diameter). On this screen, 180 deg × 50 deg segments of panoramic photographs taken at each location were displayed. Pointing in this virtual environment was accomplished by rotating the projected image until the estimated direction matched that of a demarcation line on the projection screen.

The mean absolute angular pointing error was  $11.0 \pm 0.3^\circ$  in the real environment (RE) and  $12.9 \pm 0.4^\circ$  in the virtual environment (VE). Mean signed pointing error (a measure for the systematic deviation) varied strongly between places, but was generally smaller when pointing to a place (RE:  $-10^\circ \dots 13^\circ$ ; VE:  $-10^\circ \dots 14^\circ$ ) than when pointing from a place (RE:  $-4^\circ \dots 4^\circ$ ; VE:  $-5^\circ \dots 5^\circ$ ). The pattern of systematic errors was very similar in both environments and was stable over repetitions of the experiment.

We conclude that: (i) the cognitive maps that underlie our subjects' pointing behaviour were close to the real map but not identical to it; (ii) subjects' pointing behaviour in the laboratory setting was nearly identical to that in the real world, suggesting an effortless transfer of knowledge obtained in the RE to the VE.

◆ **Spatial localisation of double flashes during smooth-pursuit eye movement.**

**I: Perception-oriented response**

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When a single LED is briefly flashed twice in quick succession (double flash), while an observer smoothly pursues a moving dot, the two flashes are perceived in distinct spatial positions. One could explain this finding by visual persistence, such that a second retinal location is stimulated while the signals from the first still persist. Our new experiments show, however, that this cannot be a complete explanation, because the relative perceived distance between the two flashes increases monotonically as a function of the time interval between the flashes, while on the persistence view this effect should peak at approximately 100 ms.

We employed four time intervals (50, 100, 200, 400 ms) between flashes with four dot velocities (1.4, 2.8, 5.6, 11.2 deg s<sup>-1</sup>) while observers pursued a dot moving from left to right. A cancellation method was used where observers set the location of the second flash to align with the first. Observers moved the second flash in the direction of eye movement (rightward) to cancel the seen spatial separation between the flashes. The largest displacement of 3.6 deg was measured at 11.2 deg s<sup>-1</sup> velocity and 400 ms interval. This effect represents 80% of the distance traveled by the moving dot in this condition.

This effect did not occur if observers held their eyes stationary (as measured by an eye-tracker), while attending to the moving dot. The results were consistent with an additional observation: When the two flashes are physically aligned, observers report a right-to-left apparent motion between the two flashes while pursuing a left-to-right moving dot.

◆ **Accuracy of estimating time-to-coincidence in approaching ongoing and oncoming cars**

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In a simulated automobile driving situation (without sound), the time-to-coincidence ( $T_c$ ) was estimated by six subjects, including both novices and experienced drivers. Simulations included self-motion and stationary observers viewing an oncoming car. The main purpose of this study was to investigate whether  $T_c$  estimation could be influenced by either the car velocity or the distance travelled when the driver could not see either car. Each subject observed the approaching car on a monitor screen (92 cm, subtending a visual angle of 42 deg) until the car disappeared (was rendered invisible) at a predetermined distance from the initial starting position. The subject was required to press a response button and then make a verbal estimate of the moment at which the vehicle would reach the right edge of the monitor screen. The approach speed was varied in the range 40–100 km h<sup>-1</sup> in four steps while the distance travelled varied from 25 to 100 m in 25 m steps from the subject. The results showed that  $T_c$  tended to be overestimated at (i) higher speeds and (ii) with more advanced driving experience. There were some differences between the key response and the verbal estimation. Even experienced drivers overestimated  $T_c$  at higher speeds and short distances. The  $T_c$  accuracy in the self-motion condition (approaching a parked car) was better than in the oncoming condition (without self-motion). These findings may be interpreted as indicating that car speed, distance travelled, and self-motion information are taken into account in estimating  $T_c$ . It is further suggested that these kinds of information may be used differently depending on the skill level of the observer.

◆ **What information is used to anticipate collision in locomotor tasks?**

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How is the redundant visual information that specifies time to contact (TTC) used when judging arrival? Lee (1976 *Perception* 5 437–459) demonstrated that the relative rate of image dilation ( $\tau$ ) can provide a temporal estimate of TTC. Empirical research supports the use of optic expansion ( $\tau$ ) in interceptive timing, but the evidence supporting an exclusive reliance on  $\tau$  has been questioned (Wann, 1996 *Journal of Experimental Psychology: Human Perception and Performance* 22 1031–1048). The issue is not whether optic expansion ( $\tau$ ) is used in interceptive timing, but how it is used in conjunction with other cues such as size and perspective or binocular motion information.

We provided participants with a simulated locomotor task in which they had to make a series of timing judgments equivalent to: avoiding collision with the eye; avoiding collision in a car (bonnet extension); initiating an emergency braking response; and continuous braking control. Systematic variations were introduced into the size of the target object (a textured cube), the binocular scaling, and the ground plane information (compression/expansion of the spatial frequency in depth).

The results demonstrate a significant effect of both 'familiar' size and binocular information on TTC judgments. Ground plane scaling introduced a depth and speed illusion that biased braking responses. The results demonstrate that a simple model, such as one based solely on optic expansion, does not provide an adequate account for such tasks, and models of interceptive timing need to address multiple cue contributions in TTC estimation.

◆ **The influence of non-visual signals of walking on the perceived speed of optic flow**

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We considered how non-visual signals that accompany walking might influence the visual processing of optic flow. During natural locomotion optic-flow speed is determined by walking speed in a closed-loop manner. In the experiments subjects were required to adjust the speed of an optic-flow pattern to match that of a reference flow pattern in an open-loop manner. The visual speed was matched while walking by turning a hand-held knob that controlled the presented optic-flow speed. Subjects were also required to change their pace according to a written instruction at the beginning of each trial to either 'very slow', 'slow', 'normal', 'fast', or 'very fast'. A nonmotorised, self-driven treadmill simulated natural walking by allowing subjects to walk at their chosen pace. The optic-flow pattern consisted of bright rectangles expanding against a dark background displayed on a large rear-projected screen. An experimental block consisted of a 15 s presentation of a reference pattern followed by five test trials, one at each pace randomly ordered. Results showed a consistent increase of matched optic-flow speed with increasing walking

speeds. However, speed settings were most accurate when subjects were walking at their chosen 'normal' walking pace. We conclude that the perceived speed of optic-flow information is influenced by non-visual signals (eg proprioception) such that optic-flow speed is overestimated at lower walking speeds while underestimated at higher speeds.

◆ **Linearity and separability of fixation control derive from properties of the extraocular muscle system**

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Treatments of eye kinematics and dynamics usually emphasise the geometric and mechanical nonlinearities of the system. Recent results, however, have suggested that there are features of the oculomotor plant (in particular the use of muscle pulleys) designed to reduce the impact of these nonlinearities. This suggestion was investigated using an eye muscle model exhibiting the important nonlinearities of the static oculomotor plant.

We have found that there is a natural separation into horizontal and vertical commands: the innervation of the two horizontal muscles is independent of the state of the four vertical muscles and vice versa. The control parameters are approximately rotation vector components. In this model Listing's law at tertiary positions is a consequence of separable control. When a simple additive controller based on retinal location is used, fixation errors are small over a wide field of view, and no extra errors are incurred by the mechanical implementation over and above inevitable geometric errors. Binocular control separates naturally into version and vergence components. If the vertical command is kept constant and equal for the two eyes, they remain in vertical alignment during vergence and version movements.

These findings indicate that the forward kinematics of the extraocular muscle system is unexpectedly simple. This may have significant consequences for both the development and calibration of fixation control. For example, the simplification in the control of binocular alignment may be particularly important developmentally in view of the relationship of amblyopia to strabismus.

◆ **Smoothing of small eye movement by wavelet analysis when gazing at a fixed target**

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Wavelet analysis of eye movements when subjects gaze at a fixed target is proposed. This enables us to get a low-noise waveform of eye movement from raw data. Time derivatives of the data, ie velocity and acceleration, can be easily obtained by this method. The results are compared with the results obtained by a method that smooths the waveform of small eye movement with the use of an FIR filter.

Three applications are discussed: a representation of eye movement with a chaotic attractor, a vector representation of acceleration of eye movement, and a statistical analysis to estimate minute skewness of small eye-movement acceleration. The decrease of the blink component by means of wavelet analysis is also discussed. These applications can be used to evaluate the picture quality of new virtual and stereoscopic displays.

◆ **Combining looming and binocular information in catching a ball**

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How are optical expansion and binocular disparity combined to provide a robust estimate of time-to-contact (TTC) for objects directly approaching an observer? Lee (1976 *Perception* 5 437–459) demonstrated that optical expansion can provide a temporal estimate of time-to-collision without the estimation of depth or relative velocity from other sources. Judge and Bradford (1988 *Perception* 17 783–802) observed gross mistiming of the grasp in a ball-catching task when binocular disparity was distorted, without altering optical expansion. Both Heuer (1993 *Perception* 22 549–563) and Gray and Regan (1997 *Vision Research* 37 499) have provided support for the use of changing size and changing disparity in TTC estimation.

We tested a model of TTC (the 'dipole model', Rushton and Wann, submitted) that is based upon the early combination of disparity and looming information, and contrasted its predictive performance against a fixed-weighting modular-summation model. Using a virtual reality system we had observers grasp for an approaching virtual ball. We introduced a subtle form of information loss by alternately 'stalling' TTC as specified by disparity or looming. The dipole model predicts that grasp time should be hardly changed, whereas simple modular summation models predict grasp should be significantly delayed.

Participants performance revealed only a slight delay when one of the streams 'stalled'. Therefore the data support a model of early summation (the dipole model) and are in direct conflict with a simple modular-summation model for the combination of looming and disparity.

◆ **Path perception from optic flow**

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A unique, veridical percept of self-motion is normally derived from a combination of visual, vestibular, and proprioceptive signals. When blindfolded subjects are passively moved they often grossly misperceive their trajectory when the orientation of the head rotates relative to the path during the movement. Linear trajectories could be perceived as circular, circular trajectories as linear. We asked whether vision would allow better path perception which could correct the shortcomings of the vestibular system.

Subjects viewed optic-flow stimuli that simulated self-movement over a random-dot ground plane. The simulated movements equalled those used in the vestibular study. Trajectories were either linear or a half-circle. Orientation of the viewpoint during the movement could be tangential to the path (A), rotate relative to it (B), or remain constant in space (C). Subjects imagined themselves being moved on an office chair which could travel across the floor and rotate around its vertical axis. Afterwards subjects had to draw the trajectory of the chair in space. The results were often remarkably similar to the vestibular study. In condition A trajectories were correctly perceived as curved or straight, respectively. In condition B linear trajectories were perceived as curved and half-circle trajectories were perceived as full circles, similar to the vestibular study. However, in condition C linear and half-circle trajectories were perceived correctly, whereas in the vestibular study both were perceived as straight. We conclude that visual and vestibular senses support path perception, but that in some conditions both systems lead to similar systematic errors.

◆ **Geometric field of view and location accuracy in a stereoscopic radar display**

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Aircraft radar displays provide the pilot with information about aircraft in the immediate environment. The God's eye-view (90° elevation) of present displays allows the pilot to ascertain the horizontal distance to displayed aircraft with relative ease. However, altitude information is usually displayed in numerical form, which requires a cognitive effort to integrate into an internal 3-D picture. A 3-D stereoscopic display should allow pilots to form their 3-D picture of the situation more easily, but there may be costs in terms of location accuracy.

We have previously shown (Banton and Thompson, 1998, AVA poster) that the inclusion of the additional depth cue of relative size in a stereoscopic display increases the accuracy of depth percepts. In the present experiment we examine the effect of geometric field of view on the accuracy of location judgments in a stereoscopic display.

In a fully crossed design a target track was placed at a radial distance from the centre of the display of between 32 and 72 mm at three azimuths: 0°, 45°, and 90°, and five elevations: -90°, -45°, 0°, 45°, and 90°. The centre of the display was marked by a dot at the centre of two coplanar concentric rings. The displayed image was distorted through four geometric fields of view: 0° (parallel projection), 6.57° (veridical), 50°, and 100°. In each field-of-view condition subjects were required to indicate the perceived radial distance by moving a standard track in the same plane as the concentric rings a similar distance away from the centre of the display.

The minimum distance-matching error occurred in the 6.57° geometric-field-of-view condition. We discuss an explanation of the errors due to geometric-field-of-view manipulation in stereoscopic displays in terms of the 'two-dimensional' and 'virtual space' effects first proposed by McGreevy and Ellis in 1986.

**NATURAL IMAGES**

◆ **Natural scene analysis: implications for cones widths?**

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A new analysis of an existing hyperspectral image data set of 29 terrestrial natural scenes (Parraga et al, 1998 *Journal of the Optical Society of America A* 15 563-569) may imply a minimum useful chromatic bandwidth for cones. As posted at our WWW site this data set is available via ftp. Each scene comprises 31 images. Each image corresponds to a nominal 10 nm

waveband, and the 31 waveband set spans the visible spectrum [400, 700] nm. The analysis reveals the degree of spatial correlation between different 10 nm waveband pairs. As expected, image pairs of the same scene that correspond to adjacent 10 nm wavebands are the most similar. As the separation between the two wavebands increases, the degree of similarity decreases sharply at first, but then levels off. On average, this levelling off occurs at around a separation of 30 nm.

Thus, designing a receptor with a half-height spanning less than 60 nm (two-tails of 30 nm) might not make much sense for a terrestrial being. To cover the visible spectrum, such narrower band receptors would require more cone types but would gain little in discrimination power—as the images seen by the new cones could often be rather similar. This assumes that the data set is well representative of natural scenes, and that receptors optimise to see average rather than extreme signals. The analysis—presented in greater detail—first derives reflectance from a greycard reference, then computes difference images, and finally measures the mean Fourier energy across a range of chromatic separations for various spatial-frequency bands.

- ◆ **Ultra-rapid visual categorisation of natural scenes : No effect of familiarity on processing speed**  
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Using a go/no-go visual categorisation task we showed that humans are highly efficient (94% correct) at detecting animals in briefly flashed (20–30 ms) natural images that they have never seen before. They are also extremely fast and the EEG showed a differential brain activity between target and non-target trials that starts 150 ms after stimulus onset [Thorpe et al, 1996 *Nature (London)* 381 520]. Familiarity is generally reported to speed up stimulus processing, so we wondered whether extensive training with a particular set of images could result in further increases in processing speed.

Human subjects were presented 1200 previously unseen images mixed at random with 1200 highly familiar images (200 images seen daily for three weeks, seen 6 times when mixed with new stimuli); evoked potentials were simultaneously recorded. As previously, subjects had to release a button when they saw an animal. Familiarity improved target detection in terms of both accuracy and speed for targets that were first identified with long response times (RTs). But the earliest responses could not be speeded up. Roughly 20% of the targets were detected with RTs < 350 ms, but the RT histograms corresponding to these early responses were strictly identical for both novel and familiar images. Moreover, the evoked potentials recorded during task performance showed that the differential brain activity between target and non-target trials started at 150 ms in both cases.

Such data support the view that the visual processing underlying ultra-rapid categorisation (RT < 350 ms in humans) probably relies on the initial feed-forward wave of processing, processing which cannot be made faster, even after extensive training.

- ◆ **Visual evoked responses to blur in natural scenes**  
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Visual evoked potentials (VEPs) have been used to measure human visual responses to the introduction of blur into simple periodic stimuli; although the accompanying changes in VEP measures are quite characteristic, the simplicity of such stimuli—in particular, the fact that they are narrow-band in spatial frequency—makes it difficult to draw conclusions regarding human visual sensitivity to blur in natural scenes.

We attempted to rectify this by investigating (a) the morphology of VEP responses to natural-image stimuli, and (b) the changes in this morphology as scenes are progressively blurred. An experiment was conducted in which a wide variety of digitised natural scenes was shown to subjects whilst their VEPs were recorded. In a single presentation, a scene was shown for 500 ms and was followed by an interstimulus interval (a homogenous grey background of the same mean luminance) of 1000 ms. For each scene, the responses to 50 such presentations were recorded from 19 scalp positions; these were averaged and subjected to bandpass temporal filtering with a bandwidth of 0.1–30 Hz. The responses comprised three complexes of positive and negative peaks, N0-P0, N1-P1, and N2-P2. Blur was introduced by changing the power-spectral falloff of the images [Thomson, 1996 *Investigative Ophthalmology & Visual Science* 37(4) S4207]. The introduction of blur into the stimuli resulted in an enhancement of the early response components, located between 60 and 120 ms. The dependence of this enhancement on the spatial-frequency composition of the original image has important consequences for perceptual mechanisms of blur detection.

◆ **Search for scale-space salient orientations in real-world scenes**

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Understanding of natural images is an active and promising research domain both in psychology for modelling visual perception and in computer science for image indexing. Taking the computational viewpoint, we show the statistics of the distribution of the dominant orientation to be a powerful metric for discriminating between several basic-level scene classes (city scenes, rooms, mountains scenes, coastal scenes, and textural scenes such as forests).

Local orientation analysis is performed by a set of steerable filters based on second-order Gaussian derivatives which allows a continuous analysis of orientation (Freeman and Adelson, 1991 *IEEE Transactions on Pattern Analysis and Machine Intelligence* 13 891–906). Such an analysis is applied at various spatial scales in linear scale-space [Lindeberg et al, 1994 *Linear Scale Space* (Kluwer: Academic)]. This approach extends previous studies (Schaaf and Hateren, 1996 *Vision Research* 36 2759–2770; Field and Brady, 1997 *Vision Research* 37 3367–3383) involving the study of power spectra of natural images in radial frequencies ( $1/f^a$  decrease). The simulations have been made with a large variety of real-world pictures. We found that the main modes of the orientation distribution are invariant in scale-space, with only the relative weights of the modes varying. These modes correspond to salient orientations in the images. Moreover, values of these orientations are quite invariant in scale-space, and they have a low within-class variance. Thus, basic predominant features extracted from the orientation distribution at various spatial scales provide enough discrimination information for scene classification.

◆ **Curvilinear component analysis: an efficient method for the unfolding and the representation of high-dimensional nonlinear data sets**

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In the field of exploratory data analysis, there are a number of methods dealing with data reduction and representation. The best known linear techniques, such as principal-component analysis (PCA), suffer from serious limitations in the case of nonlinear data structures. Other popular nonlinear methods, such as Kohonen maps and Sammon mapping, are not suited to all kinds of data (intrinsic dimension or highly folded structures). We recently proposed curvilinear component analysis (CCA, a new method which is aimed at exploring hard data structures) and finding the revealing representation by unfolding the manifold spanned by the data [Demartines and Hérault, 1997 *IEEE Transactions on Neural Networks* 8(1) 148–154]. This method has been recognised as possessing several advantages over a number of other techniques [Jain, 1997 *IEEE Transactions on Neural Networks* 8(1) 1–3], specifically with respect to speed of convergence and accuracy.

We present this method as the multidimensional scaling of similarities, in the context of image and scene representation. Some intriguing results are presented, suggesting that scene classification, visual perception of textures, and semantic distance representation could follow a principle similar to that of CCA. In particular, we asked subjects to find the similarities between pairs of randomly presented images of various scenes (eg beaches, mountains, cities, villages, rooms, forests). In parallel, we analysed the same images using a set of sixteen spatially oriented band-pass filters and analysed the results by means of CCA, reducing the 16-D data of the complex images to a 2-D space. It appeared that the non-supervised classification made by CCA matched the categories in human subjects did (Hérault, Oliva, and Guérin-Dugué, 1997, paper presented at the European Symposium on Artificial Neural Networks, Bruges, Belgium). The question which is addressed (but not answered) concerns the possibility that the brain uses an algorithm of data reduction and representation similar to that of CCA.

◆ **Detection of Gabor patches embedded in natural images**

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We measured contrast detection thresholds for Gaussian-weighted circular patches of sinusoidal gratings (Gabor patches) embedded in static digitised monochrome images of natural scenes or synthetic images with constrained statistics, and we compared these thresholds with those obtained for the same patches viewed on a spatially uniform display or against a masking

sinusoidal grating. The Gabor patch was small compared to the image and was used as a probe to measure the effective contrast within these complex images (Tolhurst and Tadmor, 1997 *Perception* 26 1011–1025) and to determine the metrics for camouflaging retrievable watermarking information in pictures. The Gabor target was presented on alternating frames of the raster display (overall frame rate 100 Hz) with either a uniformly bright background or with a fixed-contrast masking image of a digitised photograph or a sinusoidal grating. The threshold contrast for the patch was measured by a staircase procedure and a modified two-alternative forced choice. We found that the patches were most easily detected in areas of the photographs where the luminance was relatively uniform, especially in the uniformly dark areas. In areas of complex local structure, thresholds were greatly elevated. Threshold was strongly dependent on the local mean luminance and local contrast of the background image close to the target, rather than on global measures of luminance or contrast averaged across the whole image (Pelach, 1996 *Proceedings of the SPIE* 2657 216–222).

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◆ **Scene ‘shapes’ from power spectra ‘shapes’: Are power spectra families compatible with semantic scene categorisation**

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In the real-world environment, the visual system automatically recognises scenes by classifying them into semantic categories: outdoor vs indoor scenes, artificial vs natural environments, urban scenes vs landscapes, etc. Scenes belonging to each visual category have a common global organisational regularity (Schyns and Oliva, 1994 *Psychological Science* 5 195–200). For example, urban environments are mostly vertically structured with a large depth of field, whereas forest scenes show homogeneous distribution of spatial orientations. Such regularities give rise to characteristic features in the power spectrum that can be exploited for scene classification.

We show that we can differentiate between the *shape* of, at least, five families of power spectra, each corresponding to one of the five environmental categories (indoor scenes, urban scenes, textural scenes, horizon scenes such as coastal scenes, and landscapes). When dealing with individual real-world scenes, independently of their category, we observed that the shapes of the power spectra are continuously distributed between these families. Nevertheless, considering a categorisation task, decisional thresholds define the set of five spectrum-shape families corresponding to the five semantic classes. Studies have shown that images have roughly a  $1/f^a$  power spectrum (Field, 1987 *Journal of the Optical Society of America A* 4 2379–2394). A finer classification within each category is obtained by studying the slopes  $a$  of the power spectrum corresponding to different spatial orientations. Finally, we propose a more finely tuned analysis using Gabor-type filters appropriately matched to the particular shape of the power spectrum for the five categories. In summary, the features of the families of power spectra correlate well with the set of families of semantic scenes, thus allowing a robust categorisation.

◆ **Natural image statistics and visual processing. Are they matched?**

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It has been suggested that the overall organisation of the visual system, including the response properties of individual neurons, might be optimised for encoding the statistical information content of natural scenes. However plausible it might be, the suggestion still remains to be fully validated experimentally. Here we propose a new method for investigating whether the presence of natural statistics does indeed optimise the discriminability of natural scenes. Our aim is to use a set of stimuli which, while plausible, still allows good experimental control. A morphed sequence of natural scenes was presented to observers in a modified two-alternative forced-choice experiment. They were asked to discriminate between reference (original) images and a slightly morphed version of these. Discrimination thresholds were obtained by fitting the measured psychometric function with the integral of a normal distribution. The statistics of each morphed sequence were manipulated by controlling the falloff of Fourier amplitude with spatial frequency ( $\alpha$ ), and thresholds for morphed sequences with different  $\alpha$  values were measured. Eleven different conditions were explored with amplitude slopes ranging from  $-0.5$  (whitened or edge-enhanced pictures) to  $-2.5$  (blurry pictures). The results show that morphed scenes having an  $\alpha$  value close to that reported for natural scenes ( $\alpha = -1.2$ ) are optimally discriminated by the human visual

system. We conclude that natural stimuli are optimally discriminated, and suggest that this method may be suitable for more general investigations with naturalistic stimuli.

◆ **Self-similar bandpass channels and the  $1/f^2$  power spectrum of the natural environment: a rate distortion analysis**

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The basic properties of visual neurons can be seen to result from an efficient adaptation to the natural environment. According to this information-theoretic approach, visual information processing takes advantage of the specific statistical redundancies of natural images. Corroborating this, it could be demonstrated, for example, that retinal lateral inhibition is well adapted to the second-order statistics (autocorrelation function, power spectral density) of natural images. However, it is unclear whether other elementary features of biological visual systems can also be explained within the restricted context of second-order statistics. Cortical orientation selectivity, for example, seems to require the consideration of higher-order statistics. It has also been questioned, whether the second-order approach suffices for a convincing derivation of the localisation and self-similarity of cortical receptive fields.

Here we show, that for the latter property such an explanation can indeed be found. Therefore, we analysed the exploitation of the  $1/f^2$  power spectra of natural images by technical subband coders, which are closely related to the frequency-selective bandpass filters in biological vision systems. We evaluated the coding performance of the system in terms of the rate distortion theory of communication engineering, and found that an optimal partitioning of the frequency domain is only obtained by bandpass channels with an approximately constant bandwidth in octaves, whereas a partitioning with constant linear bandwidth yields a clearly suboptimal performance. A more detailed analysis revealed a slight, but systematic deviation of the optimal partitioning from perfect self-similarity: a decrease of the bandwidth with increasing centre frequency. This corresponds exactly to the neurophysiologically observed distribution of the bandwidths of cortical simple cells.

◆ **Early use of configural information in rapid scene perception**

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We investigated the use of configural information for the first 30 ms in a scene-perception task, using colour photographs of natural scenes. To remove configural information, a jumbled version of each picture was constructed by dividing the picture into 80 small squares and randomising their positions. A coherent picture (C) was paired with its jumbled version (J), a blank (B), or a random mask (M) to form a display sequence, which was bracketed by a fixation point (500 ms) and a mask (1 s). Two small images were displayed after each sequence. Subjects indicated which of the two was a cut-out from the coherent picture. In experiment 1, three types of display sequences were studied in a within-subjects design: 2B3C (ie 2 frames of blank followed by 3 frames of a coherent picture, at 14 ms per frame), 2J3C, and 2M3C. The sequences beginning with a jumbled image led to significantly higher accuracy (88%) than those starting with either a blank (79%) or a mask (75%). This suggests that a jumbled image carries usable information. In experiment 2, the 2J3C sequences were compared against 3C2J and 5C (5 frames of a coherent picture alone) sequences with new subjects. The sequences that began with a jumbled image produced a lower accuracy (82%) than both the 5-frame coherent-picture sequences (93%) and the jumbled-last sequences (92%). We conclude that during the first 30 ms, visual information other than configural information can be used to facilitate scene perception (experiment 1); however, performance can improve further if configural information is available from the very beginning (experiment 2).

◆ **Ultra-rapid visual categorisation of natural scenes: order of spiking in ganglion cells as a code**

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Recent data on the speed of processing in the human visual system [Thorpe et al, 1996 *Nature (London)* 381 520–522] indicate that information about an image can reach the brain very quickly. With as little as 10–20 ms available for information transfer, codes based on firing rate seem unlikely to be fast enough since few ganglion cells will have time to emit more than one spike. An alternative hypothesis considers ganglion cells as analog-to-delay converters—strongly

activated ones will tend to fire first, whereas more weakly activated cells will fire at longer latencies or not at all. Under such conditions, the order in which cells fire can be used as a code.

To test this hypothesis we determined the minimal number of ganglion cell spikes required for categorisation of natural images using a model in which the image is encoded by ON-centre and OFF-centre ganglion cells having a range of receptive-field sizes. The total number of cells was roughly 2.5 times the number of pixels in an image. By giving maximum weights to the first cells to fire, and progressively weakening the effectiveness of spikes that arrive later, we found that it was possible to reconstruct a recognisable image using surprisingly few spikes. Typically, less than 2% of the cells need to fire one spike in order to obtain a good reconstruction of the original image. We believe that this result goes some way to understanding the remarkable rapidity of visual processing, while at the same time providing evidence for rank order coding in the visual system.

◆ **Exploitation of natural scene statistics by orientation selectivity and cortical gain control**

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The optimal information processing strategies for visual recognition and sensorimotor control are essentially dependent on the statistical properties of the natural environment. Some of the basic neural properties, like lateral inhibition, or self-similar bandpass filtering, can be understood by use of second-order statistics (Röhrbein and Zetsche, this issue), but in general the standard principal component approach leads to logical inconsistencies (Zetsche et al. 1997 *Neuroscience Letters* 228). The necessary higher-order properties can be measured indirectly by the computation of polyspectra (Krieger and Zetsche, this issue), or, as done here, by a direct identification of the basic structure of the multivariate probability density function (pdf).

We first show that the joint multivariate statistics of natural images exhibit a concentration of probability mass in a noncompact quasi-orthogonal subspace structure. This causes a maximally sparse distribution if projected onto axes which correspond to oriented filters. Hence this structure is the key for understanding the advantages of cortical orientation selectivity.

Analysis of the response statistics of linear filters which are jointly localised but differ in symmetry (even/odd), spatial frequency, or orientation, reveals a specific spherical structure of the local multivariate pdf: it is inseparable in Cartesian coordinates but exhibits radial separability in spherical coordinates. The information-theoretic approach thus predicts that a nonlinear transform to a feature space with a radial organisation would be required for an efficient encoding. The suitable neural implementation of this nonlinear transformation turns out to be provided by gain-controlled mechanisms. Interestingly, the resulting encoding bears close similarities to shape-gain vector quantisers in technical image compression. Psychophysical tests on the discriminability of localised Gabor patches lend further support to this hypothesis of a radially structured representation in early vision.

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**LEARNING AND MEMORY**

◆ **Perceptual learning effect on spatial summation**

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In a psychophysical experiment we measured detection contrast thresholds of a central vertical line in the presence of two lateral lines by the standard method of subthreshold summation (Kulikowski and King-Smith, 1973 *Vision Research* 13 1455–1478). The width of the lines was 1 min of arc, the length was 1.4 deg. Contrasts of the lateral lines were always equal to half the contrast of the central line. Distances between lateral lines varied up to 30 min of arc. The luminance was 5 cd m<sup>-2</sup>. A two-alternative forced-choice method was used. Detection thresholds were estimated by a staircase procedure separately in the first half of the experimental session and in the second half. Not less than 500 presentations of each stimulus were carried out in each half-session. Six observers took part in the experiment. Line-spread functions were calculated as difference of two Gaussians (Wilson, 1978 *Vision Research* 18 971–981) for the first and the second halves of the experimental session. We found changes of the contrast thresholds in the second half of the session compared with the first half. The contrast sensitivity increased at many distances between the central and the lateral lines (for some distances significantly— $p > 0.01$ ). But improvement of sensitivity depended on distance. The greatest sensitivity increase was found near the central line with a summation zone. As a result, two different line-spread functions were obtained for each observer in two such cases. The second function was more

narrowly tuned and its amplitude was larger.

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◆ **What determines the response: test or reference?**

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The stability of sensory memory has been studied by presenting a reference stimulus, a delay, and a test stimulus. As has been pointed out by Lages and Treisman (1998 *Vision Research* 38 557–572), the usual measure of performance depends only on the effect of test variations on the responses. The Weber fraction characterising performance is more properly called the test-stimulus Weber fraction. We measured the relative contribution of the test and reference to the response by the ratio of the test Weber fraction to the reference Weber fraction. The stimuli were two dark lines on a bright background. Seven reference separations, varying from 9.5 to 16.7 min of arc, were intermixed in each run. Interstimulus intervals (ISI) of 50, 200, and 2000 ms and intertrial intervals (ITI) of 500 and 2500 ms were investigated. When the ISI was short (50 or 200 ms), for both ITIs, responses were determined equally by the test and reference. For the long ISI (2000 ms), the reference stimulus contributed less. However, only for the 500 ms ITI (and not for all observers) was the contribution of the reference stimulus negligible, as Treisman's criterion-setting theory might suggest.

◆ **Perceptual learning and orientation specificity**

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The bandwidth of orientation specificity in perceptual learning was investigated and compared with other estimates of orientation bandwidth. Five groups with forty observers were trained on Vernier discriminations (right versus left offset) in a binary forced-choice task for 1 h, leading to a mean improvement of performance by almost 50% of the initial level. Subsequently the stimulus was rotated by 90°, 45°, 20°, 10°, or 4°, respectively, for the five groups. Another group of eighteen observers was trained on Vernier, curvature, and orientation discrimination for 1 h each in counter-balanced order.

Improvement through training was specific for stimulus orientation in the groups whose stimulus was rotated by 10° or more. Performance of observers in these groups dropped, on average, to initial baseline levels after the change of orientation. In the group training on different hyperacuity tasks, there was no transfer of improvement between the Vernier, orientation, and curvature detection tasks.

The results indicate that perceptual learning improves performance not primarily by narrowing the bandwidth of early orientation-sensitive filters—since these filters have far wider tuning curves for orientation as revealed by single-cell recordings in animals, or by adaptation or masking studies in humans. Moreover, one would expect some transfer between different hyperacuity tasks, all based on orientation-sensitive mechanisms if these mechanisms improved through training. The best possible explanation, therefore, is based on top-down signals modifying all visual inputs in a task-dependent way.

◆ **Practicing a Vernier discrimination task with nonuniformly distributed stimuli**

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Both neural network models and signal detection theory propose that display probabilities of stimuli may influence learning and decision processes. To investigate these hypotheses we used a Vernier discrimination paradigm. We show that without feedback no improvement of performance occurs if Verniers offset in one direction are more frequently displayed than stimuli displaced in the opposite direction. Providing feedback results in a modification of decision criteria and improves performance. However, it is not clear whether or not learning processes contribute to this improvement. To assess the possible role of learning we presented Verniers offset to the left to the left eye and offset to the right to the right eye only. Display probabilities for both eyes were identical, and so were offset directions, after binocular fusion. We found an improvement of performance that is not due to a change of decision criteria but results from monocular learning processes which are not sensitive to the display probability of the stimuli. Changing display probabilities of stimuli during the experiment stops improvement of perfor-

mance—even if feedback is provided and both offset directions are on average displayed with the same probability.

◆ **A localisation test of visual spatial working memory: application to normal subjects and patients with frontal lobe lesions**

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Following Baddeley's model of visual spatial memory (VSSP), previous research used a length-way paradigm to test its capacity. These studies have shown that performance decreases with increasing distance between the items and their number. The object of the present study was to test the ability of localisation within a fixed spatial arrangement. Normal subjects and brain-damaged patients with frontal lobe lesions (aged between 20 to 30 years) were tested. The task was to recall the sequential location of four successively lighted squares within a matrix of  $5 \times 5$  (horizontal and vertical lines). Each square was illuminated for 500 ms and the interstimulus interval was 300 ms. Thus progressing across the whole matrix took 3.2 s after which the matrix appeared again on the screen without any illumination. The spatial and temporal order of stimulus presentation had to be reproduced by positioning a tick on the screen at the respective location in the matrix. Normal subjects showed a good localisation accuracy with few errors which mostly concerned presentation order of the item. In contrast, brain-damaged subjects exhibited many more errors mainly in localisation. Thus the present test appears to be sensitive to functions impaired by brain damage of the frontal lobe and highly discriminating between normals and brain-damaged patients.

◆ **Memory and learning in identification of low-pass-filtered images by low-vision patients**

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We have studied identification of low-pass-filtered images by patients with age-related macular degeneration (ARMD), before, 3 weeks after, and 3 months after laser photocoagulation treatment. An improvement of performance over time was shown. The question asked was whether it is an effect of (i) treatment, (ii) learning of the experimental task, or (iii) memory? To test these hypotheses, we introduced some new images at each session. We used images belonging to 12 different semantic categories (tools, animals, furniture, etc) and 3 graphic types (Snodgrass line drawings, isolated objects, and photos). Images were low-pass filtered with a set of Gaussians varying in bandwidth from 0.25 to 8 cycles  $\text{deg}^{-1}$  in octave steps. For each image, the minimal bandwidth for identification was determined with an ascending method of limits. The best eye of ten ARMD patients was tested, and the worst eye of ten others. Ten age-matched and ten younger subjects were tested as controls.

The first session contained 27 images; the second 9 images from the first session and 18 new images; and the third 9 original images, 9 from the second session, and 9 new images. Thus, some images were seen three times, some twice, and some once. Learning effects were evaluated by comparing recognition of new images across sessions. Memory effects were evaluated by comparing the recognition of new images and images already seen.

◆ **Modeling the decay of the McCollough effect: pre-induction, post-induction, and drug interactions**

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The McCollough effect (ME) is a classic example of a contingent aftereffect—after pairing colour and orientation a negative coloured aftereffect is reported contingent on the orientation of a test pattern (McCollough, 1965 *Science* **149** 1115–1116). A number of models have been proposed to account for this phenomenon. However, barring the recent reports of McLoughlin and Savoy [1993 *Investigative Ophthalmology & Visual Science* **34**(4) 785; 1995 *Perception* **24** Supplement, 94], none has ever attempted to fit quantitative ME data. McLoughlin and Savoy proposed that the ME is encoded in weights between unoriented monocular colour units, and both monocular and binocular achromatic oriented units. Obvious physiological correlates exist in primate visual cortex.

In previous studies we have reported on the model's ability to replicate data collected in our laboratory from a variety of monocular and binocular variations of the ME. In this study an attempt is made to have the same model replicate the decay of the ME strength over time

(a) under normal control conditions, (b) when a subject previews an achromatic test immediately prior to induction, (c) when a subject previews an achromatic test 15 min before induction, (d) when a subject inspects an achromatic test after induction, and (e) the effects of various cholinergic drugs on the strength and decay of the ME (Skowbo, 1988 *Perception & Psychophysics* **44** 295–303; Byth et al, 1992 *Psychopharmacology* **106** 75–84). These findings support our claim that the ME is in fact encoded between two separate populations of units—one sensitive to wavelength and the other sensitive to orientation.

- ◆ **Discrimination of point-light display and full-colour display of conspecies by homing pigeons**  
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Johansson (1973 *Perception & Psychophysics* **14** 201–211) investigated perception of the movements of living creatures by using point-light display films with moving spots. Light spots on a dark screen represented major joints of the human figures. Observers easily recognised a walking human from these achromatic motion sequences.

In my experiment, eight pigeons (*Columba livia*) were trained by operant technique to discriminate between moving sequences of a pigeon and a toy dog. Two types of display were given: either full-colour object or point-light displays that contained white dots on the invisible body surface of the object (three dots on each side). Each sequence lasted for 10 s. The eight pigeons were divided into two groups according to the display type used during training. Each group was divided into two subgroups: pigeons required to peck on the window when scenes with the pigeon were present (PigeonS+ group) or when scenes with the toy dog were present (DogS+ group). All pigeons reached criterion discrimination ratio except for those in the full-colour DogS+ group. This group was excluded from further analysis because its discrimination ratio did not improve after 87 sessions. The pigeons were then tested with another display type to see whether they could still perform the discrimination task. Only the full-colour PigeonS+ group showed transfer above chance. I found effects of both the display types used in the training and a feature-positive/feature-negative effect of conspecies. To test that their discrimination was not based on memory, the response was checked with novel scenes of the training display type. All eight pigeons passed.

- ◆ **The visual psychophysics of baby chicks: new context-dependent colour and size data**  
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Two groups of newborn chicks were trained in a simultaneous-discrimination task to peck selectively either at a blue (or red) versus green, or at a small versus large box. The correct pecking was reinforced by a combination of (a) a hen's 'maternal' call, (b) the delivery of a stream of (pleasant) warm air, and (c) the access to grain food. The training phase started with the first day of life; after reaching the 70% criterion of performance subsequent generalisation-testing followed. Lawful generalisation-test as well as psychophysical context-effect data were obtained with colour and size. Furthermore, large inter-individual differences between the so-called 'good' and 'poor' learners resulted during the training and the testing phase. The findings corroborate and extend some of our earlier psychophysical data obtained with baby chicks (cf Sarris et al, 1995 *Perception* **24** Supplement, 64; Sander et al, 1996 *Perception* **25** Supplement, 98).

- ◆ **Passive and active decay of visual information in the short-term memory**  
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Dependence of identification accuracy of nonverbal 2-D geometrical figures on the duration of information retention in short-term memory (STM) was investigated in psychophysical experiments on human subjects. Geometrical figures composed of a different number (4–8) of vertical and horizontal line-segments were presented with a tachistoscopic backward-masking technique. The stimulus sequence in each trial was as follows: test figure (10 ms), an individually determined interstimulus interval, masking figure (200 ms), a pause *P*, and three sample figures (1.7 s). The task for subjects was to identify which one of the three sample figures was the test figure. Passive retention of visual information of the test figure in STM was varied by changing the value of *P*: 0, 0.3, 0.5, 0.8, 1.5, 1.8, 2.5, or 4.5 s. Active decay of visual information took place in the STM during the presentation of three sample figures when they were matched with the test figure, and it was caused by the interference between visual information from the test and sample figures.

Identification accuracy of the test figure did not depend on the *P* value, ie no decay of visual information was detected in the STM during the 4.7 s period of passive retention. But identification accuracy was dependent on the matching order: the test figure was identified with the highest accuracy when it corresponded to the first sample figure in a matching sequence, and the lowest identification accuracy resulted when the test figure coincided with the last (third) sample figure, ie when the interference process was maximum. As a theoretical interpretation of experimental data, we propose that the processing of visual information is not based on a spatiovisual code in working memory.

#### CLINICAL ASPECTS OF PERCEPTION; READING

##### ◆ A two-stage model of kanji reading

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The present study attempts to explain some aspects of kanji (Japanese logographic symbols representing lexical morphemes) reading behaviour through neural-network simulation. In view of the large number of kanji characters (hundred times more than in European languages), it is impractical to apply simple perceptron-type layered-network models like those generally applied to model European letter recognition. A two-stage neural-network model for reading kanji characters was constructed. The model is an implementation of the roles that neurologically different parts of the brain play in kanji reading behaviour.

The first stage of the model (Kohonen's self-organising feature-mapping algorithm) roughly and rapidly classifies the visual input into groups on the basis of similarity of shape. This grouping can be regarded as a representation of the topological organisation which is frequently observed in the brain. The result of the first stage is forwarded to the second stage (a backpropagation network), which identifies the character from among the candidates within the group. This model demonstrates two neuropsychological phenomena, paralexia and alexia. Damage in the first stage corresponds to that seen in paralexia in which patients cannot read characters accurately. Damage in the second stage or to the connection between the output of the second stage and the phonological processing unit causes pure alexia.

##### ◆ Motion discrimination in blindsight

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Some patients with damaged striate cortex, which renders them clinically blind in the field defect, may nevertheless be able to discriminate stimuli in their scotoma when forced-choice procedures are used, even though they may deny seeing anything. Motion is a particularly effective stimulus in such patients, though there are conflicting reports as to whether or not the ability to discriminate motion direction is preserved in the scotoma.

We investigated the latter by testing a patient with right homonymous hemianopia for his ability to detect the motion and discriminate the direction of motion of a variety of moving stimuli, ranging from simple spots and bars to random-dot kinematograms depicting translation and motion-in-depth. We found that although he could detect the presence of movement in any kind of stimulus, and could discriminate the direction of motion of simple spots and bars, he was unable to discriminate the direction of motion of the more complex random-dot kinematograms, implying a selective impairment of global motion processing in his scotoma.

We conclude that extrastriate cortex, despite its ability to process the direction of motion of simple stimuli such as bars in the scotomata of both monkeys and people with striate lesions, is unable to integrate the motion signals inherent in more complex stimuli such as random-dot kinematograms in the absence of inputs from striate cortex.

##### ◆ Assessing poverty of emotional displays in Parkinson's disease from facial information

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Patients suffering from Parkinson's disease (PD) show increasing poverty of movement of facial features. This affects their ability to communicate facial signals important in expressing their emotional disposition. Measurement of the magnitude of the six basic facial expressions may prove a useful visual guide as to the severity of the condition.

Photographs of male and female faces producing the six 'universal expressions' from FACS [Ekman and Friesen, 1978 *Facial Action Coding System Manual* (Palo Alto, CA: Consulting Psychologists Press)] instructions were used to generate a statistical database containing descriptions of dispositions of facial parts. Measurements taken from each face were analysed with the use of Bayesian inference. The solution generated 100% correct classification and included an explanation of the influence of individual feature actions in achieving this solution. PD patients were asked to pose each expression in response to verbal and written and photo-imitation instructions. These were measured in the same way and the idealised model used to predict expression category membership.

Each PD patient posed the six expressions with varying degrees of success. Goodness of fit of each PD expression to the model showed: (i) Happiness was most easily distinguished but was relatively weakly expressed. (ii) Anger, sadness, and disgust were poorly represented with only a few exceptions. These expressions were insufficiently clear in production and were interpreted as blended displays. (iii) Fear and surprise were also blended. [Supported by grant JSMF 95-59.]

◆ **Morphological segmentation of neurons and axon terminals in rat visual cortex**

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A novel approach to morphometric characterisation of NADPH-diaphorase-positive neurons and biocytin-labeled axon terminals in the rat area 17 is presented. Malnutrition in the earliest periods of life can alter brain structures and functions, both in laboratory animals and in humans. Clinical studies in underweight newborns and children have pointed to relationships between reduced neurodevelopment and visual functions such as stereoacuity, colour vision, and contrast sensitivity (Dowdeswell, 1995 *British Journal of Ophthalmology* 79 1–6; Levitsky, 1995 *Journal of Nutrition* 125 2212–2220). To study these effects, measurements such as branching order, branch lengths, tortuosity, dendritic tree area and volume must be extracted.

Our approach is based on computer vision techniques and has two stages: image segmentation and three-dimensional reconstruction of neurons. We focus on the segmentation process for neuron-contour detection based on morphological grayscale reconstruction (Meyer, 1990 *Journal of Visual Communication and Image Representation* 1 21–46; Vincent, 1993 *Transactions on Image Processing* 2 176–201). The method was applied to 79 images (optical sections from successive focal planes) acquired from slices 200 µm thick by a CCD camera mounted on a microscope. Comparison of the detected contours with manual segmentation by experts shows similar results. Initial images, manually segmented contours, and the contours of the binary images are superimposed, and two parameters are evaluated: false acceptance and false rejection of pixels in relation to manual contours and original images. An 89% accuracy was obtained. Results are shown through some images. This method improves the robustness and the efficiency by reducing the subjectiveness and amount of human intervention when large samples are necessary for statistically useful conclusions (Curcio, 1986 *The Anatomical Record* 214 329–337; Wall, 1988 *Journal of Neuroscience Methods* 24 91–100).

◆ **Motion parallax enables depth processing for action in a visual form agnostic**

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We report new observations made with the patient DF, who has an unusually pure form of visual form agnosia, causing a profound impairment in perceiving and recognising shapes. Previous studies have shown that DF is remarkably good at using visual information to guide her actions—including visual information that she is totally unable to report. We tested DF on two different tasks in order to determine whether she can derive contour orientation information from motion parallax.

In the first study, we used an observer-produced motion parallax setup based on Rogers and Graham (1979 *Perception* 8 125–134) simulating depth corrugations tilted at any one of six different orientations. Although DF was quite unable to report the orientation, she was nonetheless able to guide her hand movements in a 'posting task' (mean unsigned error of < 30°). We also

found that she was able to use binocular disparity to guide her actions in a comparable task (mean unsigned error of  $< 20^\circ$ ). In a second study, DF had to reach out and grasp a solid plaque, presented at seven different front-to-back slants in depth. Under stationary, monocular viewing, DF was very poor at this task but under binocular viewing she was highly adept at orienting her finger-thumb axis to make such prehension movements. When she was allowed to make head movements, her monocular accuracy was comparable to binocular performance levels.

We conclude that DF's visuomotor system appears to have access to depth computations from monocular motion parallax as well as from disparity information.

◆ **Visual size perception in neglect patients**

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The processes underlying the visuospatial neglect phenomenon are not well understood. One proposed mechanism to explain them is a representational deficit of perceived visual space. Milner et al (1995 *Current Biology* 5 85–89) asked three neglect patients to compare the width of two objects presented simultaneously in the left and right half of egocentric space. These patients systematically underestimated the horizontal extent of objects on the left side. We questioned whether this observation holds for all neglect patients and if it can be interpreted in terms of a systematic distortion of internal space representation. We therefore examined twenty seven neglect patients. Most of them suffered from an infarction in the territory of the right medial artery. Our patients performed three tasks: (i) a line bisection task; (ii) discrimination between the width of two simultaneously presented bars (bar task); and (iii) discrimination between patterns consisting of vertical stripes which became broader or narrower from left to right (pattern task).

In the bar task the patients showed no systematic underestimation of the width of the left bar, but exhibited a tendency to a higher decision threshold and a significantly higher internal noise level compared with that of normal controls. The point of subjective equality depended on the mean width of the two bars. Performance also depended on the side of presentation in egocentric coordinates. Cueing of the left bar led to an overestimation of its width. There was no simple relation between the performance on the line bisection task and the performance on the bar task. The patients performed the pattern task as well as the controls.

The results indicate that the abnormalities in visual size perception observed in neglect patients cannot be easily explained by distorted spatial representation.

◆ **Heterochromatic flicker photometry and brightness matching in poor readers and normal controls**

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Between 5% and 10% of children suffer from developmental dyslexia. The transient-system-deficit hypothesis of reading disability remains contentious. As part of a study assessing multiple measures of transient system function we introduced heterochromatic flicker photometry (HFP) and brightness matching (HBM) to assess visual function in reading-disabled subjects.

Thirty-one poor readers and thirty age-, grade-, and sex-matched controls with ages ranging from 8 to 12 years participated in the study. Participants were free of ocular, behavioural and neurological pathology and were screened for IQ, English as a second language, and reading ability. HFP stimuli consisted of grey and colour rectangles alternating at 15 Hz. The HBM stimulus array consisted of a bipartite field of chromatic and grey rectangles. Macintosh colour displays were used to present blue, green, yellow, and red stimuli. Matches were determined by double interleaved random staircases, and a ratio of HBM and HFP matches represented performance.

Repeated-measures ANOVA showed no significant difference between poor readers and controls classified in an initial Neale reading analysis. However, partition of the subject pool based upon an a posteriori Neale analysis produced a significant difference between controls and poor readers. Consistent with a relative deficit in transient system function, poor readers exhibited increased ratios of transient-to-sustained performance for blue and red stimuli. The results confirmed the validity of the technique as a method for investigating transient/sustained visual processing and provide support for the transient-system-deficit hypothesis. The study highlights the necessity for stringent screening of reading ability in subjects and justifies a reconsideration of the transient-system-deficit hypothesis in reading disabilities.

- ◆ **Spatial localisation changes during occlusion therapy in children with strabismic amblyopia**  
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Adult strabismic amblyopes showed defective spatial localisation in a vertical-alignment task [increased uncertainty and systematic alignment errors (Bedell and Flom, 1981 *Investigative Ophthalmology & Visual Science* 20 263–268; Fronius and Sireteanu, 1989 *Investigative Ophthalmology & Visual Science* 30 2034–2044)]. We modified the alignment tests so that they can be used with strabismic children (Fronius et al, 1995 *Perception* 24 Supplement, 53).

We investigated whether alignment errors are present in strabismic children and whether the errors are influenced by occlusion therapy. Children aligned a vertical test line (3.4 min by 32 min) with the apices of two vertically aligned reference triangles separated by 5 deg. After a binocular test run, right and left eyes were tested monocularly (15 trials in each condition), followed by an orthoptic examination. We tested nineteen children (aged 5 to 11 years) with various histories of strabismic amblyopia. Twelve children were tested repeatedly during occlusion therapy. Thirteen age-matched control children with normal or corrected-to-normal vision were tested for comparison.

Compared with the data of the control children and of the dominant eyes of strabismics, amblyopic eyes showed markedly increased uncertainty with good correlation to visual acuity. Mainly in severe amblyopia, systematic alignment errors also occurred. During treatment uncertainty decreased as visual acuity improved. In several cases we observed changes of systematic vertical alignment during therapy, sometimes in the sense of an initial increase and later decrease of errors. These data suggest that spatial localisation is susceptible to change in children experiencing enforced use of their usually suppressed amblyopic eye.

- ◆ **Use of colour information in motion perception without striate cortex**  
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Previous studies have reported that some patients with damage to striate cortex retain the ability to detect monochromatic light and discriminate direction of achromatic movement in their blind visual fields. We investigated the residual chromatic visual capacity of a well-studied patient (GY) who has a homonymous unilateral lesion of his left striate cortex (area V1). A rating scale (0 = 'unaware', 5 = 'fully aware') was used to assess levels of visual awareness. Discrimination judgment confidence was assessed in the same way.

The data show that GY was able to detect and discriminate the direction of movement of colour targets presented within his blind right hemifield. The velocity and contrast of moving chromatic stimuli affected GY's levels of conscious experience of these movements. As the velocity or contrast increased, discrimination performance improved in line with rising visual awareness and judgment confidence. At isoluminance, GY continued to discriminate motion direction with above chance accuracy and, on average, with non-zero awareness.

These results indicate that chromatic signals can also be used to process motion information in the absence of primary visual cortex and that such residual visual capacity must be mediated by a subcortical pathway projecting to extrastriate cortices.

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- ◆ **The effects of different viewing conditions on performance in simulated minimal access surgery**  
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The aim of this study was to assess performance in simulated laparoscopic tasks under a range of viewing conditions. Minimal access surgery (MAS) conventionally uses 2-D viewing systems which produce a flat image. However, a number of attempts have been made to develop 3-D viewing systems which produce stereoscopic depth information. In principle and everything else being equal such systems should lead to better depth perception, and consequently should help to improve performance on tasks which require an appropriate representation of layout and depth in the visual scene. A study was carried out to assess a novel 3-D viewing system in comparison to a state-of-the-art 2-D viewing system ('conventional MAS condition') and a direct viewing condition ('classical open surgery') as a point of reference. Tasks included pulling and

cutting of threads with standard laparoscopic surgical instruments. Medical students ( $n = 16$ ) were allocated to viewing conditions according to a Latin square and carried out a total of 120 tasks each. Assessment was by means of a 3-D movement-tracking device providing a number of performance parameters (time on task, velocity, number of movements, distance travelled). In addition, instrument movement was video-recorded and analysed by four observers to validate the tracking device. Results from the tracking data and the observer data were highly correlated (correlations above 0.85). While the open-surgery condition naturally scored highest, the key finding of the study was the clearly superior performance on all criteria in the 3-D condition compared to 2-D. This shows that modern 3-D viewing systems can help to improve performance in a highly realistic task.

◆ **Recognition of filtered optotypes with narrow-band spatial-frequency spectra**

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Howland, Ginsburg, and Campbell (1978 *Vision Research* 18 1063–1066) created high-pass spatial letters but nobody has used low-pass spatial optotypes in clinical practice. Recently we studied spectral features of different optotypes. We measured distance of recognition for a set of equal-size optotypes with various wide spatial-frequency spectra and for nonfiltered letters. We found that the distances of recognition for high-frequency and low-frequency optotypes were 5.1 and 7.93 m and that for nonfiltered letters was 7.0 m. The standard deviation for high-frequency letters (filter 1) was half that for low-frequency (filter 5) or nonfiltered (filter 0) optotypes.

In order to get letters with narrow spatial spectra we designed a set of double-contoured optotypes with equality of black and white components for measurements in high and middle spatial-frequency ranges using different contrast levels. The results showed that the distance of recognition was determined by the width of the black and white contour and that standard deviation was less by a factor of 1.8 than that for standard Snellen optotypes. So we conclude that in clinical practice it is possible to increase the accuracy of visual acuity measurement by using filtered optotypes.

We found that contoured optotypes with sinusoidal luminance profiles and a special curved form of borders have ideal narrow-band frequency spectra. For measurements in the low-frequency range we suggest using optotypes with Gaussian luminance profiles. The set of new filtered optotypes (eight spatial frequencies and eight contrast levels) allowed us to measure visual acuity and contrast sensitivity, controlling subjects' answers with high accuracy in clinical practice.

◆ **Evidence of left-visual-field neglect in a line-bisection task in Parkinson's disease**

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Previous evidence for visual neglect in Parkinson's disease (PD) comes from tasks such as letter cancellation (eg Villardita et al, 1983 *Archives of Neurology* 40 737–739). In the present study, observers were presented with a single horizontal line on a large back-projection screen, and adjusted with a remote switch the position of a cursor to apparently bisect the line. Over a range of line lengths, in three screen positions (left, centre, right) and at two viewing distances (60 cm, 150 cm) PD subjects showed a consistent bias in positioning the cursor too far to the right of centre (with the exception of the only left-handed subject, who positioned the cursor too far to the left). This bias increased in absolute terms with the length of the stimulus line. Control subjects were either completely accurate, or made errors which were small and not systematic. This finding suggests that visually perceived extrapersonal space may be compressed in PD, with visual neglect of the hemifield mediated by the non-dominant (usually, the right) hemisphere.

◆ **Stereopsis in persons with brain damage**

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The human visual system perceives a transparent or a translucent illusory surface from visual stimuli that are suitably arranged partially along the surface boundary or are placed beyond the overhung illusory surface (Idesawa, 1991 *Japanese Journal of Applied Physics* 30-7B L1289). When the physical visual stimuli are depicted beyond the surface or in an enclosed area, opto-geometrical inconsistencies occur in three-dimensional structures. The human visual system may generate the transparent illusory surfaces to reconcile these inconsistencies. For detecting stereo vision we used autostereograms—stereograms presented as a single image (Tyler and Clark,

1990 *SPIE Proceedings* 1256 182–197). We tested eighty-two children, 9–15 years old and whose visual acuity was 20/20, experiencing stereoscopic interpretation of artificial images by free fusion. Forty-eight of them had temporal-lobe damage. When using this method we asked the persons to come into focus at any point before the three-dimensional effect appeared. We estimated that children who had temporal-lobe damage performed this task in 62.4% of cases worse than children without damage. We suppose that children with temporal-lobe damage may have disconnection in the brain between higher visual systems through corpus callosum.

◆ **Hemifield stimuli can be used to test the quality of fixation during pattern-ERG recordings**

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Electrophysiological responses are modulated in amplitude and shape when subjects do not maintain fixation on the centre of the stimulus field. While this effect is a problem in multifocal recordings, we asked whether we can benefit from it to indicate the quality of fixation during pattern-ERG recordings.

Twenty visually normal subjects participated in the experiment. Their age ranged from 23 to 36 years. Transient pattern-ERGs ( $f = 2.2$  Hz) to reversing checkerboard patterns of check sizes (a) 18 deg and (b) 0.8 deg were recorded binocularly with DTL-electrodes. The patterns reversed either as full-field stimuli or alternately in the left and right hemifields. A fixation mark guided the attention either to the centre of the field or 14 deg to the left. Amplitudes were derived from the voltage difference between N35 and P50.

With central fixation the amplitude difference between the two hemifield stimuli was nonsignificant for all conditions. When the fixation was guided to the left, amplitude increased on average by 15% (a) and 13% (b) in the left field and decreased by 33% (a) and 50% (b) in the right field. The responses to the full-field stimuli were reduced by 16% (a) and 20% (b). P50 latency values were not modulated by the horizontal shift in fixation.

The asymmetry between the responses to hemifield stimuli may indicate the quality of fixation during ERG recordings. This method seems applicable to a wide range of check sizes and may be extended to a 2-D fixation test by using additional top/bottom hemifield stimuli.

◆ **Contrast thresholds and visual-field thresholds in persons with chiasma-opticum damage**

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Persons with pituitary tumors may exhibit selective visual deterioration because of compression of the chiasma opticum. We examined visual perception in fifty patients aged between 20–50 years using a computerised Humphrey Visual Field Analyzer to test sixty eight peripheral point thresholds. The duration of damage was from one month to three years. The age-matched control group consisted of fifteen healthy persons with normal visual acuity. The purpose of this study was to correlate visual-field thresholds with contrast-sensitivity thresholds. Contrast sensitivity was measured with Volkov's charts (sinusoidal gratings) at eight spatial frequencies from 0.4 to 17.5 cycles deg<sup>-1</sup>. All subjects had a complete ophthalmologic examination and had normal visual acuity. Mean visual thresholds in the peripheral and parafoveal visual-field locations were lower in patients with pituitary adenomas than in healthy persons with normal vision. Jankauskienė et al (1997 *Perception* 26 Supplement, 63) found that visual-field loss in patients with thyroid neuropathy (with optic-nerve compression) accompanies a loss in visual acuity. We found that contrast-sensitivity thresholds were reduced in 83.5% of cases (mainly at low spatial frequencies) especially for those persons who had peripheral visual-field loss. Our results show that visual-field threshold testing and contrast-sensitivity threshold measurement are very sensitive at detecting early damage to the chiasma and more effective than measurement of visual acuity.

◆ **The delay effect in kanji recognition produced by prolonged viewing of adaptation characters: Effects of presentation in the right/left visual fields**

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When a kanji character is viewed steadily and continuously, the character often becomes unrecognisable as a whole pattern, while its parts remain clearly recognisable. This phenomenon is a kind of 'Gestaltzerfall' which has been reported to occur in the perception of relatively complex familiar patterns after prolonged viewing of them.

In the present study, test kanjis were presented in the right or left visual field after prolonged viewing of an adaptation kanji. Subjects were asked to judge whether the test kanji was the

same as the adaptation kanji. For the different pairs, one or two parts of the kanjis had different shapes or different dispositions. When the test kanjis were presented in the right visual field, the 'different' responses were faster than the 'same' responses and there was no delay effect caused by prolonged viewing of the adaptation kanji. In contrast, when the test kanjis were presented in the left visual field, the 'different' responses were not faster than the 'same' responses. Moreover, when the adaptation kanji was viewed for a longer period, the 'same' responses were significantly delayed. The speeds of 'different' responses were almost equal in both visual fields. These results suggest that the adaptation and test kanjis were matched serially in the left hemisphere, while they were matched in parallel in the right hemisphere. Therefore there is a possibility that kanji patterns may be represented by part-based descriptions in the left hemisphere, and by wholistic configurations in the right hemisphere. The prolonged viewing may have a disruptive influence mainly on the wholistic representations.

◆ **Restoration and improvement of stereovision by means of learning to perceive random-dot stereograms**

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Standard courses for treating strabismus and/or amblyopia are usually quite effective in increasing visual acuity and eliminating eye deviation but much less effective in restoring or developing stereovision. After such treatments, many patients still remain stereoblind. We tried to achieve stereovision in such patients using interactive test and training software CLASS based on random-dot stereograms (RDSs). The patients were taught to perceive 3-D figures hidden in RDSs by means of two different procedures: (i) to facilitate separation of test figures from background, in the visual image designed for the suppressed/amblyopic eye the dots belonging to test figures were made essentially brighter than the dots of the background, thus making it possible to recognise test figures not only on the basis of disparity but also of the difference in brightness; during training, this difference was progressively decreased; (ii) to give some advantage to the suppressed/amblyopic eye, the brightness of all dots in the image designed for the better eye was gradually decreased. As a rule, in the first stage of training the first procedure was used until the patient could recognise test figures without difference in brightness, ie using purely binocular mechanisms. After that, the second procedure was added to increase the stability of stereovision. Sixty-eight stereoblind patients underwent such training. Positive effects of CLASS exercises were recorded in all subjects: stereovision was restored to nearly normal level in thirty-four subjects, and to somewhat lower level in twenty-eight subjects; only six patients remained stereoblind, but even in these cases significant positive changes in binocular functions took place.

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◆ **The detection of visual perception disorders with a size – form discrimination test and EEG data**  
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To detect visual perception disorders (VPDs), we developed an interactive computer system for size discrimination testing (Ruseckaite, Raskinis, and Lukauskienė, 1997 *Perception* 26 63). This system comprises a test procedure, a database for testing answers, and a machine learning algorithm for the creation of rules and regularities. The rules are created according to the test results. Those in whom the tests revealed the same brain lobe damage and EEG patterns were found to have the same size-discrimination thresholds. Using these data, we could derive rules for preliminary classification of brain damage, ie if ten persons had temporal lobe damage and showed similar size-discrimination thresholds, we could state that an eleventh person, whose results were similar to those of the ten, would also have temporal lobe damage.

We performed 420 computerised tests on patients with damage in temporal and occipital regions, established by EEG. In parallel, we recorded EEG data for those patients. The EEG data and the test results were evaluated by computerised methods (Ruseckaite, Raskinis, and Lukauskienė, 1997 *Biomedical Engineering*, 118) in order to establish the relation between the EEG data and VPDs. According to the computerised methods (Raskinis, 1985 *Artificial Intelligence* 56) we created rules, which allowed us to classify patients with VPDs into different groups depending on the degree of brain damage. In conclusion we can state that the EEG data correlated with the VPD size – form discrimination data. In turn, because patients exhibiting similar brain damage also have similar EEG data, their size-discrimination test results will also correlated.

These methods of VPD detection could be used for predicting size – form discrimination test results from EEG data even for healthy persons.

◆ **Residual vision in hemispherectomy**

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We have investigated residual vision in two hemispherectomised subjects using bright patterns of light as described by Torjussen (1978 *Neuropsychologia* 16 15–21) and Marcel (*Brain* in press). The particular interest of such cases is that there is no functional cortex contralateral to the blind hemifield, and hence visual processing, if it exists, is presumably mediated by subcortical pathways either in the lesioned hemisphere and/or via commissures to the remaining hemisphere.

Patterns could be projected into the blind hemifield, the intact hemifield, or both. 'Completion' refers to a situation where patterns presented in the blind field are not reported by the subjects; stimulus presentations restricted to the intact hemifield are perceived, but when both hemifields are stimulated, subjects report the complete pattern. This 'completion' phenomenon in the past has led to inferences about residual function of the blind hemifield being uncovered by facilitation provided by the intact hemifield. We have found positive evidence of completion phenomena in both hemispherectomised subjects. But, before one can draw firm conclusions, particular conditions must be satisfied to rule out other interpretations, such as the possibility that information might be conveyed indirectly by diffusion of light into the intact hemifield.

◆ **Visual asymmetries in the perception of simultaneously presented objects**

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Hints on perceptual asymmetries in normal observers have already been reported since the very beginnings of experimental psychology [Helmholtz, 1896 *Handbuch der Physiologischen Optik* (Leipzig: Voss)]. Since handedness is also considered to be correlated with findings on asymmetries, the present study aims at elaborating on the perception of the size of simultaneously presented stimuli and its possible correlation with the observers' handedness.

In the first experiment, two horizontal lines were briefly (50 ms) presented above and below a fixation cross. Participants had to discriminate, using a 2AFC method, which of the lines appeared as longer, until in an up-and-down staircase procedure the lines became subjectively equal. In the second experiment, two circles were flashed (50 ms) to the left and to the right of fixation. The task was to decide which circle appeared to be larger until the point of subjective equality was reached.

A horizontal line located above the fixation cross was perceived as longer than the reference line below. Presenting simultaneously two circles to the left and to the right of the fixation cross resulted in a larger percept of the circle to the left. These effects are seen in right-handed and left-handed subjects. Further investigations will test if eg the direction of reading is involved in these size-estimation asymmetries.

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◆ **Factors that affect the implicit processing of motion**

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When subjects are presented with two similar pictures that have motion implied in them, recognition memory for the second picture is often found to be distorted forward along the plane of implied motion. This phenomenon is known as representational momentum.

We manipulated various factors and observed the effects they had on the production of the representational-momentum effect. The freeze-frame technique of Freyd was employed: this entailed the subjects being presented with a picture of a complex scene involving motion—a kettle pouring water into a cup. After an interval of 250 ms a second picture was presented to the subjects. This picture contained the same target item but on a different plane of implied motion, either forward or backward. The first variable to be investigated was the effect of presentation time of the first picture in the pair. The pictures were presented at 250, 500, 750, and 1000 ms intervals.

It was found that a greater representational-momentum effect occurred in the 250 ms condition. The role of mental imagery (as measured by self-report questionnaire) in the production of the representational-momentum effect was then investigated by comparing the difference in reaction times between the low and high mental imagery group for the forward and the backward pictures. The results indicate that the low-imagery groups produced more of a representational-momentum effect than the high-imagery groups. These results are discussed in terms of oculomotor and visual processing dynamics.

◆ **Eye-movement impairments following damage to human prefrontal cortex**

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A patient with a lesion largely confined to the right ventrolateral prefrontal cortex (VLPFC) was assessed on a range of oculomotor paradigms. The patient's reflexive saccades were found to be normal but he was found to be unable to suppress making reflexive glances to the target ('pro-saccade' errors) in the anti-saccade paradigm. By contrast, when asked to verbally report the required direction or to make anti-pointing movements, his performance was flawless. He could also suppress his reflexive glances to a variable degree when tested on delayed-saccade, memory-guided saccade, and maintain fixation paradigms. Under these conditions a directional asymmetry was observed with more reflexive glances being made to targets in the contralesional hemifield. The patient's deficits do not, therefore, appear to reflect a loss of control over his ability to generate saccades, nor does it appear to be a generalised problem of heightened distractibility. Furthermore, the patient's lesion did not encroach on the area of cortex considered to be the location of the frontal eye fields (FEF) in man (Paus, 1996 *Neuropsychologia* 34 475–483) and so his deficits cannot be attributed to direct damage to this region. The patient was also found to be severely impaired on tests of spatial working memory, and it is suggested that his deficits may be related to the process involved in maintaining information 'on-line' for the suppression of a pre-potent response.

◆ **Effects of visual task on dark focus and instrument myopia**

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Although it is known that optical instruments can induce a myopic shift in the observer's eyes (instrument myopia) and that the accommodation system can be influenced by nonvisual factors, it is not clear whether the degree of instrument myopia can be predicted from measurement of tonic accommodation (TA). In the present study eight subjects undertook two different visual tasks through an electro-optical instrument. In one experimental session the subject was required to undertake a simple visual-search task consisting of maintaining a sharp image at all times. In the other experimental session the subject was required to view a series of photographic scenes. TA was measured, after 5 min dark adaptation, before and immediately after the visual task which lasted 40 min.

All subjects exhibited instrument myopia in both experimental sessions. There was no effect of task on the level of instrument myopia. There was a shift in TA between the pre-task and post-task conditions. For the visual-search condition pre-task TA was weakly correlated to the level of instrument myopia ( $r^2 = 0.24$ , ns) whereas post-task TA was more closely correlated with instrument myopia ( $r^2 = 0.59$ ,  $p = 0.05$ ); there was no significant correlation for the other condition. These findings suggest that instrument myopia is task-insensitive, but can induce changes in the accommodation system which are reflected in a subsequent shift in TA. The low correlation between pre-task TA and instrument myopia also suggests that, unlike the other anomalous myopias, factors other than TA level are important in determining the level of instrument myopia.

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◆ **The methods for rehabilitation of visual perception disorders in persons with damaged temporal lobe of brain**

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Exploiting the data of Bertulis and Bulatov (1994, *Perception* 23 Supplement, 25) and Ruseckaite, Raskinis, and Lukauskienė (1997, *Perception* 26 Supplement, 63) we developed a computerised interactive system for rehabilitation of patients with damaged temporal lobes and a variety of visual perceptual disorders such as visual hemineglect and impaired spatial vision. Our objectives were: (a) to better diagnose these kinds of visual perceptual disorders; (b) to train and rehabilitate patients; and (c) to collect and analyse data from patients who can be treated, and provided with new skills as a result of intensive training. Patterns of the test program depended on the nature of visual perceptual deficit and consisted of several kinds of procedures: (i) comparing various sizes and forms of geometrical figures with sizes from 0.2 to 3.0 deg; (ii) contrast-sensitivity testing at eight spatial frequencies from 0.4 to 18 cycles deg<sup>-1</sup>, and (iii) measuring visual thresholds with the Humphrey field analyser by means of peripheral 68-point screening test. We performed 72 measurements in patients with damaged right and left temporal lobes. Patients with unilateral spatial neglect had a specific disability to disengage their attention from a given object in order to reallocate it to another object positioned to its left or right. Persons with hemineglect of the visual field were unable to concentrate their attention to two simultaneously presented stimuli. After a course of rehabilitation, this handicap was not so marked, as evidenced by the changes in contrast sensitivity (especially at low and high frequencies) and visual-field thresholds. In patients without hemineglect, contrast-sensitivity changes and visual-field threshold changes were not so noticeable.

**COLOUR MECHANISMS AND COLOUR CONSTANCY**

◆ **Differential thresholds in colour perception: A consequence of retinal processing and photoreceptor nonlinearities**

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We propose here a model for just noticeable differences in colour. We start from the data of six observers found in three different studies. Observer PGN described first by MacAdam (1942 *Journal of the Optical Society of America* 32), observers WRJB and DLM found in Brown and MacAdam (1949 *Journal of the Optical Society of America* 39), and observers GF, AR, and GW found in Wyszecki and Fielder (1971 *Journal of the Optical Society of America* 61 9). LeGrand (translated by Knoblauch, 1994 *Color Research and Application* 19 4) showed that the differential thresholds of colour in the lms space follows a V-shaped curve for the chromatic variables *L* and *M*. This property was confirmed by the study of Nagy et al (1987 *Journal of the Optical Society of America A* 4 4) for the six observers. In our model, the stimulations, considered in the lms space, are converted after photoreceptor nonlinearity into an lms space [ $l = L/(L + L_0), \dots$ ]. The retinal circuits combine lms signals into a multiplexing of two colour-opposition 'ci' and one achromatic 'a' channels, providing a 'perceptual space' (a, c1, c2). Supposing that the just noticeable differences are uniformly distributed in this space as spheres of constant radii, the backward transformations of these spheres into the lms space should produce ellipsoids, as those observed in perceptual experiments. By using the experimental data, we parametrise this model in order to find a best fit to the data. We show that this produces the expected behaviour, leading also to the explanation of other results such as the V-shaped differential thresholds.

◆ **Functional equivalence of visual scenes: Implications of theories of colour constancy**

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In a given visual scene, the perceived colour of any part is determined not only by the colour coordinates of the emitted light, but also by the colour characteristics of the whole scene. This well-known fact is a necessary condition for colour constancy. Various formal theories of colour constancy differ in the description of this dependence.

We define two visual Mondrian-like scenes to be functionally equivalent with respect to a given fixed patch if they influence the perceived colour of that patch in the same manner. More precisely, two surrounds of a fixed patch (eg a circular disk in the centre of the scene) are called functionally equivalent if the perceived colour of this patch is the same in both scenes whenever the colour coordinates of the patch coincide.

Prominent theories of colour constancy imply different predictions concerning the functional equivalence of surrounds. In a series of experiments, surrounds were constructed systematically in order to test those predictions. For one class of (Seurat-like) surrounds, the average of the colour coordinates was fixed whereas their variances in colour space were varied. The criterion was a unique yellow setting, so the subjects had to determine the red–green-equilibrium point for the disc in the centre. The results contradicted most predictions, but there were hints that the spatial configuration of the codes of the other patches in colour space might play an important role in determining the perceived colour of the centre.

◆ **Spatial edges reduce colour selectivity**

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Sensitivity to 1 deg spectral spots flashed at 1 Hz on a photopic white background is determined by colour opponency. Using Maxwellian view we measured spectral sensitivity with a 1 deg spot, a 'large' bar (0.5 deg × 3.0 deg) and a 'thin' bar (0.06 deg × 1.3 deg) on a 10 deg background field (1000 td). The background was either white (3400 K) or yellow (2400 K). Temporal sensitivity was also assessed with these stimuli under similar conditions at 450 nm and 574 nm.

Elongated bar stimuli generated spectral sensitivity functions markedly different from those obtained with a 1 deg spot; particularly affected were the blue peak at 450 nm and the Sloane notch around 575 nm. The temporal data show that with the spot stimulus two peaks are obtained in the function; these are consistent with the operation of one sustained and one transient filter. With the elongated bar stimuli, however, three localised peaks are obtained, consistent with the operation of one sustained and two transient channels.

We conclude that both the distortion of the spectral sensitivity function and the presence of different channels in the temporal function, when bars rather than spots are used, demonstrate the operation of response mechanisms that are not related to colour opponency. Thus the introduction of elongated spatial edges in colour stimuli may jeopardise their colour selectivity.

◆ **Perceptually optimal quantisation of colour natural images**

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The human visual system combines signals from the three types of cone photoreceptors into two opponent-colour components (red–green and blue–yellow) and an achromatic component. In order to design an optimal perceptual image-coding scheme, we studied the perception of colour distortions due to the quantisation used in a sub-band image representation. We measured these quantisation laws on natural textures and for the two chromatic components defined by Krauskopf (1982 *Vision Research* 22 1123–1131), taking into account the spatial combination of distortion. Previous studies have shown that the optimal quantisation laws on achromatic contrast are uniform (Senane, 1995 *ICIP'95 Conference*, pp 97–100).

The results obtained for colour components of two natural textures showed that optimal quantisers on the red–green component are also uniform. However, the quantisation laws on blue–yellow component did not have the same properties. We observed that the values of the decision thresholds and reconstruction levels follow a monotonically increasing function, which has been fitted with a power function. In both cases, the quantisation parameters were dependent on image spectral features.

To inhibit such dependence, we introduced a spatial-frequency decomposition. The visual sub-bands used here are derived both from Watson's studies (Watson, 1987 *Journal of the Optical Society of America A* 4 2401–2417) and from our previous results on the achromatic component. In other words, we have separated the colour image information into five sub-bands (one low-pass and four directional high-pass frequency sub-bands) for each of the two colour components and measured the quantisation laws on each of them. Inside each spatial-frequency sub-band the measured quantisation parameters were constant for all textures used, showing, first, the uniformity of red–green quantisation laws and, second, a monotonic increase of blue–yellow quantisation parameters. Quantisation noise of red–green components must be equally distributed over its amplitude range, as opposed to blue–yellow noise which can be higher for high colour contrast.

◆ **Perceptual uniformity of CIECAM97s colour scales**

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There are three categories of colour differences (steps): JNDs (just noticeable differences), small differences (by industrial pass/fail decisions), and large differences (neighbouring elements of colour scales). It seems worthwhile to investigate the equidistance of steps in scales based on colour-appearance models. CIECAM97s is an internationally agreed colour-appearance model. One output of this model is:  $H$ (hue) +  $C$ (chroma) +  $Q$ (brightness). Our question is are  $H$ ,  $C$ , and  $Q$  scales of mathematically equal steps perceptually uniform in the viewing condition of a computer-controlled colour VDU monitor in dim surrounds?  $H$ ,  $C$ , and  $Q$  scales were displayed on a colorimetrically calibrated monitor. A colour scale consisted of eight squares separated by spaces of grey. Five observers had to find those colour square(s) where the perceptual step was too large or too small related to the average colour step between squares, and rate the equidistance of steps by a number between 1 (best) and 5 (worst). Relatively large deviations from equidistance were found in the case of hue scales. The mean rating was 2.80. Brightness scales seemed to be more equidistant with a mean rating of 2.13. Chroma scales showed best correlation with the CIECAM97s model. The mean rating was 1.95.

◆ **S-cone input into the red – green opponent-colour mechanism in a detection task**

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In previous work (Bonnardel et al, 1997 *Documenta Ophthalmologica, Proceedings* 59 145), we concluded from the comparison between spectral modulation sensitivity functions (SMSFs) for deuteranopes and normal trichromats that the extension of sensitivity to higher comb-frequencies in normal trichromat observers depended on the response of the red – green mechanism. In the present experiment we have investigated the cone inputs that constitute the colour-opponent mechanisms by measuring SMSF in two different scales.

Sinusoidal modulations of spectral energy (comb-filtered spectra) are performed over the wavelength or the wavenumber scale for 12 comb-frequencies (0.5 – 4.3 cycles per spectral window). The observer monocularly viewed a test spot of 1.8 deg. A dark annulus delimited the test spot from a background of the same luminance. In a detection task, the observer indicated whether or not a change occurred during the 2 s presentation of a drifting comb-filtered spectrum of temporal frequency of 1 Hz.

The effect of changing the scale produces differences in the profile of empirical SMSFs of two normal trichromat observers. The best fits to empirical SMSFs were obtained with a yellow – blue mechanism with an S-cone input opposed to a combination of L-cone and M-cone inputs, but the red – green mechanism required S-cone input combined to L-cone input opposed to M-cone input instead of the usual simple L – M-cone opponency.

◆ **Colour processing in the primate outer retina: a simulation study of horizontal cell function**

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Colour processing in the primate retina is not well understood. In contrast to turtle and teleost retinae there are no colour specific signals in primate horizontal cells. They only show hyperpolarisation to light stimuli of different wavelengths. Some authors conclude that primate horizontal cells are not engaged in colour processing.

The effect of horizontal cell activity is a negative feedback onto cone pedicles. This feedback modulates the cone output signal. In this way horizontal cells might well be engaged in colour processing. In a simulation study we examined the function of H1 and H2 horizontal cells in the primate retina. Primate H1 cells are bidirectionally coupled to red and green cones, H2 cells to all cone types with strongest connection to blue cones. Horizontal cells of one type are electrically coupled among each other but not coupled to the other type.

We transformed this cell network into a computer model using NeuronC, a simulation language for retinal structures developed by R Smith, University of Pennsylvania. Simulation studies with these structures show that the first steps of possible colour-opponent mechanisms could be implemented in the following way: the red and green components are realised by feedback modulated hyperpolarisations of red-cone and green-cone signals respectively. Blue – yellow opponency can be found in the blue-cone output: horizontal cell feedback causes hyperpolarisation with the short wavelengths and depolarisation in the 'yellow' band (520 – 610 nm).

◆ **Colour and lightness of a surface seen behind a transparent filter**

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We measured how the colour and lightness of a surface seen to lie behind a transparent filter depend on filter properties. A convergence model suggests that a filter's transformation of chromatic information from underlying surfaces is interpreted as a convergence in colour space (D'Zmura, Colantoni, Knoblauch, and Laget, 1997 *Perception* 26 471–492). Such a convergence is described by a transparency parameter alpha and by a colour that acts as the centre of convergence.

We used an asymmetric matching task to test the model. In computer-graphic simulation, observers adjusted the colour of a surface seen behind a transparent colour filter in order to match the colour of a surface seen in plain view. We varied the lightness and chromatic properties of both the surface to be matched and the transparent filter. We found that the convergence model fitted the matching data nearly as well as a more general affine transformation model, even though the latter has many more parameters (twelve) than the former (four). Linear transformation, translation, and Von Kries scaling models all performed poorly.

The convergence model of transparency is a general model of colour constancy. It can account for shifts in colour, such as those caused by changing the spectral properties of illumination, and can also account for shifts in contrast, like those caused by fog or by change in the spatial distribution of illumination.

◆ **Ultrarapid visual categorisation of natural scenes is colour-blind**

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Using a go/no-go categorisation task, we recently showed that both humans and monkeys are fast and efficient at detecting animals in natural images flashed for only 20–30 ms. The visual processing can be done in under 150 ms in humans and may be even faster in monkeys. Such rapid processing is likely to depend essentially on feedforward processing and on the fastest visual information transmitted. Recent neurophysiological data (Nowak et al, 1995 *Visual Neuroscience* 12 371–384) demonstrate that the earliest responses in the visual cortex originate from the magnocellular stream, whereas chromatic parvocellular information is delayed by roughly 20 ms.

To test whether longer-latency parvocellular chromatic information is used in ultrarapid visual categorisation, we tested humans and monkeys with 400 previously unseen images, randomly presented half in colour, half in black-and-white. The effect of removing colour information was marginal both on accuracy (monkey: no effect, human: 2% decrease) and on median reaction time, RT (10 ms increase). In humans, the analysis of evoked potential showed that the strong differential response to targets and distractors started at 150 ms in both conditions. Moreover, the advantage for coloured stimuli was directly related to RT, so that subjects with long RTs performed better with coloured images whereas subjects with the shortest RTs showed little or no advantage with chromatic stimuli.

Such results support our hypothesis that ultrarapid visual categorisation involves essentially feedforward processing, since even information arriving in visual cortex with a 20 ms lag appears to have no influence on behaviour.

◆ **Simple reaction time and spatial summation in the L/M-constant and S-constant cone axes**

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Previous work concerning spatial summation in the time-varying detection of stimuli was focused mainly on changing luminance. The results obtained were related to the number of photoreceptors involved. Ueno has shown the usefulness of reaction times (RTs) as a measure of spatial summation at suprathreshold levels (Ueno, 1979 *Journal of the Optical Society of America* 69 1023–1028).

In the present study, we measured RTs for equiluminant stimuli changing in size from 8 min of arc to 10 deg. The stimuli also had chromaticities that caused variations in the signal of either the L – 2M channel or the L + M – S channel, as in Boynton's two-stage colour-vision model. Thus, the L and M cones are responsible for the changes in the L – 2M channel and the S cones for the variations in the signal of L + M – S channel. We adopted the hue-substitution method to avoid the response of the luminance channel (Nissen et al, 1977 *Perception & Psychophysics* 22 457–462). All the stimuli were displayed on a CRT colour-monitor screen that was

calibrated with a Spectra Scan PR-704 computer-controlled spectroradiometer. We plotted the logarithm of the product of RT and stimulus size vs the logarithm of stimulus size at a given channel variation. Spatial summation was fulfilled for a maximum stimulus size which was less for the L – 2M channel (32 min) than for the L + M – S channel (1.5 deg), this value coming down when the channel variation was increased. Furthermore, there was no spatial summation for variations greater than 120 td in the L + M – S channel and 15 td in the L – 2M channel. These results are discussed in connection with L-, M-, and S-cone distributions in the retina.

◆ **Rod-and-cone temporal summation during dark adaptation**

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To investigate the changes in rod-and-cone temporal summation during the time course of dark adaptation, thresholds for 585 nm (0.7 deg or 2.0 deg diameter) targets differing in duration (8 to 500 ms) were determined by randomly interleaved staircase procedures. The targets were presented at 20 deg in the temporal retina following partial (62% cone, 67% rod) or full (>99%) bleaches with a white (3200 K) Ganzfeld. Two typical complete achromats, who lack functioning cone vision; an individual with the complete type of congenital stationary night blindness (CSNB), who lacks normal rod function; and three normal trichromats served as observers. Temporal summation was estimated by the critical duration method.

Temporal summation in normal observers is minimal (~30 ms) immediately upon extinction of the full bleaching light. Within the first minute in the dark, it increases to a value of ~150 ms. A prolonged, further increase to a final value of ~270 ms coincides with the cone-rod break in the dark-adaptation curve.

The delayed increase in temporal summation was not found in the CSNB observer, who displays no cone-rod break. His maximum value was ~140 ms. The minimal temporal summation value in the achromats was ~100 ms, which increased slowly and continuously to a maximum value of ~270 ms, after 25 min in the dark. The different dynamics for the three types of observer provide insight into the temporal-summation mechanisms of the rod-and-cone visual systems.

◆ **Opponent rhodopsin receptor in rod and opponent iodopsin receptor in cone to underlie the human colour perception**

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The short-wave, middle-wave, and long-wave cone receptors with their spectral curves conventionally chosen from the multitude of vector rotations in the three-dimensional colour space cannot explain some visual phenomena. Mathematical simulation of elementary visual stimuli for subject-selective image quality metrics (Gavrik, 1998 *Proceedings of the SPIE* 3409 12) has detected self-filtering colour-separation facilities of rhodopsin in rods and iodopsin in cones. The light absorption in a receptor's front displaces by over 40 nm the spectral sensitivity of the remaining part at some concentration or thickness ratios. A negative or positive difference of the partial spectral responses can determine a blue or yellow complementary saturation response of a rod and a similar red-green response of a cone. Their neutral points, 495 or 570 nm, are directly observed by dichromats lacking in cones or a partial response. Every colour impression is then induced by the saturation responses of a non-complementary pair of the basic colours whose hues are not distorted by other receptors at 570 (yellow), 420 (violet-blue), 495 (green), and 650 nm (red). With increasing light, the yellow and violet-blue colours appear at once, then green and red do so after the partial responses become comparable in rods, then in cones. The third independent colour response, grey-white, is a sum of partial responses, and in its pure state corresponds to both the receptors in neutral points. The model consistently explains all kinds of colour deficiencies, the Bezold-Brücke and Jones-Lowry effects, foveal tritanomaly, peripheral protanomaly, and E Land's two-stimulus (eg 570 and 590 nm) polychrome images.

◆ **Production of psychophysical stimuli by partitive mixing of images**

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Multiple digital images of a scene have been acquired, with modifications made between acquisitions. By partitively mixing the images (eg 70% A, plus 20% B, plus 10% C), images of other possible scenes have been created. Experiments have been made with modifications of four scene aspects: (i) geometry and intensity of the illuminants, (ii) spectral composition of the illuminants,

(iii) colour of a scene object, and (iv) reflectance properties of an object. That partitive combinations correspond to possible scenes in cases (i) and (ii) follows from the linearity of luminance with respect to the intensity of the illuminants. In cases (iii) and (iv), partitive combinations correspond to possible scenes if there are no rays that encounter the modified object multiple times. This has been confirmed by using snooker balls for the modified object. In the absence of inter-reflections, the image of a blue ball (with shading and highlights) has been partitively mixed from images of black, white, red, and yellow balls. In the presence of inter-reflections the mixed image has areas brighter than in the true image, as predicted theoretically.

The space of partitively mixed images has an affine structure. The mixed images can be used as psychophysical stimuli and responses mapped across this affine structure. For example, by allowing mixing with negative components (eg 80% black, plus 40% white, minus 20% yellow), images of snooker balls that look reasonable, too light, or too dark have been generated. The surface separating possible and impossible snooker balls has been partially mapped.

◆ **Nonlinearities in red/green equilibria and the increment–decrement distinction**

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Red/green equilibria (unique blue) were experimentally determined for central fields surrounded by a fixed homogenous surround, *S* (unique yellow). Classical two-process theories imply that in such a situation the primary colour codes of the red/green equilibria form a (*S*-dependent) plane in three-dimensional photoreceptor space. Mausfeld and Niederée (1993 *Perception* 22 427–462) proposed a specific contrast code (the so-called octant model), which, for each cone channel, postulates a different *S*-dependent multiplicative transformation for increments and decrements. This model is related to the well-known models of Walraven, Shevell, and Hurvich and Jameson, which do not introduce such an increment–decrement distinction, however. Such a distinction has been supported by data of Mausfeld and Niederée (unique yellow settings for red surrounds). These predictions have turned out to be also in line with the data of Chichilnisky and Wandell.

In the present study the geometrical implications of a two-process model are considered which assumes a linear opponent transformation of the aforementioned contrast code assumed by the octant model. Such a model implies that the primary codes of red/green equilibria form a creased plane, with creases occurring at the octant boundaries and joining in *S*.

Thus the novel prediction is made that in certain colour-cancellation experiments multiple kinks should show up in the data. This prediction was confirmed in the case of unique blue settings in yellow surrounds. Previous studies allowed us to identify only single kinks of this kind. The present study is the first to deal with the occurrence of multiple kinks. Such multiple kinks indicate that the relevant increment–decrement distinction occurs at the level of cone channels (as opposed to a luminance-based increment–decrement distinction).

◆ **Effects of surface perception on colour splitting in transparency**

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When transparency occurs, we can simultaneously perceive two surfaces in an overlapping area. For chromatic transparency, the overlapping area has physically a single chromaticity, but perceptually it is split into two surfaces with two different chromaticities. In this study, we show that the perception of a surface could change the chromatic appearance of the overlapping area.

The stimulus surface was filled with random dots with 50% density. The display was divided diagonally into two regions. A square region (1 deg × 1 deg) was presented at the centre of the display. The left upper and the right lower surrounding regions consisted of red dots ( $x = 0.367$ ,  $y = 0.303$ ) and green dots ( $x = 0.249$ ,  $y = 0.359$ ), respectively. The centre square region had white dots whose chromaticity was drawn from the additive colour-mixture line between the red and the green in the surrounding regions. Two squares (3 deg × 3 deg) appeared in motion in each surround. These were arranged so that the centre square became the overlapping region. We measured the percentage of trials in which the centre region was perceived to be transparent as a function of the speed in the centre. We found that the centre square dramatically changed in appearance from opaque to transparent with its speed. Transparency occurred when the red, green, and white regions moved at the same speed. When all regions were static, and only the centre region moved, observers did not perceive transparency. It appears that transparency occurs only when all regions are perceived as the same continuous surface.

◆ **Understanding colour appearance phenomenology: Can variation in photopigment opsin genes give rise to individuals with perceptual tetrachromacy?**

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Research on cognition and colour appearance often uses the accepted theory of trichromatic colour vision for the purposes of modeling higher-order colour sensations. Existing results in the molecular genetics of colour vision imply that certain individuals express more than the standard three retinal visual photopigments posited by trichromacy. Can individuals with retinæ composed of more than three types of cone photoreceptor visual pigments experience colour sensations which differ from those experienced by an individual expressing only three 'normal' visual pigments?

We investigated this question by assessing the colour perception behaviours of individuals grouped by their classes of photopigment opsin genes as identified through polymerase chain reaction (PCR) genetic assays. Individuals genetically identified as dichromats, trichromats, and varieties of individuals with nonstandard photopigment genetic variations (including heterozygous and polymorphic variants) were assessed for colour perception capabilities by empirical methods similar to those previously found in the literature (Smeulders, Campbell, and Andrews, 1994 *Vision Research* 34 927–936). The results clarify to what extent gender-based differences in colour appearance are mediated by variations in photopigment opsin gene expression. We discuss the implications of these results for cognitive models of colour appearance phenomenology.

◆ **Comparison of visual reaction time for chromatic changes under monocular and binocular conditions**

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We tested visual reaction times for luminance changes and visual reaction times for L – 2M and L + M – S variations at isoluminance according to Boynton's two-stage colour-vision model. All the reaction times were determined binocularly and monocularly for each eye. Three observers took part in the experiments. The stimuli were presented on a colour monitor at a 2-deg field size. The condition of isoluminance was achieved by the flicker method, under binocular as well as monocular conditions for both eyes. For stimuli at equal luminance, we used the hue-substitution method, for which we selected twelve stimuli with L – 2M variations and another twelve with S variations. The results obtained for all the observers confirm the binocular summation over the reaction time for changes in luminance, whereas for chromatic variations at isoluminance there were no significant changes between the binocular and monocular reaction times, or the magnitude of the summation was much smaller than for luminance variations. These results show that chromatic variations are processed by the visual system less efficiently than those of luminance, as reported in previous works concerning stereopsis (J R Jiménez et al, 1997 *Vision Research* 37 591–596) and do not involve, at least significantly, binocular summation.

◆ **Modelling the human blue–yellow chromatic channel**

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Human colour vision is based on three cone types (S, M, and L) in the human retina. The cone signals are first combined in the retina and then processed further to create an achromatic (luminance) and two chromatic channels (red – green and blue – yellow), which allow us to see and discriminate colours.

According to our model of human spatial vision (Rovamo et al, 1994 *Vision Research* 34 1301–1314 and 2773–2778) contrast sensitivity  $S$  depends on the spectral density of noise  $N_e$  as follows:  $S = S_{\max}(1 + N_e/N_c)^{-0.5}$ , where  $S_{\max}$  is the maximum sensitivity and  $N_e$  the spatial equivalent of the spectral density of internal neural noise.

Let us now assume that the blue–yellow channel is

$$c_{BY} = [a(ds + s)/s + a'(dm + m)/m + a''(dl + l)/l],$$

where  $a$ ,  $a'$ , and  $a''$  are the weights of cone contrasts. Their sum is nil, as the blue–yellow channel is assumed to carry no luminance information. Thus,  $N_e = (ac_s + a'c_m + a''c_l)/p^2$ , where each  $c_w = dw/w$  and  $p^2$  is the noise check area.

In order to determine the weights of the cone contrasts in the blue–yellow channel we measured contrast sensitivity in a 2AFC detection task as a function of noise spectral density by using various combinations of S-, M-, and L-cone-specific spatial noises to mask an S-cone-specific horizontal 1 cycle  $\text{deg}^{-1}$  grating stimulating only S cones. By fitting the above equations of  $S$  and  $N_c$  to the contrast sensitivity data measured we determined the cone weights in the blue–yellow channel, which was found to be:  $c_{BY} = (0.619c_S - 0.338c_M - 0.281c_L)$ .

◆ **Difference scaling of image quality in compression-degraded images**

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Lossy image compression techniques allow arbitrarily high compression rates but at the price of poor image quality. Two of us (Charrier and Cherifi, 1998 *Proceedings of the SPIE 3308*, in press) have been studying vector quantisation as a compression technique for colour images. We applied the method of difference scaling to evaluate image quality of a series of fifteen images, each compressed to ten different levels ranging from 1 : 1 (uncompressed) to 30 : 1, and within each of eight different colour spaces. On each trial, the subject views two pairs of images representing four different compression rates. He judges whether the perceptual difference is greater between the first pair or between the second pair. Over the course of the experiment, the subject judges the differences of a subset of all possible quadruples (pairs of pairs). Using maximum likelihood methods (Maloney and Yang, 1997 *Perception 26* Supplement, 128), we then estimate a perceptual scale from the ensemble of judgments on quadruples of the ten compression levels from an image/colour space condition. In general, perceptual difference is an S-shaped function of compression rate. Some images, however, tolerate higher compression rates before they are perceived as different from the original. Thus, the maximum compression rate with the minimum image degradation should be tailored to the image. A challenge for image processing is to predict this optimum on the basis of indices calculated from the original image. Our data make possible a direct test of whether an image quality model is in agreement with human observers.

◆ **Language affects colour perception: evidence from multiple linguistic groups**

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The Sapir–Whorf hypothesis (SWH) asserts that language (or culture) affects colour perception (or cognition). We report here a large study of ten linguistic groups, including five quite different language types: Daghestanian (Caucasus), Niger-Khordafanian, Khoisan (both Namibia), Indo-European, and Sepik Ramu (Papua, New Guinea), carried out as a further test of the SWH. There were at least twenty first-language speakers in each sample; they were tested in their home villages usually by a first-language speaker of the appropriate language. The stimuli (65 coloured ‘tiles’) were an evenly distributed sample of colour space. Subjects named each tile and sorted them into groups on the basis of their appearance. The mean number of groups formed by each sample was similar (range 10.1–13.5), and correlations among the similarity matrices (number of subjects that put each pair of tiles in the same group) were high (range 0.7–0.9), indicating the group contents were similar. Principal-components analysis of the similarity matrices derived from naming and grouping showed independent factors with high loadings for each language for naming and grouping, suggesting that differences in language did not influence grouping. There were, however, some small but significant differences among the languages. Most notably, samples from the same linguistic family (and geographical area) were more similar to each other on the grouping task than to samples from more distant linguistic families and areas. Our data support the universalist position, but leave the door open for modest linguistic or cultural influences.

◆ **The effect of luminance and spectral adaptation upon subjective colours**

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The achromatic pattern of a rotating Benham disk induces subjective colours. The colours depend upon the phase relationship and the contrast between luminous signals of the arc and the background. Furthermore, colours vary with the luminance and the spectral power distribution of the light. Most explanations of the phenomenon are given in terms of low-level mechanisms.

We studied the effect of luminance and spectral adaptation upon subjective colours produced by a Benham disk (7 arcs, 45°) illuminated by various lights. The light spectral power distribution

was modified by means of colour filters (39 filters) and specified in terms of LMS cone excitation. Results of colour naming by four observers show that (i) the attributes of subjective colours are determined by post-receptoral channels combining L and M cone excitations in a synergetic (L + M) and in an antagonistic (L - M) mode; (ii) the effect of the (L + M) signal interacts with the effect of the (L - M) signal; (iii) the colour attributes resulting from this interaction vary with the arc onset; (iv) the effect of S cone signals is small and restricted to the arcs in contact with the black part of the disk. These observations lead us to propose that the mechanisms underlying subjective colours take place in a neurophysiological site high enough to allow the effect of the interaction between the synergetic and the antagonistic signals to be modulated by the duration of the white phase preceding the arc.

◆ **Colour naming by dichromats is more accurate than the standard model predicts**

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We report a study of colour naming by dichromatic boys under free viewing conditions. Thirty dichromats (twelve protanopes and eighteen deuteranopes) and twenty-nine normal trichromats were selected from a colour survey of 1631 5-9-year-old boys in Alcorcon City (near Madrid). The two samples did a colour-naming task with eleven stimuli, each a focal exemplar of one of the eleven basic colour categories. The stimuli were large (8 deg) and the exposure times were long (3 s). The normal trichromats named all the stimuli correctly. The dichromats were more accurate at naming the saturated (primary) stimuli—red, green, yellow, and blue—(90% correct), than the less-saturated stimuli—black, white, grey, brown, purple, pink, and orange—(about 60% on average). However, the dichromats' performance was more consistent with anomalous trichromacy than dichromacy (see Montag, 1994 *Vision Research* 34 2137, for similar results with adults). These data imply that standard tests such as the Ishihara or the City University Colour Vision Test will underestimate the dichromats' ability to use colour information. It appears that dichromats may have a red-green channel but with reduced capacity, perhaps mediated by an anomalous third pigment in the peripheral cones as suggested by Montag (1994).

◆ **Activation of human area V4 in a delayed match-to-sample colour task**

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Recent human-brain-imaging studies have shown that the ventral occipito-temporal cortex contains localised areas that contribute to 'higher-order' cognitive tasks involving colour, such as colour naming and colour knowledge. In this study we were particularly interested in short-term colour memory and the possible involvement, or otherwise, of area V4.

We employed positron emission tomography to measure changes in regional cerebral blood flow in a group of male volunteers ( $n = 6$ ) whilst they performed a delayed match-to-sample task. During scanning, subjects were asked to identify verbally either the colour or shape of a briefly presented (1 s) stimulus from four alternatives which were displayed after an interval of 8 s. During the delay they were also asked to perform a mental arithmetic task. Twelve scans were performed for each subject (six for colour and six for shape identification). The data were analysed with the use of SPM96b.

The comparison of the colour versus the shape versions of the task revealed bilateral activations in the ventral occipito-temporal cortex, on the fusiform gyrus (Talairach coordinates: left hemisphere = -20, -76, -24,  $Z$  score = 3.05; right hemisphere = 26, -70, -20,  $Z$  score = 3.14). The position of these cortical activations corresponds to the region previously identified by us as human area V4. This suggests that V4, as well as being activated by the passive viewing of colours, may also be involved in the short-term retention of colour sensory information.

◆ **Functional organisation of chromatic and spatial coding**

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The early stages of colour coding are well established in that a trichromatic receptor stage is followed by a set of opponent colour channels. One interpretation of the sequence is that opponent channels carry unrelated aspects of the colour stimulus, unlike the cone channels. The overlap of the cone channels can be removed by decorrelating their spectral sensitivity functions, and this procedure has been found to give opponent channels which match those found psychophysically.

Since the known spatial-frequency channels also show considerable overlap, it is reasonable to ask which aspects of the spatial stimulus are captured by decorrelating the spatial-frequency channels.

We have carried out such an analysis. The results of decorrelating the spatial-frequency channels are that the first decorrelated spatial filter acts as a broad bandpass filter which has a peak at approximately 12 cycles  $\text{deg}^{-1}$ , and the second decorrelated spatial filter acts as an opponent spatial-frequency channel, with a minimum output at a low ( $\sim 7$  cycles  $\text{deg}^{-1}$ ) spatial frequency and a maximum output at a high ( $\sim 20$  cycles  $\text{deg}^{-1}$ ) spatial frequency.

The characteristics of the first decorrelated filter closely resemble the properties of the foveal perceptive fields which have been used to explain the Hermann grid illusion. Thus, the decorrelation analysis produces a model for the functional organisation of chromatic and spatial filtering in the early visual pathway which is independent of the implementation at the neural and psychophysical levels, but which directly relates to the subjective appearance of stimuli.

◆ **Failures of relational colour constancy in achromatic and isoluminant images can be predicted from violations of invariance in cone-excitation ratios**

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Relational colour constancy refers to the constancy of the perceived relations between the colours of surfaces in a scene under changes in the spectral composition of the illuminant. Failures in this constancy may explain observers' ability to discriminate between colour changes caused by changes in illuminant and colour changes caused by changes in surface reflectance ('non-illuminant' changes). A possible physical basis for the constancy lies in the stability of ratios of cone excitations associated with light reflected from pairs of surfaces. But other quantities, such as ratios of sums and of differences of cone excitations, corresponding to luminance and chromaticity signals, are also highly stable under illuminant changes and could also provide a basis for constancy.

An experiment was undertaken to test whether relational colour constancy depends on either luminance or chromaticity cues alone. A two-interval forced-choice design was used in which pairs of computer-generated images of illuminated Mondrian patterns comprising  $7 \times 7$  patches were presented in sequence: in one interval, image pairs were related by an illuminant change; in the other, by a non-illuminant change. Observers had to identify which was which. The images were colorimetrically unconstrained or constrained to be either achromatic or isoluminant. For all three image types, observers made reliable discriminations, and their performance levels were accurately predicted by assuming that they based their judgments on the extent of violations of invariance in cone-excitation ratios. Relational colour constancy thus seems not to depend solely on either non-opponent or opponent signals, and may be subserved under all stimulus conditions by invariant cone-excitation ratios.

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◆ **Opponent responses under variable illuminant conditions: evaluation of red-green and blue-yellow signals in colour constancy**

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Colour constancy is usually defined as the constant colour appearance of surfaces independently of the illuminant. According to previous studies, colour constancy seems to be principally mediated at pre-opponent sites (Bäumli, 1995 *Journal of the Optical Society of America A* 12 261–271); other experiments, however, suggest that opponency could facilitate colour constancy [Brown, 1997 *Investigative Ophthalmology & Visual Science* 38(4) S898]. We have addressed the problem of how changes in chromatic signal influence colour-vision mechanisms under variable illuminant conditions.

We made asymmetric colour matches to analyse the influence of the illuminant in successive colour constancy. Sixteen colour surfaces were matched under five illuminants and with Mondrian surrounds as adapting fields. Surfaces were chosen along different critical axes in the cone-excitation space with an equienergy illuminant used as reference illumination.

Subjects' matches showed a deviation from colour constancy depending on both the surfaces matched and the colour-vision mechanism considered. When predicted and obtained colour constancy were evaluated along the blue-yellow axis, a significant dependence upon illumination was found. Along the red-green axis colour constancy was more uniformly processed. As expected, a general trend of increasing luminance was found for all matches. Results suggest that colour constancy is linked not only to an adaptation state at receptor sites but also to an adjustment of red-green and blue-yellow signals at opponent sites.

◆ **Categorical effects in colour perception: cross-language differences and category learning**

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The hallmarks of categorical perception are enhanced cross-category discriminability and reduced within-category discriminability. We have previously shown, using a successive same-different task, that speakers of English show categorical effects across the blue-green boundary, whereas speakers of languages with a generic blue-green (grue) category show no such effect (Davies et al, 1996 *Perception* 25 Supplement, 102). We explored the nature of the categorical effect further by using both a successive and a simultaneous same-different task. We assume that the perceptual component of the task is highest for simultaneous presentation, whereas the memory load is highest for successive presentation. English speakers showed a categorical effect under both conditions, whereas speakers of languages with a grue term showed no such effect in either condition. In experiment 2 we tried to induce a category effect within a pre-existing category (either blue or green). Subjects were trained on four successive days to categorise the stimuli into two adjacent non-overlapping sets in colour space based on either hue differences or lightness differences. On the fifth day we sought for categorical effects using the same-different task and for transfer of learning to a new stimulus set. Subjects showed more accurate judgments to the dimension they were trained on (hue or lightness) than to the other dimension, and they showed enhanced cross-category discrimination. Learning did not transfer to new stimuli. Colour perception in adults can be changed through training, and category effects can be induced within well-established categories.

◆ **The contributions of L, M, and S cones to the achromatic channel of human spatial vision**

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Human daylight vision is based on S, M, and L cones. Cone signals are combined and processed to create an achromatic channel transmitting luminance contrasts. According to our model of human spatial vision (Rovamo et al, 1994 *Vision Research* 34 1301-1314 and 2493-2502) contrast sensitivity  $S$  depends on the spectral density of noise  $N_c$  as follows:

$$S = S_{\max}(1 + N_c/N_c)^{-0.5},$$

where  $S_{\max}$  is the maximum sensitivity and  $N_c$  is the spectral density of the spatial equivalent of internal neural noise. Let us now assume that the achromatic channel is

$$c_A = [b(ds + s)/s + b'(dm + m)/m + b''(dl + l)/l],$$

where  $b$ ,  $b'$ , and  $b''$  are the weights of cone signals ( $dx + x$ )/ $x$ , where  $x$  is average luminance in each cone and  $dx$  is a deviation from it. The sum of weights is equal to unity so that the contrast of an achromatic grating is the same in the achromatic channel and physical world. When the zero-frequency component is removed by lateral inhibition,

$$c_A = (bc_S + b'c_M + b''c_L)^2 p^2,$$

where  $c_S$ ,  $c_M$ , and  $c_L$  are S-, M-, and L-cone contrasts and  $p^2$  is the noise check area. In order to find  $b$ ,  $b'$ , and  $b''$  we measured contrast sensitivity in a 2AFC detection task as a function of  $N_c$  by using various combinations of S-, M- and L-cone-specific spatial noises to mask an achromatic horizontal 1 cycle deg<sup>-1</sup> grating. By fitting the above equations for  $S$  and  $N_c$  to the measured contrast sensitivity data we determined the cone contrast weights in the achromatic channel, which was found to be  $c_A = (0.077c_S + 0.211c_M + 0.712c_L)$ .

◆ **Macaque retinal ganglion cell responses and human performance on a parafoveal equiluminant hyperacuity task**

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We recently reported (Rüttiger and Lee, 1997 *Perception* 26 Supplement, 118) that multiple, luminance and chromatic mechanisms can support performance on a hyperacuity task—the displacement of a vertical edge. With foveal fixation, displacement thresholds ranged from 15–30 s of arc at high luminance contrast and increased to 100–200 s of arc at 3% contrast, the detection threshold for achromatic edges. Chromatic edges could be detected down to much lower contrasts. On approaching the chromatic detection threshold (0.2%), displacement thresholds increased again. A  $V_i$  mechanism may underlie the high-contrast limb and a chromatic mechanism with coarser displacement resolution the low-contrast limbs of the threshold curves.

In order to further clarify the role of chromatic mechanisms, we measured displacement thresholds for equiluminant chromatic 628–552 nm edges (red–green), foveal and at 5 deg eccentricity. For the same stimuli, neuronal responses from macaque retinal ganglion cells were recorded and threshold curves constructed by neurometric analysis.

Control experiments on colour-defective observers showed that foveal displacement thresholds for equiluminant red–green edges carried a high risk of artifact due to chromatic aberration. At 5 deg eccentricity, this was not the case. Luminance-contrast threshold curves were 5–6 times higher in parafovea than in fovea. Thresholds for high-contrast red–green edges were another 5–6 times higher than these luminance-contrast threshold curves. Their level was similar to that expected from incremental chromatic-edge data.

Neurometric thresholds from MC-cells are consistent with them supporting the detection of displacements at luminance contrasts >3%. Their performance was poorer with equiluminant edges, although the residual response was obvious. Chromatic, parvocellular retinal ganglion cells (PC) perform much better with equiluminant stimuli, and thus may support displacement detection of equiluminant red–green edges at parafoveal locations.

Data for red–green equiluminant chromatic edges support the idea of multiple chromatic and achromatic spatial mechanisms contributing to hyperacuity performance. Although chromatic mechanisms (PC) show great absolute sensitivity, they appear less sensitive in terms of displacement detection than a luminance mechanism (MC).

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◆ **The role of colour in object perception within photo-realistic scenes**

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Previous studies of the role of colour in object perception have typically used stylised drawings with blocks of fill-in colour stimuli and found that colour does not play a major part in object recognition or classification (eg Ostergaard and Davidoff, 1985 *Journal of Experimental Psychology: Learning, Memory and Cognition* 11 579–587; Biederman and Ju, 1988 *Cognitive Psychology* 20 38–64). However, stylised stimuli, presented on uniform backgrounds, greatly simplify the segmentation problem and the use of fill-in colour omits information about 3-D form which may be involved in recognition. Therefore the influence of colour in these processes may have been underestimated.

In the present study we investigated the role of colour further by using photo-realistic objects presented within natural scenes. Twenty subjects were required to decide whether a target object, initially presented for 1 s, was present or absent within a scene. The object within the scene could either have (i) same form and colour, (ii) same form, different colour, or (iii) different form, same colour as the target. The location of the object was either predefined for each trial (recognition-only task) or it appeared in one of eight locations (search-and-recognition task). Error scores and decision times were recorded. Decision times for the search-and-recognition task were longer than for the recognition-only task and the pattern of results for the three conditions differed between tasks. The findings suggest that colour plays a primary role in the location and recognition of objects.

◆ **Discrimination of linear distributions in colour space**

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Even though an object might be uniformly painted, the light it reflects to an observer's eye will consist of many different colours depending on variables such as shading and specular reflection. Shading will cause variations in the brightness of the object, which makes its representation in colour space a linear distribution rather than a single point. Specular reflections of the light source might even cause the distribution to be planar. Human observers might use these differences in colour distributions to classify materials.

In this experiment we investigate how well subjects can discriminate between two linear Gaussian distributions in colour space that have the same base colour but different orientations. We varied the angle between the two distributions in RGB space for six different base colours and two different orientations. We presented a square split stimulus containing coloured squares to our subjects. The threshold angle was obtained by having subjects judge whether the division between the two linear distributions is oriented horizontally or vertically. We found that when the width of the Gaussian distribution is varied, which amounts, effectively, to varying the line length in RGB space, thresholds can be predicted by the conservation of the average distance between the two distributions.

◆ **Spatio-chromatic processing in the human retina: Towards an optimal trade-off between spatial resolution of luminance and range colour perception**

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Colour vision is due to the sampling of incident light by three kinds of photoreceptors sensitive to different wavelengths (L, M, and S cones). As only one cone type is present at each spatial location, colour information is spatially multiplexed. By considering several models of cone distributions (regular, random, and intermediate situations) we can calculate the spatial correlation function of the colour multiplexed signal. The correlation function can be decomposed into two terms: a low-pass term obtained by averaging the cone outputs, luminance signal, and a spatial modulated term which contains the colour opponency, chromatic signal. A subsequent filtering stage allows one to separate the two signals (Héroult, 1996 *Neurocomputing* 12 2–3).

Because of spatial multiplexing, a discrepancy exists between luminance spatial resolution and colour spatial resolution. In foveal vision, the discrepancy is resolved by assigning the maximum acuity to luminance. We show that this is achieved by a regular centred hexagonal lattice with only L and M cones with densities having a ratio 2 : 1 (or 1 : 2). In such a specific sampling arrangement the chromatic signal is modulated at high spatial frequencies in order to occupy the spatial frequencies where no luminance signal is present. As a result, in such a sampling lattice, spatial resolution of the luminance signal is only limited by the space between photoreceptors. Thus, luminance has a maximum resolution of 60 cycles deg<sup>-1</sup> and the colour signal a resolution up to 12 cycles deg<sup>-1</sup>, which is in good agreement with experimental data [De Valois, 1988 *Spatial Vision* (New York: Oxford University Press)]. As spatial resolution is not a strong requirement in parafoveal vision, the three kinds of photoreceptors are present and the sampling lattice accords more importance to colour representation than in the fovea.

◆ **Psychophysics tests on the internet: an evaluation**

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Conducting psychophysical experiments on the internet might constitute a useful addition to the existing spectrum of experimental methods in behavioural and cognitive sciences. Web-experiments allow access to a huge number of anonymous subjects that spend a short amount of time on an experiment. The technique is therefore suitable for experiments that (i) need few data per subject (eg, one-shot recognition experiments), (ii) need data from many subjects to get a significant result, (iii) cover a large parameter space, (iv) are designed to catalogue possible behaviours (eg, identification of exploration strategies in navigation), or (v) have a demand for subject diversity.

We have implemented five web-experiments that investigate gender perception, perception of face orientation, visual encoding of scenes, canonical views, and memory for faces (<http://exp.kyb.tuebingen.mpg.de/web-experiment/>). In the first few months we had up to 200 subjects for the shortest and most attractive experiments, whereas experiments that took more time or required additional browser plug-ins (VRML) attracted only 20–50 subjects.

The performance of a control group ( $n = 20$ ) that ran the same experiments on a computer in our laboratory confirmed the validity of our web-experiment data. Feedback from this group allowed us to improve the design of the experiments.

We conclude that web-experiments can form a valuable method for accessing large groups of subjects, provided careful thought is given to the limitations of using anonymous subjects on remote locations. The technique is especially well suited for performing quick pilot studies and for validating laboratory experiments on larger numbers of subjects. Experiments that require precise control of timing, colour, display characteristics, etc (low-level psychophysics) should not be considered for internet implementation.

◆ **Brown is an elemental colour**

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A continuous judgmental colour-naming technique was used to evaluate the possible elemental nature of brown. Participants (thirty subjects) were normal trichromats. Stimuli (48) were selected to cover the full range of visible hues with two lightnesses. All stimuli were 0.06 units from the achromatic centre in CIE  $u'v'$  chromaticity diagram. We used 24 dominant wavelengths with a 15 deg separation between each;  $15 \times 24 = 360$ ). The 48 stimuli were evaluated in two trials. In the

first trial, half of the participants had only four categories (red, green, yellow, and blue) to judge the stimuli, and in the second trial, they had five (the previous four plus brown). The order of conditions was reversed for the remaining observers.

In contrast to other published evidence (Quinn et al, 1988 *Perception & Psychophysics* **43** 156–164), our results showed that brown is an elemental colour and that the use of this category depends on the lightness level and the dominant wavelength. Discrepancy between Quinn's data and our results may be explained in terms of purity (Quinn used a 100% purity) and dominant wavelength (Quinn used only 570 nm). Meanwhile, our experimental conditions indicated that some stimuli were similar to those considered optimal for achieving the perception of brown according to Bartleson's (1976 *Color Research and Application* **1** 181–191) classical study.

◆ **Metacontrast masking reveals narrowly tuned colour channels**

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While matching and search experiments have generally indicated broadly tuned colour channels (cosine characteristics in colour space), colour-naming studies suggest a fine structure of central colour representation. We have studied the colour dependence of metacontrast masking. A contiguous disk–ring configuration was used (disk diameter 2 deg, outer ring diameter 4 deg, eccentricity 3 deg, flash duration 28 ms, disk–ring onset asynchrony 56 or 83 ms). We tested all combinations of 14 equiluminant colours (20 cd m<sup>-2</sup>, neutral background, 40 cd m<sup>-2</sup>) which were evenly spaced in perceptual metric (5 steps of the OSA Color System). Subjects rated the visibility of the test disk relative to a comparison disk. The effects of disk and ring colour were measured by a 2-way ANOVA. The patterns of interaction were consistent across subjects and asynchronies. In general, masking was strongest when the mask had the same colour as the test, and fell off with colour distance. Drops to half-maximal strength over 5 steps of the OSA system were common. In the yellow–red region this corresponded to wavelength differences as small as 12 nm. At orange, white, pink, and purplish-blue colours the masking regions were convex islands. The main effects varied between subjects. Greenish colours and gray tended to be more susceptible to masking than reddish colours. We conclude that metacontrast is highly colour selective. The results suggest cortical colour coding in narrowly tuned channels.

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◆ **An investigation into colour constancy and colour memory**

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A series of three experiments investigating the properties of colour constancy and colour memory is reported. Forty-eight subjects with normal colour vision were required to match colours under varying illumination, time delay, or the two combined. Matches were made with the use of Munsell colour targets, or with pictures of familiar objects. Results indicate that while illuminant shift and time delay both individually cause significant deviations from targets, the addition of delay to the constancy paradigm has no further effect on matching. Moreover, matching under illuminant shift conditions shows qualitative similarities to matching under time delay. It is proposed that colour constancy is dependent on colour memory as well as physiological and cognitive mechanisms. Evidence that colour and object memory are separable is presented.

◆ **Effects of spotlight and shadow on surface-colour mode perception**

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A transition of the mode of colour appearance, from surface-colour mode to aperture-colour mode, may occur when the visual system infers that the stimulus is too bright to occur under the ambient illuminant. We investigated effects of a spotlight and a shadow on the mode of colour perception by measuring the upper limit for surface-colour mode appearance. Experiments were conducted with a CRT colour monitor. Flat, matte Munsell papers were simulated on it. The stimulus was 10 deg × 10 deg square, and consisted of several colour chips. A spotlight and a shadow were simulated by changing the luminance of a circular area in the stimulus to make an increment or a decrement. The position of the circular area and the magnitude of the increment or decrement were varied. Observers adjusted the luminance of the test stimulus so that it just appeared as aperture-colour mode.

We found that the upper-limit luminances of the test stimulus changed according to the incremental or decremental change of the circular area when the test stimulus was involved in that area. The amount of the change, however, was smaller than that of the increment or decrement. The results were not affected by the luminance change of the circular area when the test stimulus was not involved in it. Our results indicate that the judgment of surface-colour mode appearance depends on the illumination condition, and an upper limit of brightness is set for each illumination. The mode of appearance may be determined by the upper-limit brightness for that illumination.

◆ **Selective colour constancy deficits after unilateral brain lesion**

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To gain insight into the neural basis of colour constancy, we examined the colour vision of twenty-seven patients with defined unilateral lesions mainly located in the parieto-temporo-occipital cortex. Patients were tested with a battery of vision and colour vision tests. Detection and grouping thresholds for isoluminant chromatic and for luminance stimuli were measured to assess retinal and early cortical processing. To examine higher cortical functions, we tested colour memory, colour-object association, and colour constancy. For the evaluation of colour constancy, subjects had to adjust the colour of a test field until it appeared as neutral gray. The test field was embedded amid a set of coloured patches, and the illuminant was varied from trial to trial. A control group of healthy subjects was tested in the same tasks.

Five of the twenty-seven patients showed a selective deficit in the colour constancy tests. All five patients showed normal colour discrimination. A comparison with anatomical lesion data, based on CT- or MRI-scans, showed that one of the five patients had a lesion near the fusiform and lingual gyri, whose importance for colour constancy had been suggested in earlier studies. However, three other patients had overlapping lesions in a region of parieto-temporal cortex, which so far had not been associated with colour vision. These results indicate that the computations underlying colour constancy are mediated by specialised cortical circuitry, which is independent of the neural substrate for colour discrimination and for assigning colours to objects.

## HIGHER-ORDER MOTION

◆ **Second-order motion does not pop-out**

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The idea of second-order motion (defined by texture or other second-order properties) seems widely accepted, but the way it is detected is still an open question. Energy-based mechanisms that imply spatially parallel detection have been proposed (eg Lu and Sperling, 1995 *Vision Research* 35 2697–2722), but some studies reported failure of parallel detection (eg Doshier et al, 1989 *Vision Research* 29 1789–1813).

Using a conventional visual-search paradigm, we examined if second-order motion was detected in parallel. The stimuli were contrast-modulated gratings with static 2-D noise fields as carriers. Luminance-modulated (first-order) gratings were also tested for comparison. The gratings were windowed by a 2-D Gaussian and scattered at a constant distance from the centre. The task was to judge if there was a target drifting in one direction among distractors drifting in the opposite direction, and the reaction time was measured.

While the first-order motion was detected in parallel, the second-order motion was not detected in parallel and the search time exceeded 400 ms/item (when the target was present). This long search time, together with the observers' reports, implies the need of eye movement to gaze at the stimulus in the central visual field one by one. It is not likely that the results solely reflected the interference due to large receptive fields, as additional measurements of the sensitivity did not show significant effects of the direction of distractors. Attention is considered to be required for this type of second-order motion, and a role of a correspondence-based detection is suggested.

◆ **Combining the motion of first-order and second-order, chromatic and luminance stimuli: a purely local process?**

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Despite much recent work, the nature of the chromatic motion mechanism (and whether it exists at all) remains a contentious issue. The current study reviews recent criticism of a basic chromatic motion mechanism and attempts to draw together some of the conflicting data. By using contrast-modulated stimuli and masks, the effects of conflicting motion from chromatic and achromatic, first-order and second-order stimuli have been examined. Of particular interest are the conditions under which one finds predictable specific masking between each domain consistent with the use of a common mechanism. Observers were required to discriminate direction in stimuli presented at scaled contrasts in the presence of masks which varied from broad to narrow band in spatial and temporal domains. The data suggest: (i) the perceived direction of motion of the unmasked stimulus is dependent solely upon the local spatial structure of the carrier and its envelope; (ii) the conditions under which masking is seen are not consistent with some specific interaction at a common (motion extraction) site but are more reasonably explained by a non-specific addition of local spatial and temporal noise into the neural image. Once this noise reaches a certain level (either in spatiotemporal extent or in amplitude), any task of spatiotemporal discrimination is severely compromised. The current study supports the previous research which suggests the existence of a low-level chromatic motion mechanism and finds that combining first-order and second-order, chromatic and achromatic motion yields data consistent with a system operating locally on the spatiotemporal structure of the stimulus and obeying laws compatible with the structure of the natural environment.

◆ **Simultaneous adaptation states for first-order but not second-order stimuli as evidenced with visual aftereffects**

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The aim of this study was to explore centre-surround interactions in visual aftereffects for first-order and second-order stimuli. A central patch was drifted in an upward or downward direction while the surround area was either drifting in phase or in antiphase, or the pattern was static. These conditions were repeated with first-order (luminance-defined) stimuli and for second-order (contrast-defined) stimuli. Two test patch conditions were used: the test patch was either static, or flickering at 3 Hz and was always luminance-defined. The results show that for the static test patch there is a clear motion aftereffect for first-order stimuli but not for second-order stimuli consistent with previous reports. With a flickering test patch a motion aftereffect is perceived for both first-order and second-order stimuli (second-order being weaker) and they generally follow the same pattern. The most striking results reside in the observations made when the surround patch was static during the adaptation conditions while the test patch was also static. In this case there was a total absence of visibility of the test patch when it was initially presented, and when this 'contrast adaptation aftereffect' disappeared there was residual motion aftereffect. No such effect was visible for the second-order stimuli. This leads us to speculate that: (i) two simultaneous adaptation states are possible, and (ii) this appears specific to first-order stimuli.

◆ **Can drifting cyclopean corrugations elicit OKN?**

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Steinbach and Anstis (1977 *Journal of the Optical Society of America* 67 1415) reported that drifting cyclopean corrugations elicited OKN. In contrast, Harris and Smith (1991 *Visual Neuroscience* 9 565-570) found that a drifting second-order motion stimulus based on contrast modulations did not evoke OKN. A key difference between the two studies is that Steinbach and Anstis did not mask the centre portion of the display and hence their eye movements might have been voluntary pursuit rather than OKN.

For the current experiment, observers were presented with random-dot-covered vertically oriented disparity corrugations ( $0.24 \text{ cycle deg}^{-1}$ ) which drifted at  $7.6 \text{ deg s}^{-1}$  either to the left or the right. A horizontal black band could mask the central 5 deg (vertically) of the display.

Horizontal eye movements were recorded with the Scalar infrared recording system. As a control, eye movements were also recorded for both high-contrast and low-contrast drifting luminance gratings. For drifting luminance gratings, the gain of OKN was reduced from 0.85 to 0.26 when the contrast was reduced from 100% to 5%. There was little or no OKN for drifting cyclopean corrugations when the central mask was present but OKN-like movements were elicited when no mask was present (cf Steinbach and Anstis). This suggests that nonfoveal cyclopean stimuli are incapable of driving OKN. However, it does not follow that the nystagmic eye movements elicited by the foveal cyclopean corrugations are voluntary pursuit. They may instead be OKN but controlled via a cortical rather than subcortical pathway.

◆ **Poor speed discrimination suggests that there is a specialised speed mechanism for cyclopean motion**

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Harris and Watamaniuk (1996 *Vision Research* 36 2149–2157) found that speed discrimination thresholds (Weber fractions  $> 0.30$ ) for moving cyclopean corrugations were predicted by displacement discrimination thresholds (Weber fractions  $\sim 0.03$ ) when the effect of their pseudo-random exposure duration was taken into account. They concluded that there is no specialised speed mechanism for cyclopean motion and that cyclopean speed perception is predominantly based on displacement cues. A prediction of this conclusion is that speed discrimination thresholds should be comparable to displacement discrimination thresholds if exposure duration is fixed.

Two panels ( $3.0 \text{ deg} \times 7.0 \text{ deg}$ ) of dynamic random-dot stereograms were located  $0.5 \text{ deg}$  on either side of a central fixation spot. Each panel contained a horizontally oriented sinusoidal cyclopean corrugation. On each trial, the cyclopean corrugations were displaced vertically in opposite directions. Subjects judged which panel contained the faster moving corrugation. All stimuli had a corrugation frequency of  $0.4 \text{ cycle deg}^{-1}$  and a peak-to-trough disparity amplitude of  $8 \text{ min of arc}$ . The speed of the reference stimulus was either  $1.0$ ,  $2.0$ , or  $3.0 \text{ deg s}^{-1}$  while the speed of the test stimulus was determined by the method of constant stimuli. Exposure duration was fixed at  $1 \text{ s}$  for all presentations.

The mean Weber fraction for cyclopean speed discrimination was  $0.52$  averaged across three subjects and the three reference speeds. The lowest Weber fraction obtained was  $0.22$  for subject AMJ with the  $3.0 \text{ deg s}^{-1}$  reference speed. Despite employing a fixed exposure duration, Weber fractions never approached cyclopean displacement discrimination performance ( $0.03$ ). This casts doubt on Harris and Watamaniuk's suggestion that cyclopean speed perception is based on displacement cues, at least for our stimuli and subjects. Rather, we believe that there exists a specialised speed mechanism(s) for cyclopean motion but that mechanism(s) is poorly tuned.

◆ **Ocular pursuit of flicker-defined motion**

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A moving luminance-defined spot elicits smooth-pursuit eye movements which respond rapidly to changes in direction of motion. Here a study is reported of eye movements evoked by a second-order (non-Fourier) motion target defined by polarity reversal of a binary random texture within a small circular area. On each frame transition ( $60 \text{ Hz}$ ), a Gaussian probability density function determined whether the corresponding texture element reversed polarity. Moving the density function from frame to frame evoked a vivid percept of motion in spite of the fact that there were no first-order (Fourier-based) motion cues. Subjects were instructed to follow this flicker-defined spot, which moved downward at  $6 \text{ deg s}^{-1}$ , changing direction once by  $30 \text{ deg}$  (right or left) at an unpredictable height. Eye position was recorded with a video ophthalmoscope having a resolution of  $1 \text{ min of arc}$ .

Unlike a luminance-defined spot of similar size, this target did not cause rapid initiation of pursuit. Instead, the eye saccaded to the target  $400\text{--}500 \text{ ms}$  after the onset of motion. After this initial saccade, some smooth pursuit occurred, perhaps due to prediction. Similar saccadic responses were observed to the direction-change events. These results suggest that flicker-defined motion is detected by perceptual, but not oculomotor pathways.

◆ **Detection of colour-based and luminance-based motion**

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Recent studies suggest that colour-based motion and luminance-based motion are processed separately in an early stage of the visual system [Cropper and Derrington, 1996 *Nature (London)*]

379 72–74]. Similarly, Metha and Mullen (1997 *Journal of the Optical Society of America A* **14** 984–996) have proposed a model where colour-based motion and luminance-based motion are processed in a common manner and site but different front-end temporal filters. In contrast, results of a visual-search task showed that luminance-based motion was processed 'pre-attentively' but colour-based motion was not (Lüscho and Nothdurft, 1993 *Vision Research* **33** 91–104). This result implies that colour-based motion is not processed in an early stage of the visual system.

The aim of this study was to examine, using visual-search task, whether colour-based motion and luminance-based motion are processed separately and whether they are processed pre-attentively in an early stage of the visual system. Stimuli were square grating patches having different colour and luminance contrast. Target moved at  $14 \text{ deg s}^{-1}$  and was presented for 50 ms. Distractors were static grating patches with the same contrast and spatial frequency as the target. We found that the detection of colour-based and luminance-based stimuli was significantly different in both response time (RT) and the proportion of correct responses. For RT, the number of distractors affected colour-based motion detection, but not luminance-based motion detection. For the proportion of correct responses, the number of distractors affected the detection of both colour-based motion and luminance-based motion. These results suggest that colour-based motion and luminance-based motion are processed separately, and colour-based motion is not processed pre-attentively, as Lüscho and Nothdurft showed, although the processing of luminance-based motion remains unclear.

◆ **No local cancellation between first-order and second-order motion**

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Despite strong converging evidence that there are separate mechanisms for the processing of first-order and second-order motion, the issue remains controversial. Here we present compelling new evidence for separate mechanisms, which we found using a direction-discrimination task performed on a composite motion stimulus. The motion sequence consisted of a dynamic binary noise carrier divided into horizontal strips of equal height, each of which was sinusoidally modulated ( $1.0 \text{ cycle deg}^{-1}$ ) in either contrast or luminance. The modulation moved leftward or rightward ( $3.75 \text{ Hz}$ ) in alternate strips. The single-interval task was to identify the direction of motion of a central, marked strip. Three conditions were tested: uniform 1 (all first-order strips), uniform 2 (all second-order strips), and mixed (alternate first-order and second-order strips, correlated with the direction alternation). The dynamic noise was refreshed at  $15 \text{ Hz}$  and the strip motion was sampled at  $90^\circ$  phase intervals. In preliminary experiments, the two uniform conditions were run with the strip height fixed. Performance fell as modulation depth decreased and the threshold modulation depth for each type was determined. These threshold values were used to scale modulations of the two types in the main experiment so as to equate visibility of the first-order and second-order components. In this experiment strip height was manipulated with fixed modulation depth. The minimum strip height at which direction identification was possible was strikingly lower in the mixed condition than in the uniform conditions. Qian et al (1994, *Journal of Neuroscience* **14** 7357–7366) have shown that first-order motion signals cancel if locally balanced. We argue that the two uniform conditions demonstrate local cancellation of motion signals, whereas in the mixed condition this does not occur. We attribute this non-cancellation to separate processing of first-order and second-order motion inputs.

◆ **Analysis of spatial structure limits temporal resolution of second-order motion mechanisms**

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Human observers are unable to discriminate the direction of motion of patterns defined by contrast (second-order patterns) at temporal frequencies above about  $5 \text{ Hz}$  whereas they can easily do the task with patterns defined by luminance (first-order patterns) up to  $20$ – $30 \text{ Hz}$  (eg Badcock and Derrington, 1989 *Vision Research* **29** 731–739).

To test whether the temporal resolution of second-order motion analysis is limited by extraction of second-order spatial structure or by analysis of its motion we measured spatial frequency and direction of motion discrimination using beat patterns of different temporal frequencies. A  $1 \text{ cycle deg}^{-1}$  beat was formed by adding a flickering or moving grating of  $9$  or  $11 \text{ cycles deg}^{-1}$  to a static grating of  $10 \text{ cycles deg}^{-1}$ . In all experiments the  $10 \text{ cycle deg}^{-1}$  grating was kept stationary and had fixed contrast ( $50\%$  or  $6.25\%$ ). At each temporal frequency ( $1$ – $16 \text{ Hz}$ ) and mean contrast we measured performance as a function of modulation depth (the ratio of the contrast of the flickering or moving component to that of the static component) using a 2IFC procedure.

At high mean contrast, it was possible to discriminate both spatial frequency and direction of motion of the beat up to 16 Hz. At low mean contrast, discriminations were similar at 1 Hz but thresholds rose with the temporal frequency. However, the threshold elevation was considerably faster in direction discriminations. At 16 Hz both of the tasks became impossible even at the highest possible modulation depth. The results imply that second-order motion analysis is limited both by the extraction of spatial structure and by analysis of its motion.

◆ **Motion estimation of transparent stimuli using triads of Gabor filters**

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In current models, discrimination of transparent and nontransparent moving regions and motion estimation are usually treated separately instead of taking a unified approach. In our previous work (A Spinei, D Pellerin, J Hérault, 1998, European Signal Processing Conference, EUSIPCO '98) we presented a technique for the nontransparent speed estimation by using triads of Gabor filters. The speed is computed in a direct manner, unlike the typical minimisation techniques, and it fits very well with a neural interpretation. In our present work, we use a simplified energetic pattern corresponding to transparent stimuli, associating in the frequency domain an energy plane to each of the two speeds, thus minimising the contribution of 'non-Fourier' components. The triads of Gabor filters are unable to cope with all the types of transparent movement, so we restricted our study to two specific cases (the case of transparent moving objects over a fixed background and the case of a transparent motion with identical speeds but in opposite directions). We are able to estimate the speed and to perform a good transparency discrimination in both cases. Finally, we reproduced the experiment of the superimposed dense random-dot patterns as described by Murakami (1997 *Perception* 26 679–692) and the simulation results are very close to the human psychophysical performance. This strongly suggests that the mechanism underlying motion transparency in the visual system uses motion energy information both for the task of discrimination and for the estimation of transparent motion.

**MOTION**

◆ **Can information about visual motion direction be combined across different speeds?**

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The encoding of visual motion must include information about both direction and speed. We have studied the interaction of these differently encoded dimensions, by testing whether information from different speeds can be integrated in a directional judgment.

Directional performance was measured from the coherence threshold (% signal dots in noise) required to discriminate two directions of global flow, differing by  $\pm 10^\circ$  either side of vertical, in a random-dot kinematogram. In single-speed conditions, coherence threshold was found to be a U-shaped function of the speed of the signal dots between 0.5 and 64 deg s<sup>-1</sup>. In mixed-speed experiments, signal dots moved in a single direction but at two different speeds chosen to have comparable thresholds when tested alone: 'slow' (0.5 or 1 deg s<sup>-1</sup>) and 'fast' (8 deg s<sup>-1</sup>). In one experiment, signal dots of one speed were added to a constant subthreshold number of dots of either the same or different speed. Thresholds were lower when the added dots and the non-varying dots had the same speed than when they were mixed, suggesting little or no integration of directional information across speeds. In a second experiment, the total number of signal dots in the mixed signal was equally divided between slow and fast dots. In this case, some observers showed as low a threshold for the mixed as for a single speed, which implies effective integration.

These results suggest that visual motion processing may be able to operate with alternative strategies, either separating information from different speeds or combining them.

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◆ **Undefined IOC solution predicts vector-sum motion**

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The intersection-of-constraints (IOC) method for combining velocity vectors accurately predicts pattern velocity, and is empirically supported [Adelson and Movshon, 1982 *Nature (London)* 300 523–525]. However, some stimuli are perceived in a non-IOC direction. Results supporting an alternative computation, the vector-sum hypothesis (Yo and Wilson, 1992 *Vision Research* 32 135–147), do not generalise. Weiss and Adelson recently provided a Bayesian explanation for the vector-sum movement, but it does not explain the shift from perceived motion in the vector-sum

direction to the IOC direction under rotation (Bowns, 1996 *Vision Research* 36 3685–3694). An equation was derived for computing the IOC in terms of component direction and speed, ie physiologically plausible terms. The equation for stimuli perceived in the vector-sum direction is undefined, whereas the equation for the same stimuli under rotation is defined. Undefined IOC solutions also provide an explanation for a result reported in Bowns (1996), where increasing the difference between predictions from the vector-sum hypothesis and the IOC resulted in perceived movement changing from the vector-sum direction to the IOC direction. Analysis of the stimuli used showed that as the difference between predictions increases the equation becomes defined. Stimuli are perceived to move in a non-IOC direction when the IOC is undefined in an equation that computes the IOC in physiologically plausible terms.

◆ **Global motion detection is impaired in visually deprived cats: a random-dot study**

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A recent study showed that discrimination of a moving square from a stationary one was affected in binocularly deprived (BD) cats (Burnat and Zernicki, 1997 *Acta Neurobiologica Experimentalis* 57 235–245). In the present study, global motion discrimination was investigated, independently of object following. The BD cats were raised during the first 6 months of life in masks. They were not able to perceive sharp edges and patterns, but could follow moving shadows. Two control (C) cats with normal visual experience and two BD cats were trained. The stimuli were modified Newsome random-dot patterns. The positive stimulus was a moving random-dot pattern; the negative stimulus a stationary one. In stage 1, the size of the stationary stimulus was 30% to 90% that of the moving stimulus. Size difference between stimuli was diminished in steps. The velocity of the moving stimulus was 7 deg s<sup>-1</sup>. The BD cats reached criterion level of performance with a 20% or 30% size difference, while C cats reached the same level with a 40% size difference. In stage 2, each cat started with the size difference achieved in the previous stage, but the velocity was increased to 25 deg s<sup>-1</sup>. The BD cats did not reach the criterion level with a size difference of 10%, whereas the C cats did when both stimuli were of equal size. In stages 3 and 4, dot density was reduced and velocity was increased to 200 deg s<sup>-1</sup>. The BD cats performed at the random level. Surprisingly, the results showed that global motion perception can be strongly impaired by pattern deprivation.

◆ **Long-range interactions in the integration of 2-D and 1-D motion signals**

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An oblique grating moving within a cross-shaped aperture with vertical and horizontal arms appears either as a coherent pattern moving in a single direction (coherence), or as two independent surfaces moving in two different directions parallel to the arms of the cross (segregation), ie like two superimposed barber-pole illusions. We studied the balance between segregation and coherence in variants of this multi-stable stimulus for a number of parameters. On each trial, observers gave a first response to indicate the initial percept (segregation or coherence) and a second response (which terminated the trial) when the initial percept was replaced by the alternative one. Reaction times for the two responses were measured.

Our main findings are: (a) the percentage of initially perceived segregation grows from 0 to 60% when the length of the arms (width: 1 deg) increases from 2 deg to 8.3 deg (distance from the centre of the cross); (b) a higher percentage of segregation (from 50% to 70% as a function of arm length) is observed in a control condition where the small sides of the arms are made parallel to the grating, instead of being perpendicular to the long sides.

Altogether, our results support the idea that the representation of independent moving surfaces depends on a hierarchy of processes which operate at different scales (Braddick, 1997 *Perception* 26 995–1010). From the local combination of 1-D and 2-D motion signals, a new velocity field with a coarser scale emerges, so that each cross-arm is represented by a single velocity 'patch' whose spatial extent is flexible. We suggest that the respective reliabilities of the patches determine their reciprocal interactions over large distances.

◆ **The direction of walk affects the perception of biological motion**

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Previous studies of biological motion have been largely confined to spatiotemporal patterns of point-light displays which specify 'walkers' moving across the visual field orthogonal to the line

of sight. However, this is a limited case as in everyday life we view humans walking in many different directions. In the present experiments we investigated whether the direction of walk affects the perception of biological motion.

Real walks in five different directions ( $0^\circ$ ,  $22.5^\circ$ ,  $45^\circ$ ,  $67.5^\circ$ , and  $90^\circ$  to the line of sight) were video recorded and converted into light displays containing thirteen points (one on the head and two on the shoulders, elbows, wrists, hips, knees, and ankles). Sequences therefore contained information that specified the biological motion in addition to changes in position and changes in overall size which accompany actual walks in 3-D space. These were shown to ten subjects in a 2AFC design where an interval containing 'the walker' plus noise had to be identified from an interval containing only noise. The SNR for this discrimination was determined for four types of walk where (i) the walker changed position and size appropriate to the direction of walk, (ii) the walker did not change position, (iii) the walker did not change size, and (iv) the walker did not change position or size.

Surprisingly, thresholds were highest in the condition where the walker changed position and size appropriate for the direction of walk. Thresholds in all conditions were lowest when the walker moved at  $0^\circ$  or  $22.5^\circ$  (unlike displays used previously). In conclusion, the direction of walk substantially affects the perception of biological motion.

◆ **The effect of stereoscopic depth on the perceived speed of transparent motions**

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Neurophysiological studies have shown that motion transparency suppresses the response of speed-selective cells in cortical area MT (Snowden et al, 1991 *Journal of Neuroscience* **11** 2768–2785). However, we have argued that the inhibition stems from constraints on a relative velocity signal: transparency augments the perceived speed. More recent findings have suggested that transparent motion processing in area MT is facilitated when the motions are in different depth planes because disparity information constrains opponent inhibition. Nevertheless, the relative-velocity argument would account for this effect if depicted speed varies as a function of disparity. To test this hypothesis human observers matched the speed of transparent and unidirectional motion and 'the point of subjective equality' was determined. Transparent motion was generated by assigning opposite directions of horizontal motion to alternating rows of a random-dot pattern, one of the two motions was always in the plane of fixation whilst the disparity of the other was varied (0–40 min of arc, crossed and uncrossed). The unidirectional matching motion was always presented in the plane of fixation. The results show that (a) for the zero-disparity condition the speed-up effect for transparent displays is about 50%, confirming our previous results; (b) this speed-up effect falls off rapidly as the disparity between the two transparent planes increases. The relative-velocity signal is lost with increasing disparity leaving a velocity corresponding to the cell's optimum unidirectional speed.

◆ **Motion-transparency perception in central and peripheral vision**

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Random-dot kinematograms, in which individual elements are assigned different speeds, lead to the perception of motion transparency. In previous studies, we reported that the minimum speed difference required to perceive two moving superimposed surfaces was quite high, in excess of 20%, with display durations of 250 ms. Using a 2AFC adaptive method, we evaluated the variation of speed difference thresholds with eccentricity.

In the first experiment, the reference stimulus was a random-dot pattern, moving at average speed. Thresholds were inferior to 15% in central vision. They increased to about 20% at 10 deg eccentricity. These results replicate classical data relating the evolution of speed-discrimination thresholds with eccentricity. In the second experiment, the reference stimulus consisted of a random-dot pattern containing five randomly distributed speeds (a 'moving cloud'). Thresholds were then higher in central vision, superior to 30%, and their dependence on eccentricity was similar to that observed in the first experiment. From these data, we conclude that, in the first experiment, subjects were dealing with local speed discrimination. In the second experiment, they had to single out surfaces from motion.

The elevation in threshold between the first and the second experiment may therefore reflect additional processes involved in the perception of transparent surfaces in motion, such as global segmentation and integration of visual motion. The similar increase of the threshold with eccentricity might be related to the spatial scale of local motion segmentation.

◆ **Analysis and modeling of the visual processing of spatiotemporal information:**

**Influence of temporal and spatial separation on the discrimination of trajectories**

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The problem of representation and processing of motion information is addressed from an integrated perspective covering the range from early visual processing to higher-level cognitive aspects. At the earliest level we assume a spatiotemporal memory as a basis for the recognition of spatiotemporal patterns. We suppose that a similar spatiotemporal organisation will also occur on higher levels of the visual processing hierarchy. The modeling of the respective representations is derived from known empirical findings regarding the representation and processing of spatiotemporal information and from newly initiated experiments. In experiments on the discrimination of the trajectories of moving dots we found evidence indicating that information about direction and position of simple straight trajectories is not stored independently but is only available in the form of a spatiotemporal compound. This is suggested by the fact that direction discrimination of two sequentially presented trajectories is not influenced by their temporal separation (ISI) but by an offset of the start-points.

Our formal representation of the higher levels of the motion-processing system is based on a two-layered architecture which uses qualitative means for the representation of motion trajectories. In the lower layer, the motion information is represented in a relatively accurate vectorial representation. This layer allows a switch between deictic and intrinsic frames of reference. The higher layer is operating in a more abstract propositional fashion and uses the shape of the course of motion as a representational primitive. The propositional representation is constructed from the vectorial representation by generalisation, segmentation, and classification of the vector sequences. This enables the system to reveal structural similarities and regularities in the course of motion which will be useful for motion prediction.

◆ **The transition from assimilation to contrast in induced motion**

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Motion assimilation is induced motion in the same direction as that of the inducing stimulus. Motion contrast is induced motion in the direction opposite that of the inducing stimulus. The two types of induced motion are produced under remarkably similar stimulus conditions. In these studies, apparent-motion sequences consisted of moving sine-wave grating patches which influenced the perceived direction of motion of a spatially disparate, ambiguously moving test patch.

In experiment 1, vertically oriented sine-wave gratings at the top and bottom of the display (inducers) oscillated back and forth through 90° of their spatial phase in one, two, six, or twelve steps, while a central test grating oscillated through 150°, 160°, 170°, 180°, 190°, 200°, or 210° of their phase in a single step. Observers reported that the test grating appeared to oscillate in phase with the inducers in the one-step conditions (motion assimilation), but out of phase in the multistep conditions (motion contrast). In experiment 2, inducers oscillated through 90° in two steps while the test grating oscillated 150°, 165°, 180°, 195°, or 210° in one step. The displacement size of the inducers' first step was varied from 0° to 90°. When the displacement size of the first step was near 0° or 90°, in-phase oscillation was reported (assimilation), whereas out-of-phase oscillation was reported for the 45° first-step condition (contrast). The results indicate that the quality of the inducing motion stimulus determines the type of induction effect that is produced. Abrupt displacements induce motion assimilation, whereas smooth, multistep motion induces motion contrast.

◆ **Walking in the crowd: emergent coherent motion captures biological motion**

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When four overlapping sets of dots oscillate horizontally out of phase, two transparent layers are perceived [Gerbino and Berneti, 1984 *Perception* 13(1) A38–A39]. The two emergent layers appear clearly segregated in depth, and often are perceptually unified in a rotating cylinder. For most observers the front layer consistently moves in the same direction, either rightwards or leftwards. Such a bias depends on retinal coordinates. For other observers the dominant direction of the front layer spontaneously reverses. Perception of two emergent layers is maintained also

when a single dot is attentionally tracked and its local oscillations become salient. Awareness of individual motion paths coexists with the perception of emergent coherent motion.

A new effect occurs when a configuration of 3 or 4 oscillating red dots is embedded in a field of hundreds of oscillating green dots. The red dots are perceived as a biological-motion pattern (a sort of random-dot walker) whose properties depend on two factors: (i) the phase relations of the red dots; (ii) the perceived motion direction of the layer that appears closer to the observer. This second factor determines the polarisation of the elementary walker, who always appears to move in the same direction as the front layer. When the emergent coherent motion spontaneously reverses, also the biological pattern changes its perceived motion polarisation. Motion capture was confirmed by a forced-choice experiment in which participants were asked to match the apparent direction of translation of the random-dot walker with the real translation of a comparison stimulus.

◆ **Eccentricity scaling of perceived velocity at a constant viewing distance**

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It has often been reported that motion perception can be equated across the visual field if stimulus size is varied in accordance with an appropriate spatial eccentricity scaling function (ESF). However, stimulus size is typically varied by changing viewing distance, and there is evidence that viewing distance affects both perceived size and perceived speed. We have, therefore, estimated an ESF for perceived speed by varying stimulus size at a number of eccentricities while keeping viewing distance constant. Stimuli were arrays of luminous dots moving within vertically oriented rectangular strips centred at eccentricities of 0.5, 2, 5, 10, 20, and 35 deg. The stimulus at 0.5 deg was always the standard, and the velocity of the stimuli at the other eccentricities which appeared to match the standard was determined by a staircase procedure. The amount that the peripheral data had to be displaced in order to match the 0.5 deg data was taken as an estimate of the ESF. Quantitative differences were found between the present data and those obtained when viewing distance was not controlled. These differences, as well as interobserver variability, generally increased with eccentricity. Further, the differences are in a direction consistent with the data of our previous studies, which indicate that stimuli perceived closer to the observer appear to move more slowly than the same stimuli perceived to be farther away.

◆ **Cuts in cinematic displays: the effect on phenomenal continuity**

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Cuts between shots (for example transitions from long shot to close-up) are widely used in cinematographic editing. Many perceptual aspects are still unresolved or have not been investigated at all in this field [Hochberg, 1986, in *Handbook of Perception and Human Performance* Eds K R Boff, L Kaufman, J P Thomas (New York: John Wiley)].

A kind of launch effect [Michotte, 1963 *The Perception of Causality* (London: Methuen)] was used as a prototypical event to investigate the influence of an abrupt transformation in size of two colliding squares (corresponding to a close-up) on the impression of continuity of the event itself. Two experiments were carried out; in both subjects had to evaluate the impression of continuity of a displayed launch.

In the first experiment there could be a sudden magnification of the squares (sides were doubled or quadrupled) at the moment of contact; at the same time the temporal continuity of the displayed event could also be altered (from a flashback to a flashforward). Results indicated that the impression of spatiotemporal discontinuity was accurate when the cut was not present (objects unmodified in size) whereas the abrupt transformation required a brief flashback to allow the continuity to be perceived. In the second experiment only the unmodified and quadrupled-in-size events were presented. Cuts were all positioned before the moment of contact (at five different locations) and temporal continuity could range only from actual continuity to flashforward. Results showed that the presence of cuts substantially prevents the discontinuity to be perceived.

◆ **Interocular transfer does not imply binocular sum of motion aftereffect**

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A model of the motion aftereffect (MAE) has been proposed that explains how transparent motion causes a nontransparent MAE [Grunewald and Lankheet, 1996 *Nature (London)* **384** 358–360].

To extend that model to include binocular interactions, we studied the effect of interocular transfer on the direction of the MAE. Subjects were adapted with a rivalrous stimulus. The left-eye stimulus contained dots going up and to the right, the right-eye stimulus contained dots going up and to the left. During testing, a balanced random dot motion stimulus was presented either to both eyes, or to only one eye (left or right). Subjects indicated the direction in which they saw motion during the test phase.

With binocular test stimuli, observers see motion in the direction opposite to the vector sum of the adaptation directions. With monocular test stimuli, observers see MAE directions opposite to the corresponding monocular adaptation directions. In a second experiment, subjects were adapted with monocular stimuli, and tested with stimuli in the same eye, or in the opposite eye with respect to the adaptation stimulus. As expected, subjects indicated for each adaptation condition the same direction of the MAE irrespective of the eye of testing, that is interocular transfer was taking place.

Together, these results suggest that binocular sum of adaptation directions (as measured in the first experiment) is distinct from interocular transfer of adaptation effects (as measured in the second experiment), and that they do not necessarily co-occur.

◆ **Analysis of direction and orientation changes in plaid stimuli**

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There are at least four cues, two static and two dynamic, that the visual system might use to analyse changes in direction of a moving object or surface: (i) discrimination of direction of motion at two discrete times; (ii) comparison of orientation relative to the observer at two discrete times; (iii) dynamic analysis of direction change over time; (iv) dynamic analysis of orientation change. We have measured the lower threshold for discriminating clockwise versus anticlockwise direction change of a drifting plaid. By introducing an ISI between the initial and final directions of the plaid, we have found evidence that the visual system can use (i), (ii), and (iv) but not (iii). The direction of a moving plaid may be changed by altering the relative speeds of the components (type V) or the orientations of the components (type O). Psychometric functions for type V direction changes in drifting plaids showed no alteration in sensitivity or bias point with added type O orientation change. Likewise, discrimination of type O orientation change was unaffected by added type V direction changes. Thus, detection of type V and type O angular motions can be independent. However, dynamic sensitivity to changing orientation is 4–10 times greater than sensitivity to changing direction, and we present theoretical arguments and experimental evidence indicating that this dynamic orientation sensitivity is equivalent to the detection of curl.

◆ **Temporal biases in speed perception rely on stimulus distribution as well as temporal order**

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Biases in perceived speed have commonly been found by applying spatial manipulations to motion stimuli. We have recently reported (Harris and Rushton, 1997 *Perception* 26 Supplement, 74) a temporal bias during speed perception. In a 2IFC task, for matched physical speeds in the first and second interval, the speed of motion in the second interval is consistently perceived as faster than that in the first interval. Here we explore temporal biases in speed perception further, by asking how speed biases are affected by the overall population of stimuli displayed. We were interested in whether an observer's response is based solely upon the stimuli presented within each trial, or whether it is biased by previously viewed stimuli.

Stimuli consisted of circular patches (~2 deg) containing fifty translating dots. In a 2IFC procedure, the task was to judge whether the motion was faster in the first or the second interval. We randomly interleaved five sets of stimuli. Each set consisted of a reference speed, always presented in the first interval, and seven test speeds, spaced evenly around the reference, and presented in the second interval. In each run there were four repetitions of each set of stimuli. We collected data for eight experimental runs.

For all sets we expected to find a small negative bias (second interval faster) if observers base their judgments solely on the current stimulus pair. However, the biases found differed between sets: for the slowest set there was a positive bias, for the fastest set there was a large negative bias.

The fastest reference speed produced the largest bias of around 10%. This is consistent with the perception of speed as being biased, not just by the order of presentation (first interval or second), but also by the distribution of stimuli previously viewed.

◆ **A study of motion aftereffects in a neuromorphic model of motion detection**

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We have recently established a new model of motion processing [A Torralba and J Hérault, 1997 *From Retinal Circuits to Motion Processing: A Neuromorphic Approach to Velocity Estimation* (Brugge, Belgium: ESANN)], based on a neuromorphic architecture. The model is made of a series of neurons coupled with asymmetric reciprocal synapses. The combination of the outputs of two arrays of elementary motion detectors tuned for two opposite motion velocities produces an estimation of local velocity. It has proved to be a very simple and efficient solution to optical flow estimation in a wide range of image sequences. We are interested in the adaptation capabilities of such a circuit and its ability to account for some motion aftereffects. Two possibilities of adaptation processes are considered: the first one deals with some fatigue at the neuron level (it acts directly on the output combinations) and the second one takes into account the synaptic plasticity (of Hebb type) between neurons (it acts as a decorrelation process between elementary motion detectors). Using the same stimuli, we compared the results of the model to the data from human perception, since the first hypothesis seems well suited to account for the 'waterfall aftereffect', the second one is more likely to explain the rotary motion effect [D M MacKay, 1967 *Models for the Perception of Visual Form* (Cambridge, MA: MIT Press)], due to a specific property of gain control.

◆ **The extrapolation of visual motion trajectories**

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Owing to the delays incurred by neural transmission and processing, there is an inevitable delay between the occurrence of an event and our ability to perceive or respond to it. Thus, if we attempt to catch (or avoid) a moving object, we must extrapolate its trajectory in order to produce an appropriate response: if we were simply to attempt to respond according to our representation of its instantaneous position, the object would have moved by the time that representation could be computed.

This presentation concerns mechanisms by which the brain might extrapolate motion trajectories. Phenomena of 'representational momentum' reported in the cognitive-psychology literature have been examined, whereby small forward shifts in the finishing position of a moving visual stimulus are less detectable than backward shifts of equal magnitude. Psychophysical forced-choice methods have been used to study the effect, to obtain objective measurements of motion direction discrimination thresholds following apparent motion of the stimulus. The lag between the end of the motion sequence and the onset of the target for discrimination was varied, and the complexity of the apparent motion trajectory was also manipulated.

Results indicate that more than one mechanism operates to produce motion extrapolation: short latencies allow only for 'low-level' mechanisms which are relatively impervious to training, whereas at longer latencies, 'higher-level' mechanisms are able to use more of the stimulus information to extrapolate motion trajectories, and are correspondingly more flexible in their operation.

◆ **Spatial interaction of motion signals: a dual mechanism?**

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We examined the 'antagonistic' model of spatial interaction of motion signals, which assumes integrative interaction between nearby regions and differentiating interaction between distant ones (eg Nawrot and Sekuler, 1990 *Vision Research* 30 1439-1451). The stimulus consisted of three rows of rectangular fields with no physical contours. In each field, a random-dot kinematogram (RDK) composed of signal and noise dots was presented. Between the frames of the RDK, the signal dots were shifted by a fixed amount either leftward or rightward; the noise dots were shifted in random directions by the same amount as the signal dots. First, spatial extent of integrative interaction was determined. The extent was defined as the maximum stimulus height below which the three fields of the RDKs with different signal-dot ratios were perceived to move in one direction as a whole. Next, the effect of the RDKs in the upper and the lower fields

on the apparent-motion direction of the RDK in the centre field was investigated. The results showed that the apparent-motion direction of the centre RDK was biased by the surrounding RDKs which were located outside the integrative region for the centre RDK. This bias could be either differentiating (motion contrast) or assimilatory (motion assimilation), depending on the number of frames, the exposure duration of each frame, and the amount of the shift of the dots. These results suggest that spatial interactions of motion signals are mediated by a 'non-antagonistic' mechanism as well as by the antagonistic one.

◆ **Apparent direction of the global moving pattern including a drifting grating**

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The apparent direction of movement of a circumscribing disk with a sinusoidal grating was measured in order to examine whether or not local movement affects global movement. The disk was made to drift horizontally from left to right at a velocity of  $28.3 \text{ deg s}^{-1}$ . The sinusoidal grating was made to drift vertically, and the velocity was varied from  $-32$  to  $+32 \text{ deg s}^{-1}$  (negative values refer to downward drift and positive values refer to upward drift). The spatial frequency of the grating was 0.2, 0.4, 0.8, 1.6, or 3.2 cycles  $\text{deg}^{-1}$ , and the luminance contrast was 15% or 100%. The disk was seen to move diagonally upwards when the grating was made to drift upward, and it was seen to move diagonally downwards when the grating was made to drift downward.

The results indicate that the apparent direction of the disk was not affected by the velocity but rather by the temporal frequency of the grating, and that the apparent direction of the disk was most affected when the grating drifted at 6.4 Hz. Moreover, it was found that the apparent direction of the disk was not concordant with the direction predicted by the simple vector-sum operation for directions of the disk and the grating. The mechanism of direction constancy might have caused this discordance.

◆ **Acuity for relative motion is better than acuity for detecting absolute motion**

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Visual acuity for small movements is known to be better than that for small positional differences. We have found similar hyperacuties for detecting differences in the relative motions of spatially separated features.

Using three collinear Gaussian blobs ( $SD = 10 \text{ min of arc}$ ) separated by  $100 \text{ min of arc}$ , we measured acuities in three types of tasks. Position acuity was measured in a static bisection task, with the central blob displaced slightly from the centre position defined by the two outer blobs. Absolute-motion acuity was measured as the smallest detectable amplitude of phase-locked sinusoidal oscillations of the blob positions. Relative-motion acuity was measured by moving the central blob antiphase to the outer blobs.

Positional acuities ranged from 40 to 53 s of arc. Absolute-motion thresholds were 17% to 30% of position thresholds, ranging from 9 to 12 s of arc. Relative-motion thresholds were lower still, ranging from 6 to 10 s of arc.

This demonstrates that the visual system is exquisitely sensitive to the relative motion of spatially separate image features. Also, relative-motion thresholds seem to remain low over increases in spatial separation and temporal frequencies of feature movement.

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◆ **Electrophysiological manifestation of first-order motion perception**

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Brain electrophysiological activity (electroencephalogram—EEG and evoked potentials—EPs) related to motion-onset perception of a pattern in the visual field was studied.

A group of four healthy subjects was examined with the use of first-order motion. The stimulus consisted of a regular high-contrast checkerboard (96%) moving at a velocity of  $7 \text{ deg s}^{-1}$  for 0.5 s with subsequent 2.5 s stationary presentation. Recordings were performed at eight locations:  $F_3$ ,  $F_4$ ,  $C_3$ ,  $C_4$ ,  $P_z$ ,  $O_z$ ,  $O_L$ , and  $O_R$  (5 cm to the left or right from the  $O_z$ ). Thirty-two single EPs with 500 ms pre-stimulus and 500 ms post-stimulus period (starting at the time of motion onset) were recorded twice from each subject. The EEG was analysed in the spectral domain by Fourier analysis

with emphasis on the comparison of pre-stimulus and post-stimulus records. An increase of power spectral density (PSD) was found in all electrode locations for delta (90%), theta (100%), and alpha (40%) bands. In contrast, a decrease of the PSD was revealed in the beta (18%) and the gamma band (10%). The PSD enlargement was accompanied by strong synchronisation in the aforementioned bands; however, it was also observed in the beta band with overall reduction of the PSD in the post-stimulus part.

The average EPs analysed in the post-stimulus recordings were unbiased. Grand average EPs were also computed over the group and decomposed into space-time independent components (Makeig, 1997 *Proceedings of the National Academy of Sciences of the USA* 94 10979–10984). The main negative component of motion-onset EPs typically observed in the occipital region at the latency of 160 ms was split into two independent components: the first—with spatial localisation in frontal region at 120 ms after motion-onset and the second—spatially placed in temporo-occipital areas with the latency of about 160 ms.

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◆ **Mechanisms for identifying the 'sign' of speed change between successively presented motions**

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The accuracy with which people can identify the 'sign' of the speed change in a two-motion paradigm strongly depends on the presence/absence of an interstimulus interval (ISI) between the two motions that are being compared.

In the present study we varied the ISI and the motion duration with a random-dot pattern moving within a 9.5 deg aperture. The ISI was either 1000, 500, 250, 125, 63 ms (separated-motions condition), or 0 ms (contiguous-motions condition). Motion durations of 125, 350, 500, and 1000 ms, and mean velocities of 8 and 16 deg s<sup>-1</sup> were used. Subjects were asked which of the two successively presented motions was faster, ie whether the change of the speed was from a high to a low speed level or vice versa. Weber fractions, determined by the method of constant stimuli, were used to specify the performance accuracy. When Weber fractions obtained from both conditions were expressed as a function of the stimulus onset asynchrony (SOA), the data points fell on a common smooth curve. With increasing SOAs the Weber fractions decreased, reaching an asymptotic level at SOAs longer than about 500 ms.

We suggest that (i) the decrease of the SOA (the sum of the first motion duration and ISI) below this critical value might be the crucial factor for the impairment of the accuracy of the identification of the sign of the speed change at both separated-motions condition and contiguous-motions condition, and (ii) a common mechanism might operate at these conditions. The results are discussed in relation to possible underlying physiological processes and models of speed perception.

◆ **From corrugated to transparency motion perception: density effects**

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Random-dot kinematograms, in which two velocities are interleaved in adjacent stripes, lead to the perception of corrugated moving patterns. Van Doorn and Koenderink (1982 *Experimental Brain Research* 45 189–195) reported that, for small bar widths, perception switches to motion transparency. In the present study, subjects had to detect, in a 2AFC procedure, which stimulus contained two motions. Motion segmentation thresholds were defined as the minimal speed difference between adjacent stripes needed to give 75%-correct responses. The effects of bar width and dot density were investigated.

For a constant dot density, speed difference thresholds changed as a sigmoidal function of bar width. When bar width decreased, thresholds rose up to an asymptotic value found for bar widths smaller than 0.4 deg and perception switched from motion corrugation to motion transparency. The transition occurred in the range 2–0.4 deg. The amplitude of the sigmoid function was dependent upon dot density: increasing dot density resulted in a decrease in motion segmentation thresholds for corrugated pattern and in an increase in thresholds for transparent patterns. Such dependence was modeled as the result of a signed local (0.4 deg diameter) motion interaction. As a function of bar width, increasing dot density would change the ratio between local coactivation of units tuned to similar speeds and local inhibition between units tuned to different speeds.

◆ **Simple and choice reaction times to changes in direction of visual motion**

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Subjects observed a random-dot pattern that moved within an invisible aperture. The pattern moved vertically, then abruptly changed the direction of motion without changing its speed. In experiment 1 the subject was asked to perform a simple reaction to the change in the velocity vector. In experiment 2 he/she had to perform a choice reaction: pushing a left button when the direction changed to the left and a right one when the change was to the right. The same angles of change between  $10^\circ$  and  $170^\circ$  and speeds of 4 and  $12 \text{ deg s}^{-1}$  were used in the two experiments. With  $12 \text{ deg s}^{-1}$  speed both simple-reaction and choice-reaction RTs were shorter than those obtained with  $4 \text{ deg s}^{-1}$ . The simple-reaction RT asymptotically decreased with increasing angle of change from  $10^\circ$  to  $170^\circ$ , whereas a U-shaped curve was obtained for the choice-reaction RT. It is argued that position-sensitive and orientation-sensitive mechanisms may be involved in the process of the choice reaction, but not in the process of the simple reaction. Further it is demonstrated that the simple-reaction RT is a decreasing function of the absolute value of the difference between the two velocity vectors, before and after the change. This result is in agreement with the model of Dzhafarov, Sekuler, and Allik (1993 *Perception & Psychophysics* 54 733–750) that deals with the simple-reaction RT to unidimensional velocity changes. An extension of the model for the two-dimensional case is proposed.

◆ **Neural model of superimposed motion discrimination**

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Our main goal is to develop a neural-network architecture dedicated to navigation and implemented on an autonomous robot. Owing to the specificity of the robot navigation, an essential task is to separate the ego movement from the motion of moving objects. Most of the optic-flow techniques used in image processing try to compute a unique movement direction for each position in the image. The computational cost can be very high and the methods are not well adapted to attributing several movement directions to a single image position. The problem of the separation of an arbitrary number of superimposed optic flows seems to be difficult to solve. A good starting point is to understand how several optic flows can be perceived simultaneously by humans.

We performed a psychophysical experiment which consists in presenting two sequences of superimposed random dots and asking subjects to tell in which of them there is the largest number of superimposed movements. The results show that we are very efficient in separating 1 vs 2 and 2 vs 3 superimposed movements. But the errors grow up to 50% when subjects are asked to separate 3 vs 4 superimposed movements.

We conclude that only two superimposed movements can be separated effortlessly. In the case of three superimposed directions, subjects appear to compute a vectorial sum of two of the vectors to reduce the number of perceived directions. Therefore, a dynamic-neural-network model of motion perception that uses two superimposed neural maps connected in a competitive/cooperative structure is proposed. Inhibition between orientations for a position on a map allows a single orientation for that map to be selected, and competition between two maps for neighbouring orientations allows subjects to perceive two different movements at a single position at the same time. This mechanism also allows us to explain why two movements separated by an angle of less than  $90^\circ$  appear to be orthogonal. Moreover, a cooperative mechanism between neurons associated with the same orientation on the same map allows us to account for the barber-pole illusion and induces a robust perception of movement. Our model accounts for much of the experimental data and seems to be simple enough to be applied to our mobile robot and efficient enough to let it follow moving objects in a complex environment.

◆ **When does noise affect perceived velocity?**

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In random-dot kinematograms comprising dots moving in coherent 'signal' directions or random 'noise' directions, displays with high signal coherence appear faster than those with low coherence (Owen, Raymond, and Thompson, 1997 *Perception* 26 Supplement, 80).

To investigate the extent to which noise dots influence the perceived velocity of signal dots we examined the role of signal-noise segmentation by manipulating segregation cues based on colour and direction of motion. In the colour-cue conditions, signal and noise dots were of the 'same' or 'different' colours (luminance controlled). In the direction-cue conditions, signal dots

moved in a single coherent direction (eg eastwards), noise dots moved in either of two trajectories, 45° from the signal direction, either 'forward' (NE and SE) or 'backward' (NW and SW).

Using speed matching judgments in a 2AFC staircased paradigm we quantified the effect of coherence on the perceived velocity of signal dots.

We found that, for the 'same' colour conditions, increasing coherence increased perceived velocity. Coherence had no effect on perceived velocity in the 'different' colour conditions. No difference emerged between the two noise types ('forward' vs 'backward').

The results of the colour-cue conditions support the proposal that signal and noise are segmented where possible, and that segmentation leads to accurate velocity estimates. The direction-cue conditions pose a problem for this interpretation as 'forward' noise motion should be more difficult to segment than 'backward' noise motion, yet we failed to observe any such difference. Possible explanations for this latter result are discussed.

◆ **Some aspects of visual evoked potentials to global-motion onset**

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We investigated the components of global-motion-onset visual evoked potentials (VEPs). The onset was a sudden transition from random motion to coherent global motion. The purpose of this stimulus was to reduce the effect of the low-level generators in the VEP and to reveal the components truly related to global motion. In the random phase, small squares with a triangle-shaped temporal luminance profile moved on the screen along linear trajectories. The directions of the squares were random as was the location where a new square was created for each faded one. At the onset of global motion the squares suddenly changed their direction resulting in a coherent expanding motion. VEPs were recorded from sixty-four electrodes referenced to Fz. There were three prominent temporo-occipital components in the VEP: a positive peak at 200 ms, a negative component at about 300 ms, and another negative component in the range of 400 to 500 ms. There was one possible low-level generator present in our stimulus: the sum effect of the simultaneous change in the direction of motion of the squares. For this reason, we did a control experiment in which the stimulus was a random change of the directions of the squares. The distribution of all the direction changes was the same as in the main experiment. The resulting VEP showed two major components that were very similar to the first two in the main experiment. Thus, only the third component at about 400 to 500 ms seems to be related to global motion.

◆ **The contributions of motion onset and form-from-motion to a transient negativity in the visual evoked potential**

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Recently we measured visual evoked potentials (VEPs) elicited by a computer-generated random-dot kinematogram in which subjects had to detect the position of the gap in a form-from-motion Landolt ring (Rutschmann and Wist, 1997 *Perception* 26 Supplement, 134). VEPs were dominated by a negative peak (N2) whose latency varied with the motion contrast between the ring and its background. A high correlation between N2-latencies and the gap-recognition times indicated a relation between the generation of N2 and form detection rather than between N2-generation and motion onset.

In a further study, we compared two conditions: (i) coherent movement of the background pixels with the ring being defined by stationary pixels in the screen centre; (ii) coherent movement of the background pixels in the absence of the ring. N2-amplitudes were smaller for the latter condition than for the former even though the absolute number of moving pixels was lower. For ten of the sixteen subjects N2-amplitudes were reduced by more than 50%, and three of the sixteen subjects did not show a measurable N2 in the second condition. The results are interpreted as being consistent with the hypothesis that the N2 measured here is the product of the superposition of two processes: one involving the response to motion onset and another more dominant one involving form processing.

◆ **Short-term and long-term extrapolation of visual motion**

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Extrapolation of visual motion is most common in daily life (eg to allow for advance specification of corresponding motor acts when catching a ball). A linear model has been proposed to describe extrapolation performance (Yakimoff et al, 1993 *Human Factors* 35 501–510), based on

extrapolation times (ETs) up to 2.7 s. We investigated whether Yakimoff's model also applies to longer ETs.

The target (a luminous dot) moved from left to right over 12 deg and then disappeared. Subjects pressed a key to indicate the moment at which the occluded target reached a stationary reference. Six extrapolation distances (2 to 12 deg) and four target speeds (1, 2, 4, 8 deg s<sup>-1</sup>) were used, resulting in twenty-four (randomly presented) stimulus conditions with fifteen different ETs (0.25 to 12 s). Mean performance, ie response time (RT) minus ET, of twelve subjects was best described by a cubic rather than linear function: overestimation (RT > ET) peaked at 1.65 s, while underestimation occurred increasingly for ETs above 3 s. However, for data sets split into short (< 1.65 s) and long (> 1.65 s) ET-ranges, two linear functions were appropriate: RT = 1.022ET + 158; RT = 0.759ET + 727.

Thus, the present data confirm and extend Yakimoff's linear model, suggesting two different (short-term and long-term) mechanisms of motion extrapolation. Such a distinction might also account for the reversal of velocity transposition in motion extrapolation, recently found for longer ETs (Sokolov et al, 1997 *Perception* 26 875–889).

◆ **Global motion segregation does not depend on detection of steep motion gradients**

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The mechanisms underlying the parsing of a spatial distribution of velocity vectors into two adjacent (spatially segregated) or overlapping (transparent) motion surfaces were examined with the use of random-dot kinematograms. Parsing might occur on the basis of either of two principles. Surfaces might be defined on the basis of similarity of motion and then sharp perceptual boundaries drawn between different surfaces. Alternatively, detection of a high gradient of direction or speed separating the motion surfaces might drive the process. To establish which method is used, we examined the effect of altering the motion-direction gradient. In the case of a sharp direction gradient, each dot had one of two directions differing by 135°. With a shallow gradient, most dots had one of two directions but the directions of the remainder spanned the range between one motion-defined surface and the other. In the spatial-segregation case, the gradient defined a central boundary separating two regions. In the transparent version, the dots were randomly positioned. In both cases all dots moved with the same speed and existed for only two frames before being randomly replaced (total duration 11 frames, 0.5 s). The ability of observers to parse the motion distribution was measured in terms of their ability to discriminate the direction of one of the two surfaces. Performance was hardly affected by spreading the gradient over at least 25% of the dots (corresponding to a 1-deg strip in the segregation case). We conclude that detection of sharp velocity gradients is not necessary for distinguishing different motion surfaces.

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◆ **Timing accuracy in motion extrapolation: Reversed effects of spatial properties at low and high velocities**

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We extended and reanalysed our recent data on motion extrapolation (Sokolov et al, 1997 *Perception* 26 875–889) to examine the timing accuracy as a function of target size, speed, and visible motion path. A target (horizontal pair of dots separated by either 0.2 deg—small, or 0.8 deg—large) moved at a constant speed of either 2.5, 5, or 10 deg s<sup>-1</sup> across a horizontal path (2.5 deg—short, or 10 deg—long) and then vanished. Observers pressed a key when they judged that the leading dot of the occluded target had reached one of seven randomly presented positions between 0 and 12 deg.

Similar to earlier findings (eg Yakimoff et al, 1993 *Human Factors* 35 501–510), mean extrapolation response time was found to exceed the arrival time. With long visible paths, the timing accuracy (as indicated by absolute error) was better for moderate and high than for low velocities. This difference increased with increasing extrapolation interval owing to a progressive loss of accuracy for low velocities. However, with short paths, performance was much more accurate for the low than for the moderate velocities even across long extrapolation intervals. The magnitude of errors increased as intervals got longer, with a markedly steeper increase for moderate speeds. Similar

effects as those with the short path were also found with different-sized targets; they were stronger for large than for small targets. The findings suggest that the visual system implements different scaling algorithms for motion perception and extrapolation of different-sized stimuli depending on target speed. At higher speeds, processing of visible and occluded motion is likely to share a common scaling mechanism.

◆ **Sex-related and age-related properties of gait signal displayed by point-light walkers**

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Subjects observed walkers whose gaits were depicted in point-light displays. LED lights were affixed to the backs of the walkers (four men and four women aged 18 to 62 years) at their eight major joints (shoulders, hips, knees, and heels). The walkers were videotaped as they walked on a treadmill at a speed of 1.0 to 3.0 km h<sup>-1</sup>. Their gaits, depicted in point-light walkers (PLWs), were projected on a screen and subjects made judgments about their sex and age.

The results, obtained from 400 undergraduates (206 female and 194 male), revealed that, on average, there was 72% correct identification of the gender and the PLWs of older walkers were 85% or more correctly identified. Classifying the male gait as male signal and a female gait as non-male signal (or noise), we applied signal detection theory to the results and found that the detectability ( $d'$ ) of male signal was larger in female observers (0.74) than in male ones (0.69), while the detectability of the female signal was larger in male observers (0.78) than in female ones (0.73). The PLWs of old walkers were presumed to be 20 years or so younger than they were and a kind of rhythmic motion-pattern produced by the movements of both shoulder and heel made the PLWs of younger walkers look older in age. These findings suggest that sex-related and age-related properties of the gait signal displayed by PLWs are given by three kinds of perceptual processes: rhythmic motion-pattern set up by shoulder and heel movements (which is typical of the walker); spatial arrangement of point-lights which comprise the PLW; and the detectability of the gait signal which characterises the observer's behaviour.

◆ **Centre-surround interactions in the rotary motion aftereffect**

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The rotary motion aftereffect (MAE) was examined with a central sector disk surrounded by a similarly sector annulus in two experiments. The durations of MAEs were measured independently for the centre and surround. In experiment 1, robust MAEs were recorded for the centre and for the surround when they alone rotated during adaptation. An induced central MAE was also produced following rotation of the surround alone, but no surround MAE was induced after rotation of the centre alone. The induced MAE was about 30% of the surround MAE duration. In experiment 2, the interactions between a rotating surround and centres that were either static or moving (in the same or opposite directions) were examined. The centre MAE was of similar duration following surround rotation in the same direction and a static surround. However, the central MAE was shorter when the surround MAE was in the opposite direction. The longest MAE in the surround was following centre and surround rotation in the same direction. The results are contrasted with those previously reported for linear MAEs.

◆ **The effect of disparity on transparent-motion perception for two oppositely moving gratings**

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We present a new illusory perception of motion transparency arising from the binocular presentation of counterphase flickering stimuli. The stimuli consisted of two vertically oriented sinusoidal standing waves at each eye with no spatial phase difference between them. When the interocular temporal delay was about zero, the observer perceived one binocularly integrated counterphase flickering-wave. When the interocular temporal delay was 45°–135°, the observer perceived two sinusoidal waves moving on different depth planes in the opposite direction to each other. This suggests that the visual system is able to decompose the moving images into Fourier components, and that the decomposition of the flickering standing wave may be mediated by the first-order motion system such as direction-sensitive and disparity-sensitive motion energy detectors. On the other hand, for the interocular temporal delay of 0°–45° and 135°–180°, only one flickering standing wave was perceived. This perception may be caused not by the motion energy system but by the higher-order motion system such as feature-tracking system. Lu and Sperling (1995 *Vision Research* 35 2697–2722) have shown that the cut-off frequency of the motion detection of the feature-tracking system is 3 Hz. If the perception of flickering is mediated by the feature-tracking

system, the probability of flickering perception will be reduced at higher temporal frequency of flickering. Analysis of observers' responses to varying temporal frequency of flickering supports this prediction. An observer's motion perception in the cyclopean domain may be determined by either the first-order system or the higher-order system—by the process with relatively larger activity between them.

◆ **Evidence of a gradient effect in processing hidden periodic movement**

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One of the abilities of the visual system is the processing of motion information when an object passes behind an occluder (the tunnel effect). To investigate what happens if the hidden movement stretches over a long time, we devised a new experimental paradigm: two diametrically opposite white dots rotating at a constant speed on a circular trajectory were presented on a black background. One of the dots, indistinguishable from the other one, was the target that subjects were required to follow for a fixed number of revolutions (exposure period). Then the dots disappeared for a number of revolutions varying from 0.1 to 4 ('blackout' period). When they reappeared on the screen, subjects had to stop their movement and indicate which one was the target. Results show that overall performance decreased as the number of revolutions increased. However, we observed a gradient effect when analysing the data as a function of phase, independently of the duration of the blackout period: best performance was obtained at 90° subsequent to the position of target disappearance and it gradually decreased in the successive parts of the trajectory. These results support the idea that in processing hidden periodic movement, subjects are accurate in detecting the period but not the speed within it.

◆ **How common must common fate be?**

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We studied the perception of coherent motion produced by the Gestalt grouping factor of common fate. We determined how much motion coherence was needed to detect a small group of moving dots in a dynamic-visual-noise background. A line of dots moving perpendicularly to the line's orientation served as the stimulus. The observer's task was to decide which of two dynamic noise fields contained the coherently moving group. The lifetimes of the coherent trajectories of the target dots and that of each of the noise dots were the same (1140 ms). In addition to parallel trajectories and linear dot arrangements, divergent, convergent, or crossing trajectories and non-linear dot arrangements were also tested as was the effect of lifetime.

Threshold was reached for stimuli containing as few as 4 dots in 100 and with an interdot distance of 22 min of arc. Detection varied little with divergence and convergence (up to 8 deg) from parallel trajectories, suggesting that only the initial or terminal phases, respectively, may have influenced detection. This assumption is consistent with the threshold saturating at a lifetime of between 600 and 700 ms. Crossing trajectories generally had a small effect, but nonlinear forms greatly impaired performance. The two factors appear to interact, with the best performance coming from the combination of parallel trajectories and linear form.

The results help to understand the effects of both dot masking and figure-ground segregation. They also permit specific predictions regarding the spatial grouping ('binding') of individually moving targets by means of spatiotemporal synchronisation as a type of dynamic form perception ('form-from-motion').

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◆ **Changes and invariances of motion detection with luminance level**

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It is well known that spatial and temporal visual resolution change drastically upon dark adaptation. Yet the consequences of these changes for motion vision have hardly been studied quantitatively with modern psychophysical techniques and stimuli.

We studied the monocular detection of coherent motion in moving random-pixel arrays (RPAs) at adaptation light levels from 50 to  $0.005 \text{ cd m}^{-2}$  in terms of the threshold luminance signal-to-noise ratio (LSNR) as a function of velocity. The four subjects wore light-tight goggles with calibrated neutral density filters of 1–4 log units attenuation (F1–F4) or without filter (F0). To compensate for differences in the visibility of RPAs at the different adaptation levels we first determined the viewing distance  $D_{20}(F_i)$  at which a static RPA has a contrast threshold of 20%. These viewing distances were then used to determine the threshold LSNR as a function of velocity. (Monocular viewing; constant rms contrast of 70%;  $128 \times 128$  pixels viewed through a circular aperture; Quest staircase converging on 85% correct).

The equalisation of static visibility across adaptation levels leads to an approximate light-level invariance of the minimum threshold for direction discrimination. The velocity-tuning curves coincide well at low speeds if plotted in terms of retinal velocities, suggesting a constant ratio of spatial to temporal resolution regardless of adaptation level. The high-velocity limit in terms of object speeds decreases and in terms of retinal speed increases with dark adaptation (and its concomitant distance decrease). We found no obvious qualitative differences between rod-dominated and cone-dominated motion detection.

◆ **Motion coherence thresholds: effect of dot lifetime and comparison with form coherence**

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Motion coherence thresholds in random-dot displays have become increasingly used as an indicator of global motion processing, including applications to neurological and developmental pathologies (eg dyslexia, Williams syndrome). Functional imaging and primate studies support the idea that motion coherence reflects function of the extrastriate dorsal pathway, including areas V5 and V3A [Braddick et al, 1997 *Investigative Ophthalmology & Visual Science* 38(4) S919]. A 'form coherence' task may provide a comparable measure of global processing in the ventral stream (Braddick et al, 1997 *Neuroreport* 8 1919–1922).

Coherence thresholds, and their interpretation, may be affected by variations in the signal/noise display, such as the lifetime of signal dots. We measured fifteen subjects' signal/noise thresholds for random-dot displays (Wattam-Bell, 1994 *Vision Research* 34 877–883) in which individual signal dots had lifetimes of 2, 3, 6, or unlimited 20 ms frames. Form coherence thresholds for identifying line segments arranged in concentric circles among randomly oriented segments were also measured. Thresholds rose from an average 4% for unlimited lifetime to 50% for two frames. Motion coherence thresholds for different lifetimes were highly correlated across subjects, but uncorrelated with form coherence thresholds.

Decreasing lifetimes might reduce performance because of (a) replacement of signal dots at the end of their lifetime adds to effective noise; (b) reduced temporal integration over individual dot trajectories; (c) subjects' strategies of tracking individual dots when lifetime is unlimited. All three factors appear necessary to account for the pattern of our results. To avoid effects of differential use of tracking strategies, dots with limited lifetime over 100 ms are recommended, especially when studying neurodevelopmental anomalies of dorsal stream function.

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◆ **Subjective orbit of spinning objects**

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Why is it that objects sometimes seem to move along a track which is physically impossible? Our hypothesis is that the local movements of the object influence the perception of its global motion. In order to test this hypothesis, we did the following psychophysical experiment. Structured stimuli (grey-level patterns consisting of a first derivative in two directions of a Gaussian function) moved along a slightly curved path on a computer monitor, from right to left or vice versa. While moving along the global path the stimuli rotated around their own centre. Both the global and the local velocities were systematically varied. The local velocity direction could be clockwise or counterclockwise. Subjects had to decide whether the global path of the stimulus was curved upwards or downwards.

Our results show a clear influence of the local velocity direction on the perceived curvature of the global path. Within the range of velocities used, the influence is larger with increasing magnitude of global velocity. The magnitude of the local velocity does not seem to influence the results.

## DEVELOPMENT AND AGEING

### ◆ Larger VEP signals from nasal-to-temporal displacements in infants' directional motion asymmetry

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When young infants view monocularly a horizontally oscillating grating, the VEP shows a prominent first-harmonic component (Norcia et al, 1991 *Investigative Ophthalmology & Visual Science* 32 436–439). This implies an asymmetry between neural responses to nasal-to-temporal (NtoT) and temporal-to-nasal (TtoN) responses. However, such steady-state VEPs cannot show which direction in the oscillation generates the stronger signal.

For a grating stimulus undergoing successive displacements in the same direction (Mason et al, 1998, ARVO), the NtoT direction gave a consistently larger amplitude in 5–21-week-old infants. In the present study we tested whether the same asymmetry is found between the transient VEP responses to the two directions of an oscillating stimulus. Simultaneous EOG recordings tested whether any asymmetry was related to eye movements.

Infants aged 8–14 weeks viewed monocularly a vertical grating of 1 cycle  $\text{deg}^{-1}$ , oscillating through  $\frac{1}{4}$  cycle at 1 Hz. Amplitude of the initial VEP peak was measured for displacements in each direction. For 17 eyes, NtoT responses were on average 80% larger than TtoN, a significant difference ( $p = 0.007$ ). Simultaneous EOG records showed no evidence of directional oculomotor responses synchronised to the displacements. Surprisingly, this stronger neural response for NtoT displacements is opposite to the asymmetry of optokinetic responses at this age. It does not appear to be an artifact due to retinal slip with differential eye movements. Oculomotor and VEP asymmetries in development may be related. However, this relationship does not seem to be simply that stronger neural responses lead to stronger optokinetic responses.

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### ◆ Young infants' perception of moving illusory contours is influenced by contour velocity

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We investigated infants' ability to perceive illusory contours, where no mean luminance contrast exists, generated by aligning line terminators. Stimuli comprised black and white sinusoidal lines on a grey background; aligned terminators defined an illusory contour on one side of the display, while on the other side of the display the sinusoidal lines were broken by non-aligned terminators. The illusory contour was presented oscillating horizontally at  $6.6 \text{ deg s}^{-1}$ ; the equivalent motion on the other side gives the appearance of the individual lines growing and shrinking. Infants from three age groups (8–10, 12–14, and 20–22 weeks) were tested by forced-choice preferential looking. A control condition showed a significant preference for a moving luminance-defined contour over individual terminator motions. All but the 8–10-week olds exhibited significant preferential looking behaviour in favour of the illusory contour side of the stimulus. The speed used for the illusory contour is below the narrow velocity range over which 10-week olds can discriminate motion direction (Wattam-Bell, 1996 *Vision Research* 36 1671–1677). To test whether the change in illusory-contour perception with age is a consequence of maturing motion-processing mechanisms, we tested 8–10-week olds with the same stimuli at a higher velocity ( $9.5 \text{ deg s}^{-1}$ ) and found a preference for the illusory contour. Together these results suggest that perception of dynamic illusory contours can be demonstrated in 2–5-month olds, provided the development of motion-processing mechanisms is taken into account.

### ◆ Newborn infants can perceive the continuation of partly occluded gratings

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There have been several studies that confirm the ability of visual completion in infants aged 2 and 4 months by the habituation method, but never in newborn infants. In the present study, thirty two newborn infants (average age, 3 weeks and 4 days) were habituated to one of four displays consisting of a vertical sinusoidal grating of low ( $0.4 \text{ cycle deg}^{-1}$ ) or high ( $1.2 \text{ cycles deg}^{-1}$ ) spatial frequency, whose central portion was covered up with a horizontal white occluder which was narrow ( $1.33 \text{ deg}$ ) or broad ( $4.17 \text{ deg}$ ). Posthabituation-test displays consisted of a complete grating of the same frequency as the habituated grating, or comprised a separate grating whose central

portion was replaced with a black gap of the same height as the occluder in the habituation display. The infants habituated to the low-frequency grating with the narrow occluder stared significantly longer at the separate grating than the complete grating in posthabituation-test trials. The dishabituation to the separate grating indicates that the infants perceived the occluded grating as a complete one in the habituation period. In contrast, the infants habituated to the high-frequency grating with the broad occluder showed a tendency to stare longer at the complete grating than the separate grating, suggesting that the infants perceived the occluded grating as a separate one in the habituation period. The infants habituated to the low-frequency grating with the broad occluder or to the high-frequency grating with the narrow occluder stared at both posthabituation-test displays almost equally. Therefore, the observed dishabituation patterns did not depend on the frequency of grating alone, but on the combination with the occluder height. These results indicate that newborn infants can exhibit their visual completion ability under the low-frequency grating with the narrow occluder.

◆ **Preferential looking and preferential reaching in infants: neurobiological models of dorsal stream development**

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Young infants show clear preferences which are dependent on the eccentricity, contrast, size, and shape of objects in preferential looking. Functional onset and increasing sensitivity of specifically tuned neurons within visual cortical streams are postulated as the neurobiological underpinnings for these preferences.

Here we report studies comparing preferential looking (PL) and preferential reaching (PR) in 5–15-month-old normal infants for pairs of small objects (red, high-contrast 6-cm-long cylinders, diameter 1–6 cm), using the Elite motion analysis system to record the detailed kinetics of reaching. In all studies we found a strong bias towards reaching on the ipsilateral side to the reaching hand. This bias lessens with age and is significantly reduced when the object on the contralateral side is of graspable size. In study 1, there were significantly more first reaches to the smaller of the two objects displayed. In PL, where the objects were 2-D renderings of the cylinders displayed either side of a fixation point on a monitor, we found an age-specific bias for looking first at the object in the right visual field in 6 to 12 month olds and significantly more first looks to the larger object when that edge of the object was nearer to the fixation point. In study 2, PR and PL were compared simultaneously for the same solid objects. Confirming study 1, more reaches were once again made to the smaller of the two objects, and with the same ipsilateral bias. Differential development of dorsal action streams for reaching and looking are suggested to account for these results.

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◆ **Visual performance in auditory-handicapped children**

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Recently, it has been found that in auditory-handicapped children, some visual capabilities (eg visual search, stereoscopic vision) are, on average, lower than in children with normal hearing (Marendaz et al, 1997 *Perception* 26 Supplement, 104; Golubkov and Krasnoperova, 1997 *Perception* 26 Supplement, 58). Moreover, when mental performance of auditory-handicapped children was estimated by means of proofreading tests, the scores were also found to be lower than in control children. It is evident, however, that the results of usual proofreading tests depend both on intellectual and visuomotor capabilities and, therefore, low scores could be accounted for by lowered visual performance. To verify this suggestion, we estimated visual performance in 99 auditory-handicapped children (aged 6–10 years) and in 144 children with normal hearing (control group) by means of a computerised coding test which was modified to reflect mostly visuomotor capabilities. The subject has to compare a row of test figures with the sample showing their codes and to put the codes under the test figures by pressing keys (ten figures in one row, twelve trials). Codes were changed at each step forcing the subject to shift his/her gaze from the test row to the sample and back each time after pressing a key. All subjects were divided into four groups: pre-school children and children of the 1st, 2nd, and 3rd school forms. Two indexes were used to characterise visual performance: coding rate (average number of symbols per minute calculated for three best trials) and accuracy (total number of errors in all trials). As regards coding rate, statistically significant differences between auditory-handicapped and control groups were found only for pre-school children (10.9 vs 13.9 symbols min<sup>-1</sup>) and for the children of the 1st school form (12.0 vs 14.2

symbols  $\text{min}^{-1}$ ); in elder handicapped and control children, coding rates were practically equal (2nd forms: 17.3 and 17.5 symbols  $\text{min}^{-1}$ ; 3rd forms: 21.0 and 21.5 symbols  $\text{min}^{-1}$ ). However, as regards the accuracy of performance, the scores of auditory-handicapped children were significantly worse in all groups (eg, in pre-school and 3rd-form groups, the average numbers of errors for auditory-handicapped and control children were 8.9 vs 3.6 and 6.9 vs 2.8, respectively).

◆ **The influence of visual defects on the formation of infants notion about the visual world**

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An assessment of the basic visual functions (binocular fixation, eye movements, field of vision, visual acuity) and infant mental representation of the visual world (discrimination of form, size and colour; prediction of object movement; search for hidden toy) was conducted on about 1000 infants aged 4–14 months. Children with slight defects of basic visual functions (about 25% of practically healthy infants) showed worse results than their normal age-mates in all tests concerning visual notions. This delay cannot be explained exclusively by the delay in their general development, but may be due in part to the direct influence of the visual defects on slowing down intellectual development. An analysis of the correlation between concrete visual defects and slowing down of mental development revealed the following: (i) Instability of binocular fixation does not influence visual notion formation. (ii) Squints influence all visual notion formation only in early infancy (before 6–7 months). (iii) Visual field restriction influences the ability of searching for a hidden toy, but does not influence colour discrimination. (iv) Reduced visual acuity (non-attention to small crumbs) unfavourably influences the development of all notions about the visual world during the whole first year of life. The reasons for such correlations are discussed.

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◆ **When visuospatial and verbal functions first become two distinct units?**

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In a longitudinal study of infant twins from 3 months to 3 years of age we followed the dynamics in different domains of early mental development. The Bayley Scales of Infant Development (BSID-II, 1993) were used. Within the confines of the Mental Development Scale we constructed subscales of visual, manual, and visuo-manual coordinations, indirect actions requiring object permanence and extrapolation, control of actions, and also subscales of cooperation and vocalisations—gestures—speech development. Individual infants develop within these subscales rather heterochronically. On this basis, subscale indexes of their development can be calculated. We have made correlational and factor analysis of these subscale indexes at five ages of testing: 4 months, 8 months, and 1, 2, and 3 years. Also we analysed the influence of biological risk factors, as higher biological risk (such as lower birth weight and lower gestational age) is specific for infant twins population) in different domains of early mental development.

In factor structures of the ages before 2 years we found a varied composition of subscales within factors. Visual coordinations appear to be best protected from biological risk factors in comparison with other domains of early development. MZ and DZ twins have some specificities in dynamics of their early development. A clear separation of visuospatial and verbal functions into different factors happens only at 3 years of age in both MZ and DZ twins.

◆ **Age-related changes in wavelength discrimination (420–620 nm)**

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Losses in chromatic discrimination have been demonstrated with increasing age. We have previously shown that poorer discrimination along individually determined tritan axes in older individuals can be ascribed to either increased rates of neural noise or a loss in the ability of the photoreceptors to capture quanta. In this experiment, classical wavelength-discrimination curves were measured for four younger and four older observers. Monochromatic lights were presented in each half of a 2 deg bipartite field by means of a Maxwellian-view optical system. All stimuli were equated in luminance for individual observers by means of heterochromatic flicker photometry. A spatial 2-alternative forced-choice (2AFC) method was used in combination with a staircase procedure to determine the threshold for discriminating wavelength ( $\Delta\lambda$ ).

The results show a small but consistent elevation in  $\Delta\lambda$  for older compared to younger observers. Because age-related changes in ocular media density were compensated by equation of the retinal illuminance for individual observers, we interpret these age-related losses in discrimination as due to neural changes. The data were analysed in terms of a modified version of the Boynton-Kambe colour discrimination equations with a power law. Consistent with our previous results for an S-cone mechanism, losses in chromatic discrimination mediated by an L/M cone pathway appear to be due to increased rates of neural noise or loss in the quantal efficiency of the photoreceptors. We cannot exclude the possibility that there are age-related changes in the Weber fraction for an L/M cone pathway.

◆ **Age-related changes in human scotopic spatial mechanisms**

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Age-related enlargements of Ricco's area and losses in contrast sensitivity across low spatial frequencies have been demonstrated under scotopic conditions. It is unclear whether these changes are mediated by one or more spatial mechanisms. To address this issue, age-related changes in grating summation area were measured for two spatial frequencies in the peripheral retina under scotopic conditions.

Eleven younger (19–32 years) and nine older (52–80 years) trichromats, who were screened for retinal disease by direct ophthalmoscopy, participated in this study. Following 30-min dark adaptation, contrast sensitivities were determined by a maximum-likelihood algorithm for a series of Gabor patches (0.3 cycle deg<sup>-1</sup> and 1.2 cycles deg<sup>-1</sup>; -0.89 log scotopic trolands) of increasing area. Stimuli were centred along the horizontal meridian at 6 deg nasal eccentricity. The grating summation area was defined as the point at which sensitivity no longer increased as a function of stimulus area.

Sensitivity increased linearly with grating stimulus area up to an asymptote, but at different rates for the two spatial frequencies, implying mediation by different spatial mechanisms. The grating summation area of older subjects was 47% larger than for younger subjects with the 0.3 cycle deg<sup>-1</sup> grating (Mann-Whitney U-test:  $z = 2.545$ ,  $p < 0.02$ ), but no difference was found for 1.2 cycles deg<sup>-1</sup> gratings. Our results suggest that there is more than one spatial mechanism subserving scotopic vision and that age-related enlargements of grating summation area vary between these mechanisms.

◆ **Dynamics of visual acuity in schoolchildren**

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In most civilised countries, the number of children with lowered vision increases significantly during learning at school. This tendency appears to be preserved despite various prophylactic measures which do not produce satisfactory positive effects. It is evident that this negative tendency deserves more detailed investigation. And, first, it is necessary to have in hand latest statistical data on the dynamics of visual acuity (VA) in schoolchildren in order to determine the critical period and to analyse factors which could exert negative effects on vision at that period. Unfortunately, most available data have been acquired in the course of screening children for obvious visual anomalies and, therefore, appear to be rather rough and incomplete. To get more accurate data, we examined about 200 pre-schoolchildren and schoolchildren (aged 5.5–13.0 years) using self-made charts with Landolt rings which allowed us to obtain relatively good VA estimates in the range 0.1–4.0. The VA levels were determined for uncorrected distance vision (5 m), both monocular and binocular. It has been found that in one-year groups with the average age up to 9 years, monocular VA histograms look like single-mode distributions with peak values shifting from about 1.0 (at the age of 6 years) to about 1.5. In groups of elder children, monocular VA histograms have the appearance of two-mode distributions with main peak around 1.8–1.9, an additional smaller peak around 0.5, and a dip around 1.0. Binocular VA histograms show similar evolution with the expected shift of their main peaks to relatively higher values. The data obtained indicate that, for Moscow schoolchildren at least, the critical period begins at 9 years of age. At this age, the schoolchildren population disintegrates into two unequal parts. In members of the larger group, vision continues to improve, whereas in members of the smaller group vision begins to worsen. With age, the latter group becomes more and more numerous but the details of this process need further investigation.

◆ **Influence of macular pigment on age-related changes in the sensitivity of S cones: protective effect or gain control?**

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The relation between macular pigment (MP) density and the sensitivity of foveal and parafoveal mechanisms dominated by short-wave (S), middle-wave (M), and long-wave (L) sensitive cones was studied on fifty observers (12–88 years old). A 2AFC procedure was used to measure increment thresholds at 0, 4, and 8 deg (temporal) eccentricity. Test and background wavelengths were chosen to isolate S, M, or L cones on the plateau of their threshold vs intensity functions. Measures of individual ocular media and MP densities were also obtained.

Statistically significant age-related losses in sensitivity for each cone mechanism were found at 0, 4, and 8 deg. Sensitivity changes in S, M, and L cones specified at the retina were not significantly correlated with MP density. However, the sensitivity difference between 8 deg and 0 deg for S, but not M and L, cones was significantly correlated with MP density. Individuals with high peak MP densities are relatively more sensitive (specified at the retina) at 0 deg vs 8 deg than individuals with low MP densities, regardless of age. The latter result might be taken as support for the hypothesis that MP has a protective role that mitigates age-related losses in sensitivity of foveal S cones. That this relation is not related to age, however, suggests an alternative explanation. Rather, the gain of the S-cone mechanism in the fovea and/or parafovea is varied in a way that maintains its relative sensitivity (specified at the cornea) across the central retina, compensating for individual variations in MP density.

**TEXTURE**

◆ **Detecting gradient and discriminating shape from texture**

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Texture is a surface parameter. It characterises materials and can give information about the shape of objects. Surface textural variations can be recognised either as a local gradient or as a texture boundary (Wolfson and Landy, 1998 *Vision Research* 38 439–446). We have investigated the effect of two variables—the size and the contrast of the texture components—on the perception of texture. A visual stimulus generator was used to display 2-D textured images on a monitor. Eleven subjects were shown a test textured square (7.7 deg × 7.7 deg) against a reference textured background. The size of the texture components was chosen with reference to previously measured psychometric curves for detection threshold. Observers were asked to classify the difference between the two textures within three categories: not perceptible (weight 1), perceptible (weight 2), and highly perceptible (weight 3). Limits between categories differed significantly. This demonstrates the existence of two responses, one for the gradient detection and one for the edge detection. Average responses were plotted versus texture size ratio (reference/test). The curves exhibited an asymmetry: when the elements of the test were smaller than the elements of the background, gradient detection and boundary detection were more difficult to assess than in the opposite configuration. The former case suggests a filling-in phenomenon. Preliminary results show the same tendency for contrast. It has also been reported by the observers that the latency for detecting texture gradient was greater than for discriminating shape from texture.

◆ **Contribution of a dynamic model for texture perception**

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To be efficient, texture discrimination in complex images requires a large number of filters and is usually performed by a statistical classification which allows the dominant features of each texture area to be extracted. In the context of preattentive texture perception, a less complex system using only a small number of filters should be investigated. A simple system using competitive and cooperative mechanisms between the outputs of a filter bank allows the discrimination of a large class of textures but fails for textures that strongly activate several filters.

The idea explored here is to allow the discrimination of texture to be refined over time. First, to allow weaker outputs of filters to be taken into account, an inhibitory feedback is applied in the system. This feedback loop, dynamically computed, is used to inhibit the output of the filter corresponding to the local dominant feature. Second, based on the fact that some psychovisual tests show that low frequencies of an image are perceived before high frequencies, the outputs

of filters at different scales are processed separately and so are not directly in competition in the system. Global information of a scene is allowed to emerge prior to local information. The model is based on differential equations proposed by Amari where the average frequency of neuronal activity is taken into account. The competition term allows a dominant direction to be chosen locally when the cooperation term diffuses the activity of the filters in a neighbourhood. Finally, we show that the achieved architecture with some dynamic aspects can enlarge the discriminated texture classes and is still open to any attentional loops.

◆ **The perceived orientation of line textures corresponds to the centroid of the orientation histogram**

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Previous work on human perception of texture has concentrated on the ability of observers to discriminate or segregate textured regions. Less attention has been paid to the issue of how the visual system assesses the magnitude of various properties of textures. We have measured the perceived group orientation of textures comprising lines with orientations drawn from an asymmetrical probability density function (pdf). This was achieved by requiring observers to judge whether the overall orientation was clockwise or anticlockwise of the vertical for various orientations of the texture and thus finding the point of subjective equality (pse). We found that the pses were generally close to the centroid of the pdf, and far from the peak, although some exceptions (probably due to local orientation contrast) were found. These findings mirror results in the spatial coding domain found with skewed contrast and luminance profiles. Our results broadly support the conclusions of Dakin and Watt (1997 *Vision Research* 37 3181–3192) concerning feature coding in textures. Implications for models of texture perception are discussed.

◆ **Can attention modulate texture-integration processes?**

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Theories of line-segment-texture perception postulate automatic, low-level processing of elements by oriented filters followed by full-wave, nonlinear rectification. This implies that textures comprised of black and white lines should yield the same output as textures made from all black (or all white) lines. It further suggests that high-level selective attention mechanisms should be unable to access luminance-polarity information.

To probe this, we presented ten observers with line-segment textures in which a percentage of elements (signals) were oriented vertically or horizontally and the remaining (noise) elements were randomly oriented. Textures had 50% black lines and 50% white lines. The % signal (coherence) was varied and observers were asked to report the signal orientation of the black lines only. In one condition, signal lines were black but the noise subset consisted of black and white lines. Although for any % signal the coherence of the black lines as a subset was substantially higher than the coherence of the whole texture, observers were unable to benefit from this, behaving as if all elements had the same polarity. In another condition we presented textures with an equal number of black and white signal lines but black signal lines were oriented perpendicular to white signal lines. Noise lines were half black and half white. If luminance-polarity information was unavailable to selection mechanisms, observers should perform at chance. Surprisingly, performance was significantly above chance, indicating subtle attentional modulation. However, performance was not as good as expected if white lines were efficiently ignored. (The same results were obtained with white target lines.)

These data suggest that selection on the basis of luminance polarity can modify texture perception but that grouping factors (eg orientational similarity) may be necessary to support such interference of low-level processes.

◆ **Change detection in textured patterns**

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We investigated the representation of texture underlying the detection of scene changes. Stimuli consisted of a number of texture patches, each randomly selected from two possible textures. Display of the patches was interrupted by display of a blank field at fixed intervals. In the Change condition, one of the patches would 'flip' from one texture to the other during each

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blank interval. Subjects indicated whether or not a change occurred, and we measured response time as a function of the number of patches in the display. We tested a number of possible pairs of textures, and also ran several control experiments in which we instead changed an attribute of a simple 'object', such as a rectangular bar.

We found that even large changes in the second-order statistics of a texture may result in slow search times, on the order of 200 ms/item. This includes large rotations, and scale changes of a factor of 2 or more. Similar changes in simple 'objects' are detectable in 100 ms/item or less. However, some texture changes lead to more efficient search, on the order of 100 ms/item or less, such as the change from regular to random patterns, or from single to multiple orientations.

These results suggest a very different representation of texture than the results of texture-segmentation experiments. The determining factor for whether a change will be easily detected remains elusive. Perhaps a change in texture classification may be easily detected, eg a change from oriented texture to non-oriented, or from regular to random; or there may be a lower-level explanation. Performance seems to be worse for transformations of texture than of objects, though there is some evidence that the relevant dimension is the degree of complexity of the pattern, rather than whether the patterns are 'objects' or 'textures'.

◆ **Does fading of textured targets depend on salience?**

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A peripherally presented target segregated from the background only by a texture difference (eg orientation contrast) will fade from view within 5–20 s as demonstrated last year at Helsinki. With increasing orientation contrast, the peripheral stimulus appears more salient and requires more time to fade. It thus appears, at least for this type of stimuli, that pop-out and fading constitute the beginning and end of a perceptual continuum. The questions asked were: Is it generally the case that targets with a physically stronger texture contrast will appear more salient? and—Is there a correlation between the salience of a given stimulus and its time to fading?

Stimuli consisted of two types: polygons were shown on a background of circles (shape contrast) or targets of random dots were shown on a background of a dotted matrix (order contrast) on a computer screen. The target subtended 2 deg × 2 deg and appeared 8 deg to the left or right of a central fixation point. Subjects maintained fixation at all times. Salience was determined with a 2AFC procedure (target left or right?) for short duration stimuli (80 ms). In the fading experiment, observers fixated on the central point and pressed a key at the moment the target disappeared.

With increasing texture contrast, performance increased from 50% (chance) for weak contrast to 100% with maximum contrast. Fading time was shortest for weak contrast and increased with increasing contrast. Therefore, we have proven that salient stimuli take longest to fade.

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