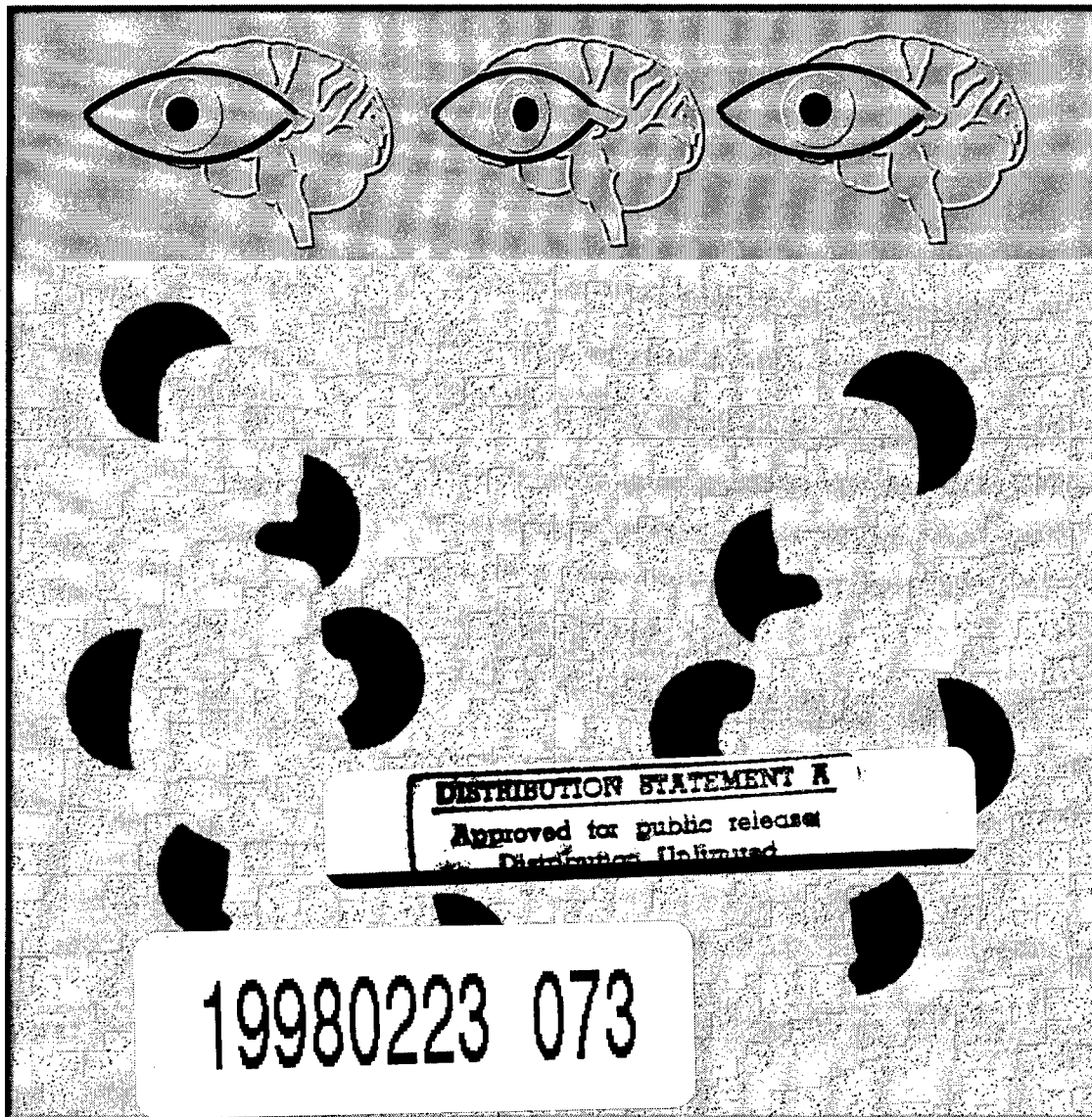


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ABSTRACTS

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Twentieth European Conference on Visual Perception Helsinki–Espoo, Finland 24–29 August 1997

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SUNDAY

THE PERCEPTION LECTURE

◆ Neural mechanisms of visual perception

T Wiesel (The Rockefeller University, 1230 York Avenue, New York, NY 10021-6399, USA; fax: +1 212 327 8900)

It is more than half a century ago since Keffer H Hartline published his classical receptive fields studies of single optic nerve fibres in the frog. World War II intervened and the full impact of his work did not become apparent until the early fifties, when Horace Barlow extended Hartline's analysis in the frog and Stephen W Kuffler showed the on-centre and off-centre type ganglion cells in the cat retina. The next advances were made in the late fifties when Jerome Lettvin and Humberto Maturana described cells in the frog tectum with very complex response properties and when David Hubel and I discovered that cells in the cat striate cortex were sensitive to orientation of contours and binocular stimulation. Vision research has gone a long distance since that time—nonetheless we have just begun the long journey towards a detailed mechanistic understanding of the neural basis of visual perception.

In this lecture I discuss the processing of visual information at the level of the striate cortex in the cat and monkey, and describe technical advances that have greatly facilitated the analysis of the neural mechanisms of visual perception.

MONDAY

ORAL PRESENTATIONS

PLENARY LECTURE

◆ The self-organising map, a possible model of brain maps

T Kohonen (Helsinki University of Technology, Neural Networks Research Centre, PO Box 2200, FIN 02015 Espoo, Finland; e-mail: teuvo.kohonen@hut.fi)

We stipulate that the following three categories of dynamic phenomena must be present in a realistic neural-network model: (i) activation; (ii) adaptation; (iii) plasticity control.

In most neural models only activation and adaptation are present. The self-organising map (SOM) algorithm is the only neural-network model that includes all the three phenomena. Its modelling laws include the following partial functions: (1) Some parallel computing mechanism for the specification of a cell in a piece of cell mass whose parametric representation matches or responds best to the afferent input. This cell is called the 'winner'. (2) Control of some learning factor in the cells in the neighbourhood of the 'winner' so that only this neighbourhood is adapted to the current input. By virtue of the 'neighbourhood learning,' the SOM forms spatially ordered maps of sensory experiences, which resemble the maps observed in the brain.

The newest version of the SOM is the ASSOM (adaptive-subspace SOM). The adaptive processing units of ASSOM are able to represent signal subspaces, not just templates of the original patterns. A signal subspace is an invariance group; therefore the processing units of ASSOM are able to respond invariantly, eg to moving and transforming patterns, in a similar fashion as the complex cells in the cortex.

SENSITIVITY AND CONTRAST

◆ Sensitivity of LGN neurons in infant macaque monkeys

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To understand the neuronal factors limiting visual sensitivity in infant primates, we studied the responses of neurons recorded in parts of the LGN representing the central visual fields in paralysed, opiate-anesthetised 1-week-old and 4-weeks-old macaque monkeys; comparison data were taken from animals older than 6 months. We tested each neuron with achromatic sinusoidal gratings varying in spatial and temporal frequency and contrast, and we also studied the effects of added spatiotemporal white noise.

In agreement with earlier reports, we found that neurons in the infant monkeys had relatively poor spatial resolution; sensitivity to high temporal frequencies was also lower than in adults. When tested with gratings of near-optimal spatiotemporal frequency, however, most LGN neurons in the infant monkeys gave brisk and reliable visual responses that were qualitatively similar to those seen in older animals. Spontaneous and evoked response rates and contrast gain were modestly lower in the infants, but response variability was also lower, and therefore statistical

measures of sensitivity and susceptibility to masking noise showed little difference between infant and adult neurons. Especially, in the 1-week-old animals, a substantial fraction of neurons lacked spontaneous activity. This resulted in 'hard' contrast thresholds not seen in adult animals. As a consequence, masking noise often paradoxically enhanced visual responses in these animals by subthreshold summation, a result not seen in the adults.

The maturation of visual responses in macaque LGN consists largely of changes in spatial and temporal scale, accompanied by modest changes in responsiveness and little or no change in sensitivity.

◆ **Adaptation to contingencies in macaque primary visual cortex**

M Carandini, H B Barlow¶, A B Poirson, L P O'Keefe, J A Movshon (Howard Hughes Medical Institute, Center for Neural Science, New York University, 4 Washington Place #809, New York, NY 10003, USA; ¶ Department of Physiology, University of Cambridge, Cambridge CB2 3EG, UK; fax: +1 212 995 4183; e-mail: matteo@cns.nyu.edu; WWW: <http://cns.nyu.edu/home/matteo>)

We tested the hypothesis that neurons in the primary visual cortex adapt selectively to contingencies in the attributes of visual stimuli. We recorded from single neurons in macaque V1 and measured the effects of adaptation either to the sum of two gratings (compound stimulus) or to the individual gratings. According to our hypothesis, there would be a component of adaptation that is specific to the compound stimulus.

We performed two sets of experiments. In the first set one grating had optimal orientation and the other was orthogonal to it. In the second set the gratings were parallel, differed in spatial frequency, and were both effective in driving the cell. The first set of experiments, but not the second, provided evidence in favour of our hypothesis. In most cells tested with orthogonal gratings, adaptation to the compound stimulus reduced the responses to the compound stimulus more than the responses to the preferred grating. In addition, in most of these experiments the responses to the compound stimulus were reduced more by adaptation to the compound stimulus than by adaptation to the individual gratings. This suggests that a component of adaptation in the experiments with orthogonal gratings was specific to (and caused by) the contingent presence of the two gratings in the compound stimulus.

◆ **Nonlinearities of near-threshold contrast transduction**

L L Kontsevich, C W Tyler (Smith-Kettlewell Eye Research Institute, 2232 Webster Street, San Francisco, CA 94115, USA; fax: +1 415 561 1610; e-mail: lenny@skivis.ski.org)

The existence of analytic threshold nonlinearities was probed with a variety of local and extended stimuli. Incremental thresholds were measured by the 2AFC procedure for same-sign and opposite-sign stationary pedestals. In contrast to the dipper effect for same-sign pedestals, subthreshold bumper effects were observed of threshold elevation (up to a factor of 4 in some conditions). The results for local difference of Gaussians (DoG) and 10 cycles deg^{-1} Gabors were consistent with accurate hard-threshold behaviour. The results for negative DoG (whose increment corresponds to the darkening of the central spot) and 2 cycles deg^{-1} Gabor profiles revealed a quadratic nonlinearity for one observer and linear transduction for the other. These results repudiate the uncertainty explanation for the steep psychometric function near threshold, and suggest that there are two different hard-wired nonlinearities: one for luminance increments and another for luminance decrements. According to our analysis, in low-spatial-frequency gratings, a contrast change is detected within those bars that become darker; in high-frequency gratings, transient changes are detected in the bars that become brighter.

◆ **Entropy masking**

A B Watson (MS 262-2 NASA Ames Research Center, Moffett Field, CA 94035-1000, USA; fax: +1 415 604 3323; e-mail: abwatson@mail.arc.nasa.gov; WWW: <http://vision.arc.nasa.gov/>)

Current vision theory admits two principal types of visual masking: contrast masking and noise masking. The former is thought to operate via mechanisms such as a nonlinear transducer, contrast gain control, and lateral inhibitory influences. The latter is understood to be due to the randomness of the target + mask combination. Here I propose a new category: entropy masking. Entropy masking is evident when the mask is a complex but deterministic signal. Because the mask is deterministic, and because experiments demonstrate that the masking power of such signals is much greater than predicted by contrast gain control, entropy masking cannot be due to either contrast masking or noise masking. Entropy masking occurs because the observer cannot discount the background, as supposed by ideal-observer theory, and hence must learn the target + mask signal. The ease with which this is done is a function of the entropy of both target and mask. Experiments that illustrate these general principles are described.

◆ **Asymmetric masking: luminance gratings mask second-order gratings, but not vice versa**

A J Schofield, M A Georgeson (School of Psychology, University of Birmingham, Birmingham B15 2TT, UK; fax: +44 121 414 4897; e-mail: a.j.schofield@bham.ac.uk)

Human vision can detect spatiotemporal information conveyed by first-order modulations of luminance and by second-order, non-Fourier modulations of image contrast. Models for second-order motion have suggested two filtering stages separated by a rectifying nonlinearity. We explore here the encoding of stationary first-order and second-order gratings, and their interaction.

Stimuli consisted of 2-D broad-band static visual noise sinusoidally modulated in luminance (first-order, LM) or contrast (second-order, CM). Modulation thresholds were measured in a two-interval forced-choice staircase procedure. With increasing noise contrast, first-order sensitivity decreased (owing to masking) but sensitivity to contrast modulation increased. Weak background gratings present in both intervals produced order-specific facilitation: LM background facilitated LM detection (the 'dipper function') and CM facilitated CM detection. LM did not facilitate CM, nor vice versa, and this is strong evidence that LM and CM are detected via different mechanisms. Nevertheless, suprathreshold LM gratings masked CM detection, but not vice versa. High-amplitude CM masks had little or no effect on CM or LM detection. A broadly tuned divisive gain-control mechanism applied to the first-order filtering stage has been proposed by Foley (1994 *Journal of the Optical Society of America A* **11** 1710–1719) to account for masking of luminance gratings, and this might also explain the masking of second-order by first-order stimuli. First-order maskers would drive down the effective contrast of the carrier, thus reducing second-order sensitivity. But for second-order maskers the mean contrast, and hence contrast gain, remained constant, independent of modulation depth. Thus second-order gratings would produce no masking effects, as observed.

◆ **Noisy template matching: a model for detection and discrimination**

W McIlhagga, A Pääkkönen¶ (Psychological Laboratory, Copenhagen University, Njalsgade 88, 2300 Copenhagen S, Denmark; ¶ Department of Clinical Neurophysiology, Kuopio University Hospital, FIN-70211 Kuopio, Finland; e-mail: william@axp.psl.ku.dk)

The detection and discrimination of simple patterns occupies a central place in visual psychophysics. A wide variety of phenomena have been observed in this paradigm, such as: Weber's law; masking (simultaneous, forward, and backward); masking by noise; spatial frequency tuning; orientation tuning; and area summation. We suggest that many of these phenomena can be explained by a simple model which we call 'noisy template matching'.

In this model, the encoded stimulus is matched to a memorised template. Both stimulus and template are corrupted by additive noise. The template matching operation yields a decision variable, to which more noise is added. This model is very simple, but it has many interesting consequences. It provides qualitative explanations for many of the phenomena mentioned above, and with additional (but we think reasonable) assumptions about lens blur, contrast nonlinearity (Whittle, 1986 *Vision Research* **26** 1677–1691), uncertainty (Pelli, 1985 *Journal of the Optical Society of America* **2** 1508–1532), and suboptimal templates, the model also provides good quantitative accounts of these phenomena.

BRIGHTNESS AND LIGHTNESS

◆ **Comparative analysis of brightness and lightness functions**

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A study is reported of twelve chromatic functions and one achromatic function of brightness, and fourteen chromatic functions and one achromatic function of lightness with the aim of establishing the change in the exponent of the functions, a phenomenon considered as being related to: (a) the brightness or lightness response of a subject; (b) the influence of hue and saturation; (c) the level of the background surrounding the stimulus; (d) the Helmholtz–Kohlrausch effect.

Different authors agree that these differences are produced by specific contributions of the tristimulus value Y and of chromaticity, the complexity of the problem arising from the fact that chromaticity would be expected to play a different role in each hue. They also agree that the Helmholtz–Kohlrausch effect is independent of the appearance of colour.

We show that the variation due to hue and saturation does not prevent the lightness and brightness functions from showing a specific response that permits differentiation between them and other functions, for instance the saturation functions.

Finally, we correlate chromatic and achromatic functions by means of the quadratic fluctuation function which allows us to define a self-correlation function. This mathematical analysis extends to all the samples without taking into account their variation in wavelength and purity.

It shows the existence of a solid and stable coding system for luminance, a system that achieves stability through its instability, reflected in the variation of the exponent of the functions.

◆ **Anchoring of surface lightness by area and luminance**

A L Gilchrist (Psychology Department, Rutgers University, Newark, NJ 07102, USA;
fax: +1 201 648 1171; e-mail: agil@andromeda.rutgers.edu)

Relative luminance is fundamental to lightness perception, but can be used to predict specific lightness values only when coupled with an anchoring rule. Empirical results indicate that, in simple displays, lightness is anchored by the highest luminance (white) rather than by the average luminance (middle gray). This implies that increasing the luminance range of a stimulus causes grayness induction: the lower luminance values become darker gray while the highest luminance remains unchanged, as many so-called brightness induction experiments have shown. Yet sometimes increasing the luminance range of a stimulus causes luminosity induction: the highest luminance becomes increasingly self-luminous while the lowest luminances remain unchanged. Whether grayness induction or luminosity induction results from an increase in stimulus contrast depends on relative area. A few simple, yet hitherto unrecognised, rules that describe how anchoring by highest luminance combines with anchoring by largest area appear to be consistent with the many published reports on area and lightness/brightness. These findings add to the accumulating evidence that many phenomena previously attributed to contrast are much better understood in terms of anchoring.

◆ **Brightness illusion induced by consistency constraints**

A Feher (Laboratory of Vision Research, Rutgers University, Psychology Building, Busch Campus, Piscataway, NJ 08854, USA; fax: +1 908 445 6715;
e-mail: feher@zeus.rutgers.edu; WWW: <http://zeus.rutgers.edu/akos.html>)

We present a novel brightness illusion (the 'Brick Illusion') that is determined by perceptual interpretation. The image is ambiguous in terms of depth layering, and the strength of the illusion depends on the chosen interpretation. When a certain interpretation is enforced by stereo disparity, and the layering is disambiguated, the strength of the illusion changes according to constraints on the consistency between depth layering, transparency relationships, and surface brightness.

We applied a 2AFC brightness comparison procedure to quantify the strength of the illusion. This procedure allowed us to measure the uncertainty of judgements on relative surface brightness in illusory conditions. The increased uncertainty of our observers among these conditions reflects the multidimensional nature of these judgements.

This paper is linked to the following World Wide Web page: <http://zeus.rutgers.edu/~feher/brick.html>. With a Java-enabled browser the reader can change the gray levels of the backgrounds and the disks, the disparity of the disks, and other parameters.

◆ **Plasmas: a new class of motion-induced brightness illusion**

P Tse (Vision Sciences Laboratory, Psychology Department, Harvard University,
33 Kirkland Street, Cambridge, MA 02138, USA; e-mail: ptse@wjh.harvard.edu)

When a white figure is set in smooth continuous motion against a dark background, a 'shadowy' region forms around and behind it, somewhat similar to the wake that a boat leaves in water. Conversely, when a dark figure moves against a white background, this 'wake' appears lighter than the background. When several such figures move, these 'wakes' can link up in surprising ways. For example, if four white circles of radius r are positioned on a dark background at the vertices of an imaginary square whose width is, say, $4r$, and this imaginary square rotates about its centre, bands darker than the background form between the four circles, linking them through the centre. This 'black cross' is nonrigid, and is accompanied by dark 'wakes' on the outside of the circles. I call these illusory brightness regions 'plasmas'.

The relation of this effect to other motion-induced brightness illusions is considered. In particular, this effect has different properties than either induced gratings (McCourt, 1982 *Vision Research* **22** 119–134) or phantom gratings (Tynan and Sekuler, 1975 *Science* **188** 951–952). Plasmas are not due to retinal afterimages or persistence, since they form in regions never traversed by the moving figure. Nor are they an artifact of the computer screen, since the illusion occurs equally well in displays constructed from paper. Plasmas have the opposite phase relative to the inducing figure, disappear when a figure stops moving, are strongest at high background/inducer contrast, and are most visible when the luminance of the inducers is in the photopic range. Experiments measuring the strength of plasmas as a function of angular velocity and visual angle are described. A model is proposed according to which plasmas are due to a phase lag in luminance-edge induced lateral inhibition.

◆ **Atmospheric boundaries in lightness perception**

E H Adelson, D C Somers (Massachusetts Institute of Technology, Department of Brain and Cognitive Sciences, E10-118, Cambridge, MA 02139, USA; fax: +1 617 253 8335; e-mail: adelson@psyche.mit.edu; WWW: <http://www-bcs.mit.edu/people/adelson>)

In judging the lightness of a surface, an observer must estimate and discount the optical viewing conditions: these include illumination level, haze, and interposed filters. The physical effects can be captured in terms of additive and multiplicative factors, which we call 'atmosphere'. Local atmosphere can be estimated by gathering gray-level statistics over a local window. If the window is too small, the statistics will be impoverished. If the window is too large, it may encompass multiple atmospheres, making the statistics unreliable. We find evidence that the visual system imposes limits on the size and shape of the window, in accord with configural cues that signal atmospheric boundaries. Junctions with proper gray-level arrangements offer powerful cues to atmospheric boundaries; T-, X-, and psi-junctions are especially important. By combining statistics and configural cues, we have generated new lightness illusions that are much stronger than those seen in typical simultaneous-contrast displays. By changing the junctions we can also generate illusions that are quite weak, also in accord with the model.

SYMPOSIUM

LIMITS TO VISUAL PERFORMANCE: A COMPARATIVE APPROACH

◆ **Which eye sees the most?**

D-E Nilsson, J Warrant (Department of Zoology, University of Lund, Helgonavägen 3, S-22362 Lund, Sweden; fax: +46 46 22 24425; e-mail: dan-e.nilsson@zool.lu.se, eric.warrant@zool.lu.se)

The performance of the eyes is ultimately limited by the physical nature of light. The diameter of the aperture that admits light to the eye sets an upper limit to the spatial frequencies that can be imaged behind the aperture. Diffraction, which is responsible for this limitation, is caused by the wave nature of light. The array of sampling stations the eye uses to detect the image is instead limited by the quantum nature of light. Each sampling station can only sample a finite number of quanta, and any such count is associated with a standard deviation being the square root of the true mean. Effectively, this limits the ability to detect differences in luminance (contrasts) across the image. Diffraction and quantum noise together sets an upper physical limit to the performance of an eye. If the eye's quantum efficiency, integration time, and thermal noise are constants, it is possible to find the optimum sampling frequency that maximises spatial resolution of a stationary image. This optimum depends on eye size and luminance, and differs from the 'camera type eye', the 'pinhole eye', and the various optical types of compound eye.

We have calculated the maximum detectable spatial frequency for a number of simple and compound types of eye, and plotted the results against luminance and eye size to produce a unique 'performance surface' for each type of eye. These performance surfaces allow a comprehensive graphical comparison of the efficiency of the various optical types of eye.

◆ **Photic environment, visual pigments, and the limits of the visible spectrum**

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The limits of the visible spectrum are set by the light available for vision, and by the visual pigment absorbance. The hundreds of visual pigments studied to the present day have absorbance maxima spread within the range from 350 to 620 nm. Yet this diversity is used for vision quite nonuniformly: rod and cone visual pigments are tightly clustered around a few preferred positions in the spectrum, eg near 500 nm in the rods of land animals. The so-called 'sensitivity hypothesis' assumes that the clustering is to maximise the number of absorbed photons available in the animals' light environment. In most cases, however, visual pigments are substantially more short-wave (blue-shifted) than is necessary for maximum quantal absorption. Examples of the 'blue shift' are the Purkinje shift during cone-rod transition in dark adaptation, the hypsochromic shift of rod visual pigments in deep-water fish, and a similar shift in the cone pigments of geckos and some snakes as a result of evolutionary adaptation to nocturnal habits. It is argued that an important limiting factor in vision is the dark noise produced by thermal isomerisation of the chromophore. Measurements of the dark noise in rods with different visual pigments show that the noise increases steeply when the absorbance maximum is shifted to longer wavelengths, thus precluding the use of long-wave pigments for vision at low intensities. The optimum spectral position of a pigment may be that which ensures a maximum light-to-noise ratio in a particular photic environment.

◆ **Speed and noise of neural membranes: ion channel limitations to visual information transmission**

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In dim light, photoreceptor cells and subsequent neural elements typically show high absolute sensitivity, implying that both phototransduction and synaptic transmission work at a high gain and even a single photon may produce a large electrical response. However, when there is more light, rapid adaptation at several levels of signal processing ensures that the information channel is not congested, but optimally filled with relevant voltage responses. All this is achieved by carefully tuned mechanisms that include several types of ion channels in the cell membrane. These ion-channel mechanisms have been thoroughly investigated in a few species of invertebrates and vertebrates, and some general principles are being revealed.

The membrane capacitance and the resistance of the cell together define the time constant of the membrane, thus the maximum speed for building up a voltage response to light. Both in vertebrate cones and in insect microvillar photoreceptors, phototransduction takes place in an enlarged part of the cell membrane, which implies a large capacitance. This can be counteracted by making the membrane more leaky by opening more ion channels. In insect photoreceptors several types of potassium channels have been identified that perform exactly this kind of function. The types of channels vary according to the required speed of phototransduction, ie depending on the life style of the animal. In diurnal dipteran insects the potassium channels are typically of the slowly inactivating type. This channel type regulates the cell impedance according to the depolarisation caused by light stimulation. In insects active in dim environments, the potassium channels found have been predominantly rapidly inactivating. The function of this type of channels is currently under debate. In vertebrate photoreceptors several potassium channel types, including channels sensitive to intracellular calcium and pH, are expressed in the inner segments and modulate photoresponses.

Opening and closing of the potassium channels also generates neural noise and thus degrades the signal-to-noise ratio (SNR). However, if the gain of phototransduction is high enough, the dominant noise comes from photon fluctuations, or from the biochemical transduction machinery, or—in some situations—from spontaneous photon-like events. Channel noise is then insignificant by comparison. Thus the optimisation of the SNR is a trade-off between bandwidth (ie speed) and amplification of the signal, and here the voltage-gated potassium channels are of prime importance.

◆ **Overcoming the limitations of eye design: two remarkable examples from the insect world**

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Light availability has driven the evolution of the two major compound-eye designs found in insects. Superposition eyes, which sacrifice spatial resolution for improved photon catch, are common in insects active in dim light. Insects active in bright light typically have apposition eyes. These eyes are adapted to provide the maximum resolution possible, often leading to 'foveal' eye regions of higher acuity.

Even though superposition eyes are typical for dim-light insects and apposition eyes typical for bright-light insects, there are many fascinating exceptions to this 'rule'. Many insects have been forced (by competition for example) to occupy niches with light intensities that are not optimal for their eye designs. This has led to surprising optical and neural adaptations which have re-optimised the eye for the new niche. After reviewing the way in which compound-eye design affects spatial vision in insects active at different light intensities, I describe two remarkable eyes which provide exceptions to the 'rule': the superposition eye of the fast-flying day-active hawk moth *Macroglossum*, and the open-rhabdom apposition eye of the cave-dwelling beetle *Zophobas*. These two eyes exemplify the ways in which the trade-off between spatial resolution and the sensitivity to light can be radically manipulated during evolution, despite its initial setting by the ancestral eye design.

◆ **Processing of natural time series of intensities in the early visual system of the blowfly**

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The first steps of processing in the visual system of the blowfly are well suited for studying the relationship between the properties of the environment and the function of visual processing (eg Srinivasan et al, 1982 *Proceedings of the Royal Society, London B* 216 427; van Hateren, 1992 *Journal of Comparative Physiology A* 171 157). Although the early visual system appears to be linear to some extent, there are also reports on functionally significant nonlinearities (Laughlin,

1981 *Zeitschrift für Naturforschung* **36c** 910). Recent theories using information theory for understanding the early visual system perform reasonably well, but not quite as well as the real visual system when confronted with natural stimuli [eg van Hateren, 1992 *Nature (London)* **360** 68]. The main problem seems to be that they lack a component that adapts with the right time course to changes in stimulus statistics (eg the local average light intensity). In order to study this problem of adaptation with a relatively simple, yet realistic, stimulus I recorded time series of natural intensities, and played them back via a high-brightness LED to the visual system of the blowfly (*Calliphora vicina*). The power spectra of the intensity measurements and photoreceptor responses behave approximately as $1/f$, with f the temporal frequency, whilst those of second-order neurons (LMCs) are almost flat. The probability distributions of the responses of LMCs are almost gaussian and largely independent of the input contrast, unlike the distributions of photoreceptor responses and intensity measurements. These results suggest that LMCs are in effect executing a form of contrast normalisation in the time domain.

◆ **Correspondence noise limits to global motion perception**

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We measured human observers' thresholds for detecting coherent motion in random-dot kinematograms and compared them with theoretical thresholds predicted by the hypothesis that unavoidable correspondence noise in the kinematograms themselves is the limiting factor. In experiments where the stimulus had two fields we varied the dot density, the ratio of the number of dots in the two fields, and the area of stimulus. In further experiments we varied the number of fields and the method of generation of the coherent dots. The observed thresholds varied in the way predicted by the hypothesis over ranges that were in some cases wide, but even within these ranges the absolute levels of performance were much worse than that calculated for the ideal observer.

Objects moving in the real world generate motion signals in their images covering broad ranges of direction and velocity, and when the spread of motion signals within each presentation of our stimulus was increased, the discrepancy between ideal and actual performance was much reduced. We conclude that correspondence noise present in the stimulus is an important limiting factor in the coherent motion paradigm. Since this noise is largely external and inextricably bound with the signal, to attain high signal/noise ratios the input signals have to be pooled over broad ranges that match the range of motion signals in the natural stimuli. This provides an insight into the design of the motion detecting system, and perhaps into the design of other parts of the cortex.

POSTERS

NEUROBIOLOGY AND COMPARATIVE VISION

◆ **Interrelation of tuning characteristics in striate neurons sensitive to cross and corner**

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In the cat striate cortex we have found 56 out of 174 neurons that respond on average by a threefold increase of the responses to cross-like or corner figures flashing in the receptive field in comparison to those to a single light bar of preferred orientation. For 27/56 of these neurons tuning to both cross and corner was investigated. 18/27 neurons responded to both stimuli, while 3/27 cells were sensitive only to cross and 6/27 only to corner. The width, selectivity, and quality of tuning to orientation did not differ on average for stimulation by the bar and figures of both types. The characteristics of tuning to the shape of a figure (the angle between its lines) were about the same for cross and corner. We have found a direct relationship between the orientation tuning width, selectivity and quality for bar, cross, and corner. The relationships between the characteristics of tuning to the shape of a figure were found to be rather more complex. Thus, among 18 cells sensitive to both cross and corner we never met a high selectivity to cross, whereas that was typical for the selectivity to corner. Of the cells sensitive to cross, 35/46 responded to figures with angles of 45° or 90° between the lines, and the rest (11/46) responded to a cross with an angle of 67.5° . The neurons sensitive to corner responded most often to the angle of 67.5° (9/26) and in nearly equal but lower proportion to all other angles. The functional implication of neuronal sensitivity to cross and corner figures is discussed.

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◆ **Visual discrimination learning in monkeys with bilateral parietal cortex lesions**

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The characteristics of visual discrimination learning were tested on rhesus monkeys during development of an instrumental reflex after bilateral extirpation of the parietal cortex area 7. The animals were trained to discriminate stimuli with different visual attributes (shape, colour, orientation, size, spatial relationships). Their decisions and motor reaction times were recorded. Bilateral extirpation of area 7 did not influence learning characteristics for shape and colour discrimination. The duration of the learning process and the motor reaction time were shortest with these visual attributes. When monkeys were required to discriminate geometrical figures of different orientations and size, these learning characteristics slightly increased. However, learning to discriminate spatial relationships was dramatically impaired. As a result, the duration of the learning process and motor reaction time significantly increased and the level of correct decisions after training significantly decreased. Visual stimuli associated with identical learning characteristics formed distinct groups in a cluster analysis.

These results support the suggestion that area 7 is a structural and functional component of mechanisms involved in evaluation of spatial relationships. The impairment of the learning to discriminate spatial relationships can be explained by a change of learning strategy upon disturbance of this mechanism, associated with visual-vestibular interactions and synchronisation processes which bind distributed neurons across different cortical areas into synchronised assemblies.

◆ **Improvement of visual short-term memory characteristics in monkeys: effect of an antioxidant**

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Visual short-term memory was tested in a delayed-discrimination task on rhesus monkeys before and after a systemic injection of the antioxidant oxymetacil ($4-7 \text{ mg kg}^{-1}$). Monkeys had to discriminate stimuli with different visual attributes (colour, orientation, spatial frequency, size, contrast, spatial relationships between visual objects) by a delayed (0–32 s) instrumental reflex. Oxymetacil had no influence upon visual discrimination without delay, but after injection of this drug the delayed discrimination (associated with mechanisms of short-term memory) of different stimuli was significantly improved. Oxymetacil increased the duration of short-term storage of spatial information by a factor of 2–4 and decreased motor reaction time. Application of oxymetacil in the same doses produced similar results for delayed discrimination of black-and-white gratings, or geometrical figures of different orientations and size. The duration of short-term information storage was doubled or trebled and the motor reaction time was decreased. If monkeys were required to discriminate colour figures, the duration of short-term information storage was also doubled, being longer than for any of the other tasks. The results are discussed in terms of effects on cortical interregional synchronisation mechanisms responsible for control processes such as attention.

◆ **Interaction of direction and speed selectivity in cat primary visual cortex**

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We have studied the selectivity for speed and direction of directionally selective (DS) cells in the primary visual cortex of the cat. Most of the 37 DS neurons tested were velocity tuned. From a set of velocities in the range from 2 to 80 deg s^{-1} , each velocity was optimal for a certain proportion of these cells. The distribution was as follows: 2 deg s^{-1} was optimal for 16% of all tested neurons, 5 deg s^{-1} for 14%, 10 deg s^{-1} for 27%, 20 deg s^{-1} for 30%, 40 deg s^{-1} for 8%, and 80 deg s^{-1} for 5%. The preferred direction determined with a single light spot was compared with that obtained with a pair of spots moving at a mutual angle of 60° over the receptive field. For 40% of the neurons tested the preferred direction to the single moving spot coincided with that obtained with the two-spot stimulus. The responses to the latter could be successfully computed as a combination of responses to single spots moving in the given directions. This result indicates a high capacity for motion processing in the primary visual cortex of the cat.

◆ **Classification of visual cortex cells with the use of a new neural network model**

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To identify the intrinsic connections within different layers of area 17 of the cat visual cortex we studied the initial neurons labelled by horseradish peroxidase retrograde axonal transport in serial sections. A computer model of visual neural networks (Dudkin et al, 1995 *Proceedings of SPIE* 122) has been specially developed in these studies to classify cortical neurons according to their specific anatomic features. There are two main stages of the recognition process in this model: feature selection by nonlinear neural operators and classification (clustering) connected with algorithms of cluster analysis. In the first stage, the primary image processing and segmentation are performed by interactive algorithms, which allow us to form several primary image descriptions and to extract the basic description elements of the cell. From these elements, a feature vector consisting of 17 normalised measures is extracted. In the second stage of the recognition process several algorithms are used to cluster the cells according to the feature vectors extracted. It was possible to group these vectors into compact clusters and to associate each group of vectors with a certain type of cells (pyramidal, spiny, and smooth stellate cells). These results are part of the task of creating a computer image data base and 3-D reconstruction of the cortico-cortical connections in the visual system.

◆ **The arrangement of corpus geniculatum laterale connections with oculomotor structures**

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The primary visual centres are known to be involved in the organisation of oculomotor acts, but the pathways of signal transmission from corpus geniculatum laterale (lateral geniculate nucleus, LGN) to the structures of the oculomotor system remain unknown. The aim of this study on 30 cats was to determine autoradiographically all the possible pathways of visual information transmission from both dorsal and ventral nuclei of the LGN to oculomotor nuclei.

It was found that there were no direct connections of the LGN with the oculomotor nucleus. The connection occurs either through the cortex or through the preoculomotor formations. These pathways are the following: (1) from the dorsal and ventral nuclei of the LGN to the visual pretectum (olivary pretectal nucleus, posterior pretectal nucleus, nucleus of the optic tract) and then to the vegetative part of III nucleus or through nucleus commissurae posterioris, Cajal and Darkschewitsch nuclei to the somatis part of III nucleus and along the medial longitudinal fasciculus to IV nucleus and periaqueductus region; (2) from the ventral LGN into the deep layers (IV and VI) of the superior colliculus, and then to the Edinger-Westphal nucleus, preoculomotor central gray substance, and VI nucleus; (3) from the dorsal LGN into the deep layers (IV and VI) of the superior colliculus with relay synapses in the parietal cortex and zona insecta; (4) from the dorsal and ventral nuclei of the LGN to nucleus pontis dorsolateralis and paramedianus, being connected with the vermis anterior lobe (V-VII lobes) of cerebellum, and then to nucleus vestibularis inferior and nucleus vestibularis lateralis.

◆ **Summation for stationary and moving visual stimuli in receptive fields of cat pretectal neurons**

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Numerous investigations have shown that the cat's pretectal region is involved in various visual habits and in visually guided behaviour. Thus visually driven pretectal neurons should possess summation abilities for integration of incoming sensory information. We investigated responses of 102 neurons in the pretectal region of cats with pretrigeminal brain stem transection using single-unit extracellular recording. Cells were examined with moving and stationary visual stimuli of different sizes. Our purpose was to compare summation characteristics for stationary and moving visual stimuli in the same neuron. Only a small proportion (5%) of pretectal neurons revealed similar summation characteristics for stationary and moving stimuli. The great majority of neurons showed different patterns of summation, depending on the type of the visual stimulus. For example, positive and negative effects of an increase of the stimulus size on the intensity of cellular response were observed. The results suggest that there are several discrete mechanisms subserving integration of sensory information concerning stationary and moving visual stimuli.

◆ **Informational estimates of neuronal responses**

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We studied responses of visually driven neurons from the associative Clare-Bishop area of the cat cortex. Interspike intervals of neuronal responses were subdivided into four constituents: intervals between all spikes, intervals between spikes inside bursts, intervals between bursts, and intervals between events (in which case it has been assumed that a burst and an isolated spike are events of equal importance). Two informational parameters based on these distributions were calculated: the information capacity of the channel (F) and the amount of information (entropy H). We found that (1) values for F and H are significantly higher when they are based on intervals between all spikes and intervals between events than when they are based on intervals inside bursts and intervals between bursts; (2) values of F and H are significantly higher for all cases where a neuronal response is present than those for spontaneous activity.

◆ **Neuronal connections in cat striate cortex as revealed by HRP staining**

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Injecting horseradish peroxidase (HRP) into area 17 of tree shrews, Rockland and Lund (1982 *Science* **215** 1532–1533) found connection-specific columnar staining superimposed on a Gaussian decrease of staining intensity with distance from the injection site. Such data are important when constructing models of neuronal nets. We have investigated in more detail the staining of different types of neurons after HRP injection into one orientation column of cat striate cortex. The intensity of staining was classified as dark, intermediate, or light. Cells with different staining intensities were found in all cortical layers and at different distances from the injection site of HRP. According to the shape of their somata and the organisation of their dendritic trees, the labelled cells were identified as pyramidal, small pyramidal, non pyramidal, or modified pyramidal (inverted and fusiform). The ratio of dark:light:intermediate cells within all identified morphological types was 2:1:1, except for the inverted pyramidal cells (1:1:1). Thus the intensity of staining depends not only on the physical uptake and transportation of HRP but also on the organisation of axonal terminals and neuron location in the functional structure of the cortex.

◆ **Single cortical column in area 17: the distribution of intrinsic connections**

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Intrinsic connections are one category of neuronal cortical connections, referring to axons that remain within the same cortical area and do not travel in the white matter. Our knowledge about these connections is based on extrapolations of results on the labelling of cells in different cortical layers, but there is no direct information about the complete connectivity of a single cortical column. To study how the population of cells sending axons to the same cortical column is distributed over the cortex we microiontophoretically injected horseradish peroxidase in single cortical columns of area 17 in cat. 3-D reconstruction of the region of labelled cells was performed by using serial frontal brain sections. It was shown that afferents from layer IV cells are short range (up to 0.5 mm) and from the supragranular (II, III) and the infragranular (V, VI) layer cells are long range (up to 5 mm). The regions with labelled cells in the supragranular and infragranular layers sending axons to the very same cortical column lie in register. For columns representing the central visual field, the distribution of labelling (in a tangential plane) is elongated in the mediolateral direction, and for peripheral columns there was a tendency towards elongation in the mediolateral and rostrocaudal directions. Moreover, the majority of labelled cells were located in regions representing peripheral parts of the visual field relative to the injection site. The described connections may represent the substrate for global linking tasks and underlie several psychophysical phenomena, such as meridional and peripheral effects.

◆ **Neuronal plasticity in the associative visual cortex of the cat after callosotomy**

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Changes in receptive field (RF) properties and connectivity of neurons in cat associative visual cortex were studied after callosotomy. Callosotomy and skull trepanation at area 21 were performed in cats weighing 2.5–4 kg (with nembutal 40 mg kg⁻¹). A total of 120 neurons in area 21 were studied. In experiments performed a short time after the operation, RF sizes were found to be

smaller on average, and more equal between the two hemispheres compared with intact brains [mean RF sizes previously found in intact brains: 39 deg (left hemisphere) and 28 deg (right hemisphere); after operation: 23 (left hemisphere) and 24 deg (right hemisphere)]. At this stage, all investigated neurons lacked ipsilateral input and were selective for the orientation of the stimulus, whereas we have previously found that 70% of the neurons in the left and 30% of the neurons in the right hemisphere of the intact brain are not selective for orientation. Two months after the operation, RF sizes had increased, associated with the appearance of extensive inhibitory zones including input from the ipsilateral hemifield (in 40% of the neurons). Connectivity was studied by injecting horseradish peroxidase (HRP) in area 21. In intact animals, this has been found to result in a characteristic pattern of staining of neurons in area 17 in groups of 2–15. In animals studied two months after callosotomy, the resulting HRP staining in area 17 was more uniform. Further, in area 7 of operated animals large numbers of cells were stained, compared with only single cells in intact brains. More than 20% of the stained area 7 neurons of operated animals were inhibitory interneurons, which might correlate with the large inhibitory zones apparent in area 21 RFs. We conclude that extensive compensatory reorganisations occur in the associative visual cortex after callosotomy, involving changing connections in at least areas 7 and 17.

◆ **Peripheral and central factors limiting spatial contrast sensitivity in infant macaque monkeys**

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To evaluate the contribution of peripheral and central factors to the development of visual sensitivity, we measured contrast thresholds for sinusoidal gratings ($0.5\text{--}4.2\text{ cycles deg}^{-1}$), presented alone and in the presence of added dynamic visual noise, in infant monkeys. We wished to use the changes in contrast threshold during development, in the presence and absence of masking noise, to establish what mechanisms might be responsible for this developmental process.

We tested *Macaca nemestrina* monkeys, aged 1–18 months, on a spatial contrast detection task, and analysed the masking functions to calculate two parameters: equivalent intrinsic noise (N_{eq} , the noise contrast at which squared contrast threshold was doubled), and signal-to-noise ratio (R_{sn} , the asymptotic ratio of threshold to noise contrast at high noise contrasts). We hypothesise, following Pelli, that N_{eq} measures a peripheral limit while R_{sn} measures a central one.

Our data suggest that intrinsic noise is high in infants and falls with contrast threshold during development, thus supporting the hypothesis that peripheral factors set an important limit on the development of contrast sensitivity. However, the relationship between N_{eq} and contrast threshold varied somewhat with spatial frequency. At low spatial frequencies, contrast threshold was well specified by knowledge of N_{eq} , whereas at higher spatial frequencies, changes in R_{sn} had a relatively greater weight. We conclude that peripheral factors set an important limit on the development of sensitivity at all spatial frequencies; central factors are needed to account for some aspects of development at higher frequencies.

◆ **A new look at primate ganglion cell receptive field structure**

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We have reinvestigated receptive field structure of macaque ganglion cells using a novel stimulus—counterphase modulation of a bipartite field—with luminance, chromatic, or cone-selective stimulation. We previously used this stimulus (Kremers et al, 1995 *Colour Vision Deficiencies XII* 399–406) to show that surrounds of middle (M) and long (L) wavelength cone opponent cells of the parvocellular (PC) pathway are cone specific, measuring on a finer scale than in previous experiments [Reid and Shapley, 1992 *Nature (London)* 356 716–718]. Modelling of response amplitude and phase now confirms this conclusion. Second, centre sizes measured were consistent with those from the literature, with PC and magnocellular pathway (MC) cell centres having similar size. Modelling on the basis of single cone centres for PC-cells plus optical blur provided a partial description of the data, but some inconsistencies were present. Last, the chromatic nonlinearity of magnocellular pathway ganglion cells appears to result from a subunit structure within the receptive-field surround.

◆ **Estimation of local and global characteristics of half-tone surfaces by the cat's lateral geniculate body**

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We investigated neuronal mechanisms in the cat's dorsal LGN that could carry information about the spatial brightness distribution across half-tone visual object surfaces. Stimuli were half-tone spheres, cylinders, toroids, etc. We have found that geniculate neuronal structures describe and estimate both local and global characteristics of the brightness distribution on these surfaces. The search for local mechanisms of perception of half-tone surfaces revealed a new property of geniculate neurons: their sensitivity to changes in both the magnitude and vector direction of the spatial brightness gradient in the test stimulus. The quantitative estimation of gradient sensitivity in each case has been calculated by the formula: $K = (N_{\max} - N_{\min}) / N_{\max}$, where $N_{\max}$ is the number of spikes (in a 500 ms interval) in response to the preferred (and $N_{\min}$ to the nonpreferred) gradient direction. The average value of K was 0.49 (range 0.15–0.95) for a mean brightness gradient of $2.7 \text{ cd m}^{-2} \text{ deg}^{-1}$. A ninefold decrease of the gradient reduced K by a factor of 6.5. The preferred direction of most (82%) neurons coincided with the radial direction from the centre of the receptive field to area centralis. The basis of this phenomenon probably lies in the influence of the spatial brightness gradient on spatiotemporal relations between excitatory and inhibitory processes in geniculate receptive fields. Global characteristics of the surface brightness distribution were represented in the population response of the neurons. The pattern of neuronal activity elicited in on-neurons and off-neurons in response to surface stimuli correlated with the isophot structure of the surface ($r_{\text{av}} = 0.86$ for 23 cases). Therefore, separate descriptions of local and global brightness distributions originate at subcortical levels of the visual system.

◆ **Lorazepam: a new tool to study the processing of discontinuities**

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The involvement of GABA_A in the computation of visual information has been suggested in numerous electrophysiological studies. It might play a role, in particular, in the generation of the responses of hypercomplex cells involved in the processing of discontinuities. Benzodiazepines like lorazepam enhance the fixation of GABA on the GABA_A receptor. We tested the hypothesis that lorazepam enhances the detection of discontinuities, with static stimuli composed of horizontal line-segments. There were four types of stimuli, with (1) collinear and discontinuous, (2) collinear and continuous, (3) parallel and discontinuous, and (4) parallel and continuous elements. A stimulus was presented on each trial in the centre of a computer screen for 160 ms. The task was to decide whether the stimulus was continuous or discontinuous. Response was given on two response keys. The results showed that lorazepam-treated subjects were faster at detecting a discontinuity when the stimulus included two aligned line-segments (– –) as compared to two parallel line-segments (=). Placebo-treated subjects displayed equivalent performance in the two conditions. These results support the hypothesis that lorazepam enhances responses to line-ends. They are consistent with previous results, obtained with static drawings, letters, fragmented squares, and dynamic stimuli. Lorazepam might be a useful tool to investigate visuo-perceptual integration processes and to link experimental psychology and electrophysiology.

◆ **Effects of aging on photoreceptors and implications for visual performance**

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Visual performance depends in the initial stages on the properties of retinal photoreceptors. In this context we consider the effects of rod outer segment (OS) renewal and OS response gradient on performance. The OS renews itself by forming new membrane near the cilium, at the base of the OS. This membrane then advances towards the tip where it is shed and phagocytosed in the pigment epithelium. Thus the OS is older at the tip than the base, and it has been proposed that it is due to this aging that the observed light responses are smaller and slower at the tip than at the base.

We have tested this hypothesis by exposing *Xenopus laevis* in a controlled manner to altered temperature and lighting conditions which are known either to slow down or to accelerate OS renewal. We have recorded the light responses of the OS base and tip and found that they are,

indeed, correlated with the age differences. In addition to OS membrane age we have also investigated the effects of animal age on the response gradient along the OS. Here we found that during development the response differences decrease and then stabilise at maturity. Concurrently with the decrease of the gradient the response kinetics are slowed down. There is thus a changing trade-off between response gradient and kinetics up to maturity in this animal.

These results have important implications for visual performance. Visual reaction times depend on photoreceptor kinetics; and since photons can be absorbed anywhere along the OS, the response gradient, especially at low light levels, directly affects the reliability of detecting stimulus intensity. We conclude that visual performance in *Xenopus laevis* is related to the rates of OS renewal and the resulting response gradient in an age-dependent manner.

◆ **Light adaptation in frog cones deviates from Weber's law in a temperature-dependent way**

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Light adaptation in cone photoreceptors is generally thought to be well described by Weber's law, ie the intensity of an incremental light stimulus needed to produce a response of small criterion amplitude (the threshold intensity, I_{th}) would depend on the intensity of a steady background light I_B according to the equation $I_{th}/I_{th, dark} = 1 + I_B/I_0$, where I_0 is a constant, the 'dark light'. We have observed, however, that light adaptation in frog cones deviates from Weber's law in a temperature-dependent way.

Pure red-cone responses were isolated by a subtraction procedure from ERG mass responses recorded across the aspartate-treated frog retina at temperatures from ca 4 to 26 °C. Photoreponses to 553 nm light flashes (20 ms) were subtracted from responses to rod-equivalent 642 nm flashes. Steady-state log threshold vs log background intensity (TVI) curves were determined over a 7-log-unit range of I_B .

TVI curves appeared to be composed of four distinct segments, corresponding to different ranges of I_B . In the lowest range, cone sensitivity was not affected by I_B . In the second range, cone threshold increased according to the relation $I_{th} \propto I_B^a$, where the exponent a (the slope of a straight line in a log-log presentation) was usually close to 0.5 ('square-root-like adaptation'). This process was temperature-sensitive: the I_B value where I_{th} started to rise increased with warming, from 3 photoisomerisations per cone per second [Ps^{-1}] at 4 °C to 10^3 Ps^{-1} at 25 °C. Thus, square-root-like adaptation spanned a wider I_B range at lower temperatures. In the third I_B range (from ca 3×10^4 Ps^{-1} one log unit upwards), the TVI curve had a steep slope, typically 2–2.5. It appears significant that this steep TVI slope is obtained at background intensities where bleaching of the visual pigment begins to become substantial. In this range, at least 30 min was needed to reach a steady state after background onset, which at lower or higher backgrounds took only about 2 min. The time constant of approach towards the steady state was temperature-dependent, increasing with lowered temperature. In the fourth, very high I_B range, the TVI slope finally settled at a value near 1 (Weber adaptation).

◆ **On the nature of the gated colour opponency in the ON-units of the frog retina: electrophysiological study and model**

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Ganglion cells of the ON-type in the frog retina produce colour-dependent responses differing in temporal patterns (short bursts to excitation of red-sensitive cones as opposed to prolonged discharges if blue-sensitive 'green rods' are excited). Their gated colour opponency (Kicliter et al, 1981 *Brain Research* **210** 103–113; Maximov et al, 1985 *Vision Research* **25** 1037–1049) becomes apparent from the OFF-responses in conditions when the test stimuli are superimposed on a background of another colour. So, when blue glass is introduced in the light beam (decreasing the excitation mainly of red-sensitive cones), an OFF-response is observed, much like the response to the onset of blue light. It has been suggested that opponency in ON-cells is asymmetric, ie that the red signal reaches the blue channel with reversed sign, but not vice versa.

A single-unit-recording study revealed the dependence of ON-cell responses both on the colour of stimuli presented in the centre of the receptive field and on the steady illumination of its surround. Surround illumination was found to favour OFF-responses in ON-units. In some cases even the cessation of blue light elicited an OFF-response with a discharge pattern resembling that of the onset of red light. In these cases an ON-response to yellow glass could also be obtained. These observations prove some degree of symmetry in the opponency of the red and

blue channels. It is suggested that feedback from horizontal cells onto photoreceptor terminals is involved in the gated colour opponency. A circuit model that reproduces the observed phenomena is presented.

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◆ **Visual illusions in frogs and toads**

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There are situations where frogs and toads radically misjudge the size of a moving object, taking an enemy for prey or vice versa. In the present work, the conditions where this occurs were investigated. Frogs (*Rana temporaria*) were shown black balls of diameters 0.25–20 cm moving at different distances and velocities, either in the presence or absence of a structured background. When the targets moved at 10–15 cm s⁻¹ (at a distance where this corresponded to ~10 deg s⁻¹) in the presence of the background, frogs turned, approached and tried to catch those with small diameters (0.25–2 cm) only. Larger targets mainly evoked escape reactions. Without the background, balls of any real size could be perceived as prey: all targets of angular size about 5 deg or less triggered a 'food' turning reaction, implying that the critical distance for this reaction depends linearly on object size. 'Food' turning towards big targets (10 or 20 cm) indicates incorrect distance estimation. Moreover, if a big target was moved at high speed (100 deg s⁻¹), the frog not only turned but also flicked its tongue at it without approaching it, even when the distance was up to 1 m. Observations on the toad *Bufo bufo* were qualitatively similar. Thus it is possible to create an illusion of closeness in frogs and toads by increasing the speed of the moving object. Conversely, it is possible to create an illusion of distance by moving a small object at slow speed close to the animal. The 0.25 cm target moving at a 12 cm distance with a velocity of 0.15 cm s⁻¹ (0.7 deg s⁻¹) in the absence of the structured background evoked the 'food' reaction on only 4% of the trials and escape reactions on 80% of the trials. When the background was present, the same stimulus evoked 'food' turning only. The escape reaction to a small object can be explained by a drastic overestimation of its distance in the absence of other cues.

◆ **Measuring frog visual acuity by a novel method**

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The sensory capabilities of animals have usually been measured either by lengthy conditioned discrimination procedures, or by using some specific unconditioned reflex. Amphibian visual acuity has previously been measured only by the latter type of method. Birukow's (1937 *Zeitschrift für Vergleichende Physiologie* 25 92–142) optomotor response experiments on the common frog (*Rana temporaria*) yielded an acuity of 4.3 cycles deg⁻¹, which is surprisingly high in the sense that the retinal cell mosaics would suggest a substantially lower acuity. I have used a new method of measuring acuity based on the frog's prey-catching behaviour, a behaviour that has proved very useful for investigations of amphibian vision. Leopard frogs (*R. pipiens*) were presented with a stimulus screen where two patches of identical black/white vertical grating were seen through two small horizontal oval windows (left and right) in a large screen displaying a horizontal grating pattern. The windows were of 'mealworm' size (18 mm long and 7 mm high, with the frog positioned 220 mm from the screen). One of the two vertical gratings was drifting in the window. If resolved, the movement triggered prey-catching behaviour in the frog: orienting, jumping towards the target, and even snapping. The spatial frequency of the two vertical gratings was varied, while the horizontal pattern of the screen was kept constant throughout the experiment. Orienting or jumping towards the moving grating was taken as an indication that the frog was able to resolve the spatial frequency in question. This method yielded a visual acuity of 2.8 cycles deg⁻¹, which is in good agreement with the eye optics and the retinal grain of frogs (very similar for the common frog and the leopard frog). The method in itself implies that this is a 'functional' acuity value.

◆ **Rhodopsins with similar absorbance characteristics but different rates of thermal activation: amino acid sequences**

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Thermal activation of the visual pigment is thought to be an important factor that in many cases limits the absolute sensitivity of vision in darkness. It has been suggested that pigments with high $\lambda_{\max}$ (ie with good absorbance at long wavelengths, allowing 'red-sensitive' vision) are associated with a cost in terms of high thermal activation rates, degrading signal/noise and

hence visual sensitivity [Barlow, 1957 *Nature (London)* **179** 255–256]. While rhodopsins in different species do show a general correlation between red-sensitivity and high thermal activation rates as measured electrophysiologically in whole rods (Firsov and Govardovskii, 1990 *Sensornye Sistemy* **4** 25–34), a comparison of the toads *Bufo marinus* and *B. bufo* with the bull-frog *Rana catesbeiana* has suggested that the two properties are not tightly coupled. Toad and bull-frog rhodopsins have almost the same λ_{max} , yet the thermal activation rate in bull-frog rods is lower by almost one order of magnitude [Donner et al, 1990 *Journal of Physiology (London)* **428** 673–692]. We have sequenced the cDNA coding for the rhodopsins of the two toad species and that of the common frog *R. temporaria* and aligned them to previously sequenced rhodopsins of *R. catesbeiana*, *R. pipiens* and *Xenopus laevis* in an attempt to identify substitutions that could underlie the greater thermal stability of bull-frog rhodopsin compared with toad rhodopsins.

The open reading frame predicted proteins of 354 amino acids. There was 96% identity between species of the same genus and 90% identity between genera. Across the six species studied, there is a total of 22 non-conserved substitutions and changes that include gain or loss of hydroxyl groups. Our study produced a list of substitutions that apparently do not significantly affect absorbance characteristics. We could not, however, unequivocally identify substitutions important for thermal stability.

◆ **Neural image enhancement allows honeybees to see at night**

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The optical design of most insect apposition compound eyes should restrict activity to daylight because at night the tiny lenses of the isolated ommatidia cannot collect sufficient light. However, several bee species have adopted nocturnal activity, taking advantage of the benefits of night foraging. By measuring behavioural visual performance in honeybees, we show that insects can possess better spatial resolution in dim light than the optics and physiology of their apposition eyes suggest, implying the presence of higher neural mechanisms which enhance vision at night. Theoretical calculations reveal that honeybees improve light capture at night by neurally summing photons in space and time. Even though summation compromises both spatial and temporal resolution, the improved photon capture enhances vision sufficiently for bees to discriminate coarse images in moonlight. This explains how bees and many other insects can adopt a nocturnal life style despite having an eye design typical of a day-active insect.

◆ **The phototactic sensorimotor mechanism of the unicellular alga *Euglena gracilis*.**

An application to the evolutionary study of vision.

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Our understanding of even basic functions of microtubules (MT) such as intracellular transport and ciliary beating, including their role in sensory cells and nerve cells, is still incomplete. For example, vertebrate photoreceptors contain a cilium whose possible dynamical function is still unknown.

A new model of microtubular dynamics, developed by me together with P Zaborski and J Tuszyński [Insinna et al, 1996 *BioSystems* **39**(3) 187–226], is capable of accounting for most of the phenomena associated with cell motility. Additionally, it sheds new light not only on the phototactic behaviour of the Protozoan *Euglena gracilis* but also on some possible evolutionary steps leading from primitive sensory organs to more complex ones such as the photoreceptors of vertebrates. *Euglena* displays simple perceptive functions (phototaxis) based on a primitive photoreceptor. This unicellular organism offers a unique possibility to study the function of MT in a simple form of vision. The model is based on classical nonlinear physics and suggests a dynamical role for MT in vertebrate photoreceptors. I am convinced that a better understanding of photoreceptor dynamics requires knowledge of the evolutionary steps leading to their development.

MODELS AND NEURAL NETWORKS

◆ The human contrast sensitivity function reflects nonlinear dynamics

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Many processes of visual perception may be modelled by nonlinear systems. I here present a novel nonlinear analysis of contrast sensitivity data. My point of departure was the similarity in shape of (i) curves giving threshold contrast as a function of spatial modulation frequency, and (ii) the envelope of bifurcational diagrams obtained from the logistic equation. It should be noted that the well-known changes of curvature for spatial frequencies above 20 cycles deg^{-1} are now being discussed in the literature as a problem of the last or finest channel [Kulikowski, 1991, in *Limits of Vision* Eds J J Kulikowski, V Walsh, I J Murray, volume 5 of *Vision and Visual Dysfunction* Ed. J Cronly-Dillon (London: Macmillan) pp 286-329].

Numerical simulations of threshold contrast as a function of spatial frequency were carried out on the basis of the logistic equation appropriately adapted to the problem. Several linear transformations of the equation were used for determining the parameters that would provide the best fit to the experimental data. The model introduces the concept of perceptual cycle that can be used for characterising the dynamics of selectivity in the spatial frequency domain in its dependence on grating contrast.

◆ A model of human contrast sensitivity as a function of retinal illuminance

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We present a mathematical model for signal transformation by the receptor-horizontal-bipolar cell triad, which gives a good prediction of the spatial-contrast modulation transfer of the visual system at different levels of retinal illuminance. We assume that rod-driven and cone-driven bipolar output signals, s_r and s_c , depend on the mean rates of photoisomerisations in rods and cones, y_r and y_c , and their derivatives, y'_r and y'_c , as expressed by the equations $s_r = c_r y'_r / (d_r y_r + d_c y_c)$, and $s_c = c_c y'_c / (d_r y_r + d_c y_c)$, where c_r , c_c , d_r , d_c are constant coefficients. The total output signal is $S = s_r + s_c$. During scotopic vision $s_r \gg s_c$ and spatial frequency characteristics are determined by the rod system. When illumination increases and rods saturate, contrast sensitivity is determined by the cone system. A formula for calculation of the spatial-contrast modulation transfer function is derived with mean illumination as a parameter. The predictions of the model are in good agreement with experimental data measured at various levels of retinal illumination.

◆ Summation of quantal noise in space and time

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Noise in visual neurons, or variability in psychophysical experiments, may be quantified in terms of photon fluctuations from an 'equivalent' steady illumination. The conversion requires assumptions on how photon signals are pooled in space and time, ie how to pass from the light flux to the numbers of photon events relevant to the Poisson statistics describing signal/noise. Real weighting profiles for the integration of photon events in space and time [the sensitivity distribution of the receptive field (RF) and the waveform of the impulse response (IR)] are commonly approximated by sharp-bordered apertures of 'complete', equal-weight summation of events. Such apertures based on signal equivalence cannot provide noise equivalence, however, because greater numbers of events summed with lower weights (as in reality) have lower variances than smaller numbers summed with full weight. Thus sharp-bordered apertures are necessarily smaller if defined for noise equivalence rather than for signal equivalence. We have calculated the difference for some commonly encountered RF and IR profiles. Summation areas, expressed as numbers of photoreceptors (cones or rods) contributing with equal weight, are denoted N_s for signal and N_N for noise, and sharply delimited summation times are correspondingly denoted t_s and t_N . We show that the relation in time is $t_N = 0.6t_s$ to $0.7t_s$ for realistic quantal response waveforms of photoreceptors. In space, the relation is $N_N = 0.5N_s$ for the Gaussian distribution (eg for the RF centre mechanism of retinal ganglion cells). For a photoreceptor in an electrically coupled network the difference is still greater, eg for rods in the toad retina $N_N = 0.2N_s$ ($N_s = 13.7$ rods and $N_N = 2.8$ rods). We introduce a third possible definition of sharp-bordered summation apertures: one that provides the same signal-to-noise ratio (SNR) for large-long stimuli as the real integration profiles. The SNR-equivalent summation area is $N^* = N_s^2 / N_N$ and the summation time is $t^* = t_s^2 / t_N$.

◆ **A formal mapping model for striate cortex**

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Cortical magnification has been measured with different techniques in many primates, including humans. The most popular models assume a value reciprocal to eccentricity, and are therefore rotation symmetric. To simulate the location of a projected stimulus, a real mapping function is needed. We use the complex logarithm $\log(z + a)$ —introduced for this purpose by Schwartz (1977 *Biological Cybernetics* 25 181–194), which is close to recent brain imaging results in humans and macaque monkeys. The model contradicts the idea of symmetric magnification and the linear model implicitly used by most anatomists. Our model gives a quantitative correspondence from visual field to striate cortex and vice versa, which we use to relate topology and geometry of cortical structures such as ocular dominance stripes, orientation fields, and cytochrome oxidase blobs in V1 to the visual field. This model may serve to relate empirical knowledge about spatial properties of these brain structures to psychophysical stimulus arrangements. Together with the description of cell densities, the point-to-point (and thus simplified) model may be used as a basis for formalising convergence and divergence properties of connections in neural maps.

◆ **A method of identification of analyser characteristics that is free of probability summation effect**

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A detection model (originally proposed by Quick) comprising, in a sequence of linear analysers, $\phi_1, \dots, \phi_n$, nonlinear transducer functions, and the Minkowski decision rule, is widely used, especially when it is necessary to take into account the effect of probability summation. However, there is a general belief that the analyser characteristics cannot be determined in detection experiments since there is a trade-off between these characteristics and the decision rule. Here we show how to overcome this problem, ie how to identify the analysers $\phi_1, \dots, \phi_n$ despite the probability summation between them.

The observer's performance is assumed to be quantitatively defined in terms of an equidetection surface (EDS). Each analyser ϕ_i is expressed as a weighted sum of linear (coordinate) analysers $\{\phi_j\}$: $\phi_i = \sum_{j=1}^n a_{ij} \phi_j$, so that an identification of the analysers $\{\phi_j\}$ is then reduced to evaluating the weight matrix $A = \{a_{ij}\}$. It has been proven that A can be uniquely recovered from an ellipsoidal approximation of EDS in the neighbourhood of at least two points. More specifically, the following equation holds true: $A^{-1}DA = H_1^{-1}H_2$, where D is a diagonal matrix, H_1 and H_2 are the matrices of the quadratic forms determining the n -dimensional ellipsoids approximating EDS. Thus, the matrix $H_1^{-1}H_2$ known from experiment is a similarity transform of the diagonal matrix, the columns of A being the eigenvectors of $H_1^{-1}H_2$. Hence, any eigensystem routine can be used to derive A from $H_1^{-1}H_2$.

◆ **A neuromorphic recurrent model for figure-ground segregation of coherent motion**

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A neuromorphic model of the retino-cortical motion processing stream is proposed which incorporates both feedforward and feedback mechanisms. The feedforward stream consists of motion integration from the retina to the MT area. Retinal spatiotemporal filtering provides X-like and Y-like visual inputs with band-pass characteristics to the V1 area (Beaudot, 1996 *Perception* 25 Supplement, 30–31). V1 direction-selective cells respond to local motion resulting from nonlinear interactions between retinal inputs. MT direction-selective cells respond to global motion resulting from spatial convergence and temporal integration of V1 signals. This feedforward stream provides a fine representation of local motion in V1 and a coarse representation of global motion in MT. However, it is unable to deal with the aperture problem.

Solving this problem requires the adjunction of local constraints related to both smoothness and discontinuity of coherent motion, as well as some minimisation techniques to obtain the optimal solution. We propose a plausible neural substrate for this computation by incorporating excitatory intracortical feedbacks in V1 and their modulation by reciprocal connections from MT. The underlying enhancement or depression of V1 responses according to the strength of MT responses reflects changes in the spatiotemporal properties of the V1 receptive fields. This mechanism induces a dynamic competition between local and global motion representations in V1.

On convergence of these dynamics, responses of V1 direction-selective cells provide a fine representation of 'true' motion, thus solving the aperture problem and allowing a figure-ground segregation based on coherent motion. The model is compatible with recent anatomical, physiological, and psychophysical evidence [Bullier et al, 1996 *Journal de Physiologie (Paris)* **90** 217–220].

◆ **Testing the hypothesis of labelled detectors**

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The hypothesis of labelled detectors (or 'lines') is the present-day version of the basic Müller–Helmholtz doctrine. Müller's dictum of *specific energy of nerves* stated: "the same internal cause excites (...) in each sense the sensation peculiar to it". Helmholtz made 'the cause' external to the body and postulated that all knowledge about the world thus comes through the senses. The key word is *specificity*. The strong version of the hypothesis must treat detection–identification as a single task: a stimulus would be identified whenever it is detected. The weak version requires only that we identify a specific mechanism by which both detection and identification are achieved, even though the latter may require additional processing. In the general case, the strong version (with its ludicrous 'grandmother cell' as the neural substrate) finds little support. Detection and recognition of complex shapes (letters, faces, etc) aside, even discrimination between simple increments and decrements of luminance is difficult to attribute directly to a specific mechanism (in this case, the activity in either ON or OFF systems, respectively). This is demonstrated by experiment 1 reported here. However, perception of relative depth seems to conform to the strong version of the hypothesis, as experiment 2, also reported here, indicates. Thus, at least some specific neural mechanisms (in this case, probably the crossed and uncrossed disparity detectors) may be indeed linked directly to perception.

◆ **A neural net for reconstructing 3-D images of object surfaces**

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There are some algorithms for reconstructing a 3-D surface from two 2-D images. Usually these algorithms are different for shaded objects and for 3-D surfaces from random-dot stereograms. We here propose a neural net for the reconstruction of images of such objects. Two arrays (matrices) of photosensitive elements act as inputs to the neural net. The real 3-D object (shaded sphere and planes) illuminated by a point light source produces two images in the plane of these matrices. The information from photomatrices is processed by many independent channels. Each channel obtains information only from a delimited area of the matrices. This area is called the receptive field (RF) of the channel. RFs of the different channels overlap. If RFs have the same coordinates on the two matrices, they form a pair of corresponding RFs. The information obtained from this pair is integrally processed, determining both the spatial position of the single object surface fragment and its averaged brightness. Two subsystems (coarse and fine) are used to determine the spatial position. First, the orientations of the matrices are chosen so as to bring down to a minimum the integral differences of light intensities between the images in all corresponding RFs. The coarse subsystems determine the disparities of the corresponding RFs, taking into account the orientation (fixation disparity) of the matrices. The fine subsystems calculate the centroids of the images within the RFs and the averaged intensity across the RFs. This information is used to calculate the exact position of the fragment in space and the averaged brightness. All calculations are carried out by neuron detectors sensitive to object location in space. These neurons form the output layer of the neural net.

◆ **The role of subcortical visual structures in target foveation control**

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The role of subcortical levels—the lateral geniculate body (LGB) and superior colliculus (SC) of cat—in the control of foveation eye movements is described by a model based on our own electrophysiological data. These data include the characteristics of eye movements elicited by local electrical microstimulation of neuronal structures in the LGB and the SC.

The model represents a multilevel system forming the program of foveation eye movements by performing the following actions in temporal sequence: determination of the position of the visual target in retinotopic coordinates, determination of its craniotopic coordinates and determination of the direction and calculation of the velocity of the moving visual target. I discuss algorithms and neuronal mechanisms (including electrophysiological data on single neurons and neuronal populations) of subcortical levels of the cat visual system taking part in foveation eye-movement control for stationary and moving visual objects, as well as the role of directional and orientation properties of receptive fields of subcortical neurons in this control.

◆ **Visual associative memory simulates the McCollough effect**

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The McCollough effect (ME) refers to the phenomenon that, after a few minutes' exposure to gratings differing in both orientation and colour, subjects perceive similarly oriented achromatic gratings as if they were tinted with complementary hues. The traditional explanation of the ME as an adaptation of detectors selective for colour and orientation suffers from a number of inconsistencies: (i) the ME lasts much longer than ordinary adaptation, the decay of the effect being completely arrested during a night's sleep, or by occluding the eye for a long time; (ii) the strength of the ME is practically independent of the intensity of the adapting light; and (iii) a set of related pattern-contingent aftereffects discovered later would require, for explanation on similar lines, new detectors specific to other patterns. These properties can be explained, however, in the framework of associative memory and novelty filters.

A computational model has been developed which consists of (i) an input layer of two (left and right eyes) square matrices with two analog receptors (red and green) in each pixel; (ii) an isomorphic associative neural layer, each neuron being synaptically connected with all receptors of both eyes; and (iii) an output layer (novelty filter). Modification of synaptic efficacies conforms to the Hebb learning rule. After a few presentations of coloured gratings the model displays the ME, which is slowly destroyed by subsequent presentations of random pictures. With a sufficiently large receptor matrix the effect lasts a thousand times longer than the period of learning. Continuous darkness does not change the strength of the effect. Like the real ME, the model does not display interocular transfer, but with other adapting patterns it shows the disparity-contingent colour aftereffect (thus confirming the connections with both eyes). The model can account for different pattern-contingent colour aftereffects without assuming any predetermined specific detectors. Such detectors are constructed in the course of adaptation to specific stimuli (gratings).

◆ **Real-world scene categorisation by a self-organising neural network**

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There is now a great deal of evidence that the visual system identifies the category of a scene before identifying its component objects. Schyns and Oliva (1994 *Psychological Science* 5 195–200) showed that scene recognition could be initiated with only coarse blobs (information from which the identity of objects could not be recognised). Thus, one possible strategy for object recognition would be first to recognise the background scene from very coarse information and then recognise the component objects from fine-scale information. However, this will only be useful to the extent that there is enough coarse-scale information for the background scene to be recognised. We present a scene categorisation model in which low and very low spatial frequencies alone offer sufficient information to produce consistent clusters of five distinct scene categories (beach, city, forest, room, and valley). A new self-organising neural network—curvilinear component analysis (P Demartines, J Hérault, 1997 *IEEE Transactions on Neural Networks* 8 149–154)—was used to project nonlinearly a filtered version of a real-world image onto a two-dimensional output space. The resulting projection preserved the semantic proximities between the scene categories. These results offer formal evidence that there is enough coarse-scale information for recognition.

◆ **A ring model for direction-selective simple cells in the visual cortex**

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Experimental studies have shown that (1) direction-selective simple cells in the visual cortex have spatiotemporally inseparable receptive fields, whose spatial profiles at a given time are described by Gabor functions: a sinusoid multiplied by a Gaussian, with a phase parameter; (2) among simple cells, the phases are distributed not merely at 0 and $\pi/2$ as for sine and cosine Gabor functions, but uniformly between 0 and 2π (DeAngelis et al, 1993 *Journal of Neurophysiology* 69 1091–1117); (3) anatomically, these simple cells receive inputs more from other cortical cells than from the lateral geniculate body (LGN) (Ahmed et al, 1994 *Journal of Comparative Neurology* 341 39–49). We accordingly propose here a neural model for the simple cells whose receptive

fields are assumed to be of the same spatial position and orientation. In the model, several cortical cells are arranged in a ring with mutual excitatory and inhibitory connections, and receive afferent signals from lagged and nonlagged cells in LGN (Saul and Humphrey, 1990 *Journal of Neurophysiology* **64** 206–224). Computer simulation shows that the cortical cells have spatiotemporally inseparable receptive fields with spatial profiles described by Gabor functions, and are directionally selective to a moving grating. The cells are found to be arranged so that their Gabor phases vary regularly from 0 to 2π with rotation along the ring. The connection among the cortical cells has a role of amplification as in the canonical microcircuit model (Douglas et al, 1989 *Neural Computation* **1** 480–488).

◆ **A neural network model of tilt aftereffects**

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RF-LISSOM, a self-organising model of laterally connected orientation maps in the primary visual cortex, was used to study the psychological phenomenon known as the tilt aftereffect. The model allows observation of activation and connection patterns between large numbers of neurons simultaneously, making it possible to relate higher-level phenomena to low-level events, which is difficult to do experimentally. In RF-LISSOM, the same self-organising processes that are responsible for the development of the orientation map and its lateral connections are shown to result in tilt aftereffects over short time scales in the adult. The results give computational support for the idea that direct tilt aftereffects arise from adaptive lateral interactions between feature detectors, as has long been surmised. They also suggest that indirect effects could result from the conservation of synaptic resources during this process. The model thus provides a unified computational explanation of self-organisation and both direct and indirect tilt aftereffects in the primary visual cortex.

◆ **A recurrent network for tilt illusions based on retinotopic coding**

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We propose a computational model for the mechanism underlying the perception of tilt illusions. Several studies have suggested that cortical mechanisms based on orientation-dependent lateral connections account for tilt illusions such as the Zöllner and Delboeuf illusions [1970 *Nature (London)* **228** 37–39; 1989 *Biological Cybernetics* **58** 35–49]. In these studies, it has been proposed that two intersecting bars evoke strong activation of V1 cells tuned to the orientations of the bars, and that, because of lateral interactions, cells tuned to orientations several degrees off those of the bars are the most strongly activated of all orientation-tuned cells. Thus the peaks in the neural orientation profiles are shifted by several degrees compared with the actual orientations of the bars. We investigate the retinotopic distribution of V1 cell activities in simulations of a large-scale recurrent network based on V1 anatomical connectivity, and show that the orientation profile of cell activities is significantly different for different retinotopic positions. For most positions, a single peak appears in the orientation profile. Taking into account population coding of the cells, we show that the bars will be tilted in a stimulus-configuration-dependent manner. The network shows angle expansion at crossed (X-shaped), branched (Y-shaped), or bent (L-shaped) intersections if the angle between the two bars is acute, and contraction if the angle is obtuse. The maximum expansion appears between 15° and 30°. These results are in good agreement with psychophysical observations on tilt illusions, including the Zöllner, Delboeuf, and Poggendorff illusions.

METHODOLOGY

◆ **ASIDT: Adaptive signal detection testing**

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Two-alternative forced choice (2AFC) methods which are routinely used in psychophysics provide criterion-free sensitivity measures but at a high price: 2AFC procedures generally need 2–3 times the number of trials than a simple yes/no design to achieve the same level of threshold variability. Similarly, signal detection methods provide measures for criterion and sensitivity, but they require predetermined signal levels for the presented stimuli and also need a large number of trials.

ASIDT (adaptive signal detection testing) combines rating responses with an adaptive stimulus placement strategy according to the accelerated stochastic approximation method (see Treutwein,

1995 *Vision Research* **35** 2503–2522). More specifically, during the course of the experiment the rating responses are collapsed into two groups (yes/no). The border between these two groups is set at the current median of the rating categories actually used by the subject. With the collapsed yes/no responses the stimuli are placed according to accelerated stochastic approximation. This placement strategy is based on very simple rules and distributes the stimulus values asymptotically according to a normal distribution around the median. After the experiment, the rating responses can be used to compute a nonparametric and criterion-free sensitivity measure, the area under the empirical ROC, which is equivalent to the percentage correct in a 2AFC experiment. The usage of ASIDT is demonstrated by psychophysical data.

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◆ **Experimental evaluation of the reliability of the method of constant stimuli**

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Although the method of constant stimuli is commonly used in psychophysical investigations, special statistical procedures for testing its reliability are rarely employed. Measurement errors are usually ignored, and their potential effect on the overall efficiency of the measurement procedure is not taken into consideration. In reality, the decision-making strategy of the subject may change during the course of the experiment, and responses may be correlated.

We suggest a completely nonparametric method for testing hypotheses about a subject's decision-making strategy. It is based on the analysis of contingency tables and includes the method of primary-data grouping. This technique was applied to address two questions: (1) whether the results of a set of experiments, conducted independently of each other, may be considered as statistically equivalent; (2) whether the subject's response depends statistically on his preceding decisions.

Specially designed experiments on discrimination of the length of lines were performed with a large number of untrained subjects. Exploratory analysis of primary data typical for experiments of this kind has revealed some features that are usually not detected by ordinary statistical data processing, but may affect the final results. It appeared that untrained subjects often used a decision-making strategy biased towards the preceding response. This does not seem to be dependent on the personal characteristics of the subject. Some psychophysical procedures in fact encourage subjects to use this strategy.

◆ **Preventing local clustering in random-dot patterns: a new method to avoid perceptual artifacts**

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Patterns consisting of random dots are frequently used in visual science. One disadvantage of using random-dot patterns is the possible clustering of dots. These clusters have a lower spatial frequency than the one derived from dot size. The cluster formation is not present in patterns in which dots are homogeneously distributed, but with these patterns other problems, eg ambiguity in stereograms, occur. A good balance between homogeneous and random distribution has to be found. This problem has often been addressed in half-toning techniques. One of these techniques is force-field random dithering. In this technique each dot has a force field that repels newly placed dots. For generating random patterns, we used a modification of this dithering technique.

This technique is empirically compared with the traditional random-dot patterns. Subjects viewed for 70 ms a 6 deg × 6 deg square consisting of 100 × 100 dots placed randomly or with a force field. Each dot subtended 0.6 min arc. The task was to detect a vertical band of 30 × 100 dots with increased luminance, which could appear either left or right of the midline. The density of the dots was varied between 5% and 25%. The results indicate a significantly larger error rate when using the force-field generated pattern.

We conclude that subjects are using clusters as local cues. These results should warn investigators using random-dot patterns that local clusters could act as serious artifacts.

◆ **Fundamental comparison of image quality metrics**

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In most image quality metrics (eg MTFA, ICS, SQF, DDD, SQR1) use is made of the modulation transfer function (MTF) of the imaging system and the contrast sensitivity function (CSF) of the human visual system. All metrics usually show a positive correlation with perceived image quality. This does not, however, say much about the correctness of the underlying equations.

Defocusing experiments where an image is defocused by one just-noticeable difference can give information about the contribution of different spatial-frequency ranges to image quality. By performing defocusing experiments with images where contrast is also varied, information can be obtained about the dependence of image quality on contrast.

In our investigation defocusing measurements from Baldwin (1940), Carlson and Cohen (1980) and Watt and Morgan (1983) were used. Comparison of the results with the fundamental dependence of some image quality metrics on spatial frequency and contrast indicates that only the SQRI (square-root integral) showed the right behaviour with respect to these parameters.

◆ **Goodness of dot patterns and completion variability: effects of equidistance and collinearity of dots**

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Visual patterns that are initially poorly specified can be perceptually completed into different Gestalten (eg dot patterns can impose the perception of different figures). In the present study the following hypothesis is evaluated. If the goodness of initial patterns is high enough (high Prägnanz), then the completion of initial patterns will result in a single Gestalt (high stability of percept). On the other hand, if the goodness is low (low Prägnanz), the completion will result in several Gestalten (perceptual multistability). In experiment 1 subjects estimated the goodness of four sets of initial 8-dot patterns. The distance between the dots was systematically varied. In experiment 2 the variability of completion of the same initial stimuli was examined. Subjects were asked to choose from a given set of figures the one that was most strongly suggested by the exposed initial dot pattern. The entropy, as a measure of the completion variability, was derived from the proportions of the choices of figures. The correlation between goodness estimates (Prägnanz level) and entropy (completion multistability) was significant: the higher the goodness, the lower the multistability of initial pattern completion. The arrangement of dots was an important stimulus constraint of the dependent variables. Increasing the number of equidistant extents between dots increased multistability and decreased goodness. Collinearity of dots induced a decrease of multistability and an increase of goodness.

◆ **Tools for investigating the perception of natural scenes**

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Research on the perception of complex half-tone images and images of natural scenes requires accurate quantitative control of the characteristics of the stimuli. The tools consist of the hardware and the software for stimulation and processing. Our hardware for stimulation includes a CCD, an IBM PC with implementing Frame Grabber, the display, and a device for photometric control. We present programs for image processing allowing control of the brightness scale, reformation, changing the number of discretisation levels, addition and subtraction, programs for convolution operations including frequency filtration approximations, the means of different methods, programs for generation of test images and for generation of noise added to these, and programs for measuring statistical and geometrical characteristics of images. We also present software for use in electrophysiological experiments.

◆ **A quantitative method to explore the assimilation effects**

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The role of central processes in the assimilation effect can easily be shown qualitatively (de Weert and Spillmann, 1995 *Vision Research* 35 1413–1419), but it is difficult to measure quantitatively because of the subtlety of the effect. In most experimental designs, the match stimulus differs greatly in appearance from the test stimulus, eg in size or configuration, and because these differences are far more striking than the assimilation effect, matching is difficult.

Central processing, eg object segmentation, influences colour spreading. It is this property that we explored with a new approach: a matching task in which the match stimulus has the same properties (eg size and configuration) as the test stimulus. Object segmentation is forced by stereopsis-induced depth. The test stimulus consists of two depth planes, one with black dots and the other with white dots, on a homogeneous gray background. The match stimulus has the same configuration of black and white dots, but now squeezed into a single depth plane. The basic idea behind this stimulus is that assimilation mainly acts on the back plane of a scene

(as can be shown experimentally). So, while keeping the appearance of the stimulus the same, subjects can focus on the assimilation effect itself. This new approach allows us to explore more aspects of the assimilation effect and gain insight into the processes involved.

◆ **Noise effects in perceptual models**

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In studies of visual perception performance is often measured by statistics that are ratios of a perceptual magnitude to its intrinsic variability, most commonly the signal-detection measure $d' = \delta\sigma$. Many models for visual phenomena treat the variability σ as a constant and describe performance exclusively by δ . However, in models for the combination of stimulus attributes, the combination process affects both terms, and an observed d' reflects both δ and σ . For example, we have shown that masking and configural effects with sinusoidal plaids can be at least partially interpreted as noise effects.

We have developed methods to analyse these noise effects. Through a series of concurrent-response experiments using grating stimuli, some reported at earlier ECVF meetings, we have measured the form and magnitude of the noise sources. Our analysis allows us to model the way that primitive Fourier components (spatial frequency by orientation) are integrated to form second-order or third-order combinations (eg spatial frequency pooled over orientation).

SENSITIVITY, CONTRAST, BRIGHTNESS AND LIGHTNESS

◆ **Detection efficiency for gratings with various frequency gradients**

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We investigated the effects of spatial frequency gradients on human grating-detection efficiency. Both polar-circular and vertical cosine gratings of different central spatial frequencies (1–4 cycles deg^{-1}) and frequency gradients were used. The local spatial frequency either increased or decreased with the radial distance from image centre. Contrast energy thresholds were determined by a 2AFC method. The gratings were embedded in strong spatial noise, which allowed us to investigate detection performance in terms of efficiency. The experimental results were described as a function of a scale-invariant measure of image complexity (Z) calculated as $Z = Af^2$, where A is the grating area and f is the highest local spatial frequency of the gradient grating.

The results showed that efficiency behaves similarly for vastly different gratings in visual noise. Efficiency for all spatial frequency gradients obeyed a single function of complexity independently of the central spatial frequency or the steepness of the frequency gradient. At small values of complexity, efficiency was constant, but decreased at higher values of complexity. Thus, the proportion of contrast information used decreased with increasing image complexity. The results can be understood by assuming that the highest local spatial frequencies of the image determine the spatial extent over which the human visual system integrates contrast information of grating images. With increasing highest spatial frequency the extent of the integration area becomes smaller.

◆ **Spatial extent of masking by sine-wave gratings**

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The contrast threshold for detection of a target consisting of 1.5 periods of a sine wave was determined as a function of the number of cycles in a sinusoidal mask with the same spatial frequency and orientation. The test frequencies were 2, 4, and 8 cycles deg^{-1} . The masks were spatial-frequency modulated so as to equate their spectral extent. Stimuli were seen monocularly in Maxwellian view at a mean luminance of 10 cd m^{-2} . The contrast threshold in a backward masking paradigm was determined by a 2AFC staircase. Data were obtained from three subjects with normal vision.

It was found that as the number of cycles in the mask was increased, the contrast threshold fell, but only to a certain level. The full range of the threshold decrement was about 2 dB. At all the spatial frequencies tested, the final threshold level was reached with 3 cycles in the mask and then remained unaffected by a further increase in the number of cycles.

The results implicate frequency-tuned mechanisms of very restricted spatial extent. It is suggested that these may underlie processing of spatially distributed information at the post-striate stages.

◆ **Calibration of a spatiotemporal discrimination model from forward, simultaneous, and backward masking**

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We have been developing a simplified spatiotemporal discrimination model similar to our simplified spatial model in that masking is assumed to be a function of the local visible contrast energy. The overall spatiotemporal sensitivity of the model is calibrated to predict the detectability of targets on a uniform background. To calibrate the spatiotemporal integration functions that define local visible contrast energy, spatiotemporal masking data are required.

Observer thresholds were measured (2IFC) for the detection of a 12 ms target stimulus in the presence of a 700 ms mask. Targets were 1, 3, or 9 cycles deg^{-1} sine-wave gratings. Masks were either one of these gratings or two of them combined. The target was presented in 17 temporal positions with respect to the mask, including positions before, during, and after the mask. Peak masking was found near mask onset and offset for 1 and 3 cycles deg^{-1} targets, while masking effects were more nearly uniform during the mask for the 9 cycles deg^{-1} target.

As in the purely spatial case, the simplified model cannot predict all the details of masking as a function of masking component spatial frequencies, but overall the prediction errors are small.

◆ **Eye-position effects on the visual transfer function**

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Light responses of neurons in several brain areas are affected by eye position (Andersen et al, 1990 *Journal of Neuroscience* 10 1176–1196). To find out if eye position may influence contrast sensitivity, measurements were made of the spatial contrast modulation transfer function at two different eye positions: with the gaze directed straight ahead and horizontally deflected by 30 deg, respectively. Eleven gratings (1.05–36.8 cycles deg^{-1}) were presented so that their retinal position was identical at both eye positions. The data obtained show a significant effect of eye position on contrast sensitivity in 4 subjects out of 8. We found a mean decrease in contrast sensitivity by 10.8% in the 'deflected' condition. The eye-position effect was pronounced at low (14.8%) and high (29.6%) frequencies, being insignificant at middle frequencies. The maximal sensitivity decrease observed was 62.1% at 25 cycles deg^{-1} in one subject. In 4 of the subjects, no significant eye-position effect was found.

Thus a horizontal deflection of the gaze direction can narrow the visual transfer function in some observers and consequently impair perception of near-threshold objects dominated by high or low spatial frequencies. Further studies will show what may account for this phenomenon: the interaction of retinal and eye position signals and/or optical changes due to compression of the eye ball.

◆ **Adaptation is faster after luminance decrements than after luminance increments, independently of test pulse polarity**

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As is well known, dark-adaptation in the human visual system is much slower than recovery from darkness. We show that at high photopic luminances the situation is exactly opposite. In psychophysical experiments on human subjects, we have studied detection thresholds for brief light flashes, at various delays with respect to decrement and increment steps in background luminance. Light adaptation was nearly complete within 100 ms after luminance decrements, but took much longer after luminance increments.

In an effort to determine the nature of the threshold dynamics, we have compared sensitivity after equally visible pulses or steps in the adaptation luminance. Flash detectability was initially the same in the pulse and step conditions, but recovered much faster after pulses than after increment steps. This suggests that the initial threshold elevation is caused by the temporal contrast of the background steps and pulses, whereas the residual threshold elevation after an increment step shows an incomplete luminance adaptation. We have substantiated this by manipulating the contrast of a transition between luminances: we found that these contrast manipulations affected only the initial part of the threshold curve, not later stages. Finally, we measured detection thresholds for brief luminance decrements. For these tests with negative polarity, threshold recovery remained significantly faster after decrement than after increment steps in background luminance. Therefore, the asymmetry in adaptation dynamics that we report is indeed related to the step direction of the background luminance, and is not caused by interaction with the test polarity.

◆ **Detection thresholds for light pulses superimposed on backgrounds with temporally modulated luminance**

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We investigated the effects of sinusoidal modulation of the luminance of a large (17 deg) spatially homogeneous field on detection thresholds for a brief (7.5 ms) light pulse 46 min arc or 17 deg in size. The average luminance of the background field was at a high photopic level (2800 Td) throughout the experiment. Temporal frequency f (0.4–200 Hz) and contrast C (0.05–0.8) of the background modulation were varied, together with the timing τ of the test pulse in the modulation cycle.

As a function of f , thresholds reach maximum around 15–20 Hz, and steeply decline at higher frequencies. At frequencies above flicker fusion, thresholds do not depend on τ , and are equal to the detection threshold on a constant background with the time-averaged luminance, in accordance with Talbot's law. At frequencies below 15 Hz, threshold elevations above threshold at constant background depend on f as a power law, with a power exponent (0.8–1.0) that is close to 1. Also threshold elevation as a function of modulation contrast conforms to a power law, with a similar power exponent (0.8–1.0). The effects of τ are complex, and depend on both the frequency and the contrast of the background modulation.

Our results yield constraints for models of luminance adaptation and contrast masking. In particular, the results at high frequencies indicate that the first stage of such models should consist of a linear low-pass filtering of the input luminance. The results at low frequency suggest a temporal derivative operation of the resulting signal. We discuss to what extent existing models can explain the dynamics of the measurements.

◆ **The effect of pedestal contrast on choice reaction times to contrast increments**

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Two-alternative forced-choice reaction times (RTs) were measured and psychometric functions constructed for ten contrast increments at seven pedestal contrasts ranging from 0% to 4.8%. Two sine gratings at 2 cycles deg⁻¹ differing only in contrast were presented on a computer screen, and the subject's task was to indicate as quickly as possible whether the stimulus with higher contrast appeared to the left or to the right of a fixation point. There were 100 trials per stimulus pair from which the percentage of correct responses and the median correct RTs were calculated. As the contrast increment increased, the percentage of correct responses increased and RTs decreased reaching a minimum with large increments. However, RTs continued to decrease even when performance reached 100% correct. Contrast increment thresholds calculated at 82% correct level formed a classical dipper-shaped function when plotted as a function of pedestal contrast. Response variability, reflected in standard errors of increment thresholds, was greater at high pedestal contrasts. When RTs corresponding to threshold increments were interpolated and plotted against pedestal contrast, the functions were also dipper-shaped. Discriminative RTs were on average faster at low and slower at high pedestal contrasts compared to detection. These findings show that equalising the percentage of correct responses did not equalise RTs, and that processing time increased with pedestal contrast. The increase of both increment thresholds and RTs with pedestal contrast may be due to an increase in signal-dependent noise which increases response variability and slows down the decision process.

◆ **Retinal mechanisms underlying pedestal effects in brightness discrimination: a model**

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The dependence of the minimal discriminable intensity difference (MDD) of two flashed stimuli on the pedestal (the intensity of the dimmer one) is known to follow a nonmonotonic 'dipper' function. When the pedestal is zero, the MDD is by definition identical to the threshold for light detection. Very dim pedestals have little effect on the MDD, but there is a range of fairly dim pedestals, of intensities around the detection threshold, where the MDD decreases with increasing intensity. Beyond that range, the MDD is a monotonically increasing function of intensity. Functions of this type have been observed with spatially very different stimuli.

We propose that dipper functions arise owing to the fact that different aspects of the primary light response of photoreceptors are relevant to near-threshold and suprathreshold visual signals. Decisions near the detection threshold are based on signals determined by the peak

amplitude of photoreceptor responses, which for dim stimuli grows linearly with intensity. By contrast, visual signals for clearly suprathreshold stimuli reflect the rate of rise of early parts of the photoreceptor response, tracing only a short segment of the photoreceptor response just after the point where it has reached threshold amplitude. The latter type of signal shows a similar intensity dependence as do psychophysical brightness judgments, starting with a supra-linear segment and passing via linearity into a compressive power function at high stimulus intensities (Donner, 1989 *Visual Neuroscience* 3 39–51; Djupsund et al, 1996 *Vision Research* 36 3253–3264). Discrimination sensitivity is in principle proportional to the derivative of this function. The transition from the 'peak-amplitude-based' linear signalling range around detection threshold to the 'early-rise-based' signalling range described by the nonlinear brightness function implies a sharp contraction of the response time window. Intensity discrimination improves, because the intensity dependence of the signal scaled by its variability becomes steeper than linear. As pedestal intensity is raised further, however, the MDD begins to increase again, basically in inverse proportion to the decreasing derivative of the brightness function.

◆ **Suprathreshold contrast increment detection is not affected by grating edge-type**

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We have shown that the spatial frequency components introduced by sharply truncating the edge of a sinusoidal grating do not affect detection thresholds (Kukkonen et al, 1996 *Perception* 25 Supplement, 117). This could be due to the fact that contrast energy at these spatial frequencies is much lower than at the nominal frequency. Any effect upon detection attributable to the broadening of the Fourier spectrum might therefore exert itself most strongly at suprathreshold rather than threshold contrast levels. To establish whether these extra components interfere with performance at higher contrasts, we measured contrast increment thresholds of circular-aperture sinusoidal gratings with a pedestal contrast of 0.5. Gratings were either sharply truncated or Gaussian-edged having a half-contrast diameter equal to that of its corresponding sharp-edged stimulus. Gratings of 0.125 and 0.5 cycle deg⁻¹ were used, each tested with 1–8 cycles. There was no significant difference between contrast increment thresholds for the sharp-edged and Gaussian-edged gratings, which were spectrally narrower. The frequency components introduced into the Fourier spectrum by the abrupt edge of the truncated gratings appear to have no effect upon subject performance even in suprathreshold contrast increment detection.

◆ **An illuminated surface may be perceived as a shining surface**

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The relationship between the whiteness of a surface (W) and its perceived illumination (E) has been described by the equation: $W + kE = Y$, where Y is brightness and k is a constant. When brightness remains constant and perceived illumination decreases, whiteness increases from black to white. If, starting from a pair of values $W = W_0$, $E = E_0$ (where E_0 is a low value of perceived illumination) at which the surface is seen as white (state A), E is further decreased while brightness remains constant, the surface may be perceived as shining (state B).

We investigated the conditions under which the perceptual transition from state A to state B occurred. The subject looked at an illuminated white paper screen on which objects cast shadows. Two test patches were presented: one on a well-illuminated area, the other on a shaded area. The scene and the patches were illuminated by two separate light sources. The brightness of the patches was held constant. The subject was instructed to set the 'scene' illumination so that a test patch was perceived as shining, separately for each patch. The results showed that the 'scene' illumination where the transition occurred was different for the shaded and the well-illuminated patches. We conclude that the perception of a surface as shining depends on local illumination.

◆ **Some new effects: phenomenal glare, luminous 'mist' and dark 'smoke'**

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The impression of glare is caused by a very intense light source. However, here I show that this impression can also be generated with normal light intensities. The strength of the effect depends on the number of elements used to produce it. The elements are 2 cm × 5 cm rectangles. A single horizontal achromatic rectangle is first used on a homogeneous white or black background. From left to right, the brightness of the rectangle varies smoothly from black to white. The left part of the rectangle appears to progressively bend toward the background when the background is black, while the rectangle appears straight and to fade into an apparent white mist near its right side when the background is white. When the background is black, two

horizontal rectangles, specularly shaded from black to white, so that their black ends face each other with a 2 cm gap between them, appear either to bend toward the background or to be straight and to fade into a sort of dark 'smoke'. When the background is white with the left rectangle varying in brightness from black to white and the right one from white to black, the rectangles look straight with a sort of white glare appearing to come out from the gap. The black 'smoke' and the white glare look more compelling when there are four rectangles forming a cross with a central square gap. It can be argued that this and the neon spreading effect are unrelated. Instead, psychophysical experiments suggest that the glare and smoke effects depend on a relation between the grey scale gradient and the background brightness.

◆ **Further evidence of the effect of gradient on lightness**

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Recently, Agostini and Galmonte (submitted for publication) reported a new effect of gradient on lightness. When two identical mid-gray squares are placed at the centre (white and black, respectively) of two crosses, the first cross having arms filled by a constant achromatic gradient from black (outer part) to white (inner part), and the second cross being the negative of the first one, the gray target surrounded by white appears much darker than that surrounded by black. In a simultaneous comparison, this phenomenon is much stronger than the classical lightness contrast effect. Further observations showed that the effect is quite robust also when the amount of black area is reduced and the gradient is discontinuous. When the gray targets are enlarged to fill the centres of the crosses, the effect is still stronger than that observed in the classical simultaneous lightness contrast display. Furthermore, the effect is independent of the shape of the configuration. The phenomenon can be explained by assuming that the gradient is perceived as a change of the level of illumination rather than as a change of the reflectance of the surfaces.

◆ **Multiphasic spatial response to flickering stimuli**

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If it is assumed that the weighting function of early vision can be described by a spatiotemporal Gabor-like function (Manahilov, 1995 *Vision Research* 35 227–237), the spatial impulse response to flickering stimuli would consist of more alternating phases than that to a brief stimulus. To test this prediction, the Westheimer paradigm and the brightness matching technique were used. The effect of a flickering inducing disk (temporal frequency 7.7 Hz, duration 195 ms, zero starting phase) of variable radius on the apparent brightness of an incremental test stimulus (1.2 min arc radius, duration 14.25 ms) was measured in foveal photopic vision. The test stimulus was superimposed on the centre of the inducing disk and presented 142 ms after the onset of the inducing stimulus. When the radius of the inducing stimulus was increased, the test brightness was enhanced, reaching a maximum at a radius of 3 min arc, then diminished below the control level at radii of 9–11 min arc and was enhanced again at radii of 14–17 min arc. This finding differed from the unimodal effect of a brief inducing disk on test brightness and suggested a multiphasic profile of the spatial impulse response to a flickering stimulus. This suggestion was supported by the dependence of the apparent brightness of a test line on the distance between the test and two flanking inducing lines. The temporal conditions were similar to those of the previous experiment. The brightness of the test line was increased above the control level at distances of 0–2 min arc, decreased at distances of 3–6 min arc and again increased to a smaller extent at distances of 10–13 min arc. Brief inducing lines evoked only the initial enhancement of the test-line brightness and its decrease at lateral positions. The data obtained are in line with the predictions of the model of the visual weighting function.

◆ **Influence of scanning eye movements on the scintillating-grid illusion**

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The scintillating grid is an example of a brightness contrast illusion in which bright disks are superimposed on a Hermann grid. Dark spots are perceived within the bright disks as flashing with each flick of the eye (Schrauf et al *Vision Research* in press). With steady fixation, stimulation must be brief for the illusion to occur. Varying exposure duration with steady fixation, we

found the maximum illusion at durations between 210–350 ms (Schrauf et al, 1996 *Perception* 25 Supplement, 78).

In the present study voluntary saccadic eye movements were used to produce brief exposures during fixations. The task of 5 trained subjects was to scan scintillation grids of five different spacings (0.5–2.0 deg separation of grid elements, observation time 60 s) in a manner yielding a maximum scintillating effect. Eye movements were recorded binocularly at 100 Hz with the Demel Debic 90 infrared corneal reflection tracker (resolution: 6 min arc). For each fixation we calculated latency and position. Durations and amplitudes of the saccades increased with decreasing angular separation of grid elements. When the illusion was maximal, roughly 60% of fixation durations were between 250 and 550 ms. These durations overlap with those obtained with steady fixation combined with variable exposure durations. Unlike the Hermann grid illusion, where illusory dark spots can be perceived at very brief exposure durations, the scintillating grid illusion takes much more time to develop. The long optimal durations found here are discussed in relation to mechanisms of scanning eye movements.

◆ **Two new dynamic effects: light explosion and night crash**

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Starting from an achromatic display used by Zavagno to study a glare and a 'smoke' effect, we show two new dynamic effects that we call (a) 'light explosion' and (b) 'night crash'.

On a uniform white or black background four black or white rectangles (inducers, $1 \text{ deg} \times 5.7 \text{ deg}$) were arranged to form an orthogonal cross with a square gap in its centre. (a) When the luminance of black inducers on a white background is transformed into a smooth gray scale gradient with the lighter ends facing the square gap, a luminous mist with a glare effect is seen. When such a transformation is performed dynamically by changing the gradient from outside to inside (with the outside ends remaining black and the inside changing toward white), a sudden explosion of light is seen. (b) When the luminance of white inducers on a black background is transformed into a smooth gray scale gradient with their darker ends facing the square gap, a sort of dark 'smoke' is seen. If such a transformation is performed dynamically by changing the gradient from inside to outside (with the outside ends remaining white and the inside changing toward black), a sudden and instantaneous black diffusion (a sort of night crash) is seen.

Both the light explosion and the night crash effects have an exponential course followed by an immediate drop. Psychophysical data show that both effects depend on an interaction between the lightness of the background, the lightness of the square gap, and the transformation rate of the gray scale gradient.

◆ **Spatial parameters affecting the Hermann grid and the scintillating-grid illusions**

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The Hermann grid and the scintillating grid are examples of brightness-contrast illusions. The scintillating grid consists of a Hermann grid with bright disks about 1.4 times the diameter of the grid elements superimposed upon the intersections. The resulting scintillation effect can be described as striking illusory spots, darker than the background, perceived as flashing within the bright disks with each flick of the eye. Although the scintillation effect is different from the classical Hermann grid illusion, one prerequisite for its occurrence is the presence of a grid eliciting the Hermann grid illusion (Schrauf et al *Vision Research* in press). At the 12th ECVF we showed that the Hermann grid illusion can be reduced by bright diagonals within the squares of the grid which have the effect of suppressing the $45^\circ/135^\circ$ components of the Fourier spectrum (Lingelbach et al, 1989 *Perception* 18 536–537). In a pilot study we successively reduced the length of the diagonals, and found that this suppression works well even if the diagonals are reduced to small tips near the grid intersections. According to Baumgartner's receptive-field account (Baumgartner, 1960 *Pflügers Archiv* 272 21–22), such elements should cause additional inhibition, thus decreasing the neuronal discharge rate and corresponding illusory percept. This is not the case: if any illusion is perceived, it is considerably weaker. The strength of the scintillation effect is similarly reduced by this manipulation. Thus the present results cannot easily be accounted for by Baumgartner's model.

TUESDAY

ORAL PRESENTATIONS

PLENARY LECTURE

- ◆ **Psychophysical studies of visual dysfunction in glaucoma: Lessons learned and questions raised**
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The study of visual dysfunction in ophthalmic disease is important for both elucidating the pathophysiological basis of visual loss and improving patient care. The application of psychophysical procedures in contemporary glaucoma research illustrates this point. Although achromatic automated perimetry (ie differential luminance thresholds) remains the 'gold standard' for the clinical diagnosis of glaucomatous optic neuropathy, psychophysical studies of other visual functions (motion discrimination, blue–yellow perimetry, temporal resolution, and contrast sensitivity) have led to the development of a more comprehensive framework for investigating the mechanisms underlying glaucoma-induced visual impairment. For example, psychophysical studies of the mechanisms mediating visual dysfunction in glaucoma suggest that neurodegenerative changes reduce redundancy in the neural circuitry in a manner that may be selective for, but possibly not specific to, particular neural pathways. In addition, psychophysical studies have significantly advanced our understanding of the nature and scope of visual deterioration in this disease. As a direct result of these studies new clinical tools have been designed which (1) increase sensitivity for detecting early signs of visual impairment, (2) more accurately predict which glaucoma suspects will develop the disease, and (3) provide a more precise metric for both monitoring disease progression and evaluating treatment efficacy (eg in clinical trials). In this presentation I describe the status of our knowledge of visual impairment in glaucoma and highlight the contributions of visual psychophysics to the evolution of this understanding.

BINOCULARITY AND STEREOPSIS

- ◆ **Interocular grouping of visual attributes during binocular rivalry**
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The need to revise the eye competition hypothesis of binocular rivalry, and to include the role of stimulus competition has been demonstrated recently by Kovács, Papathomas, Feher, and Yang (1996 *Proceedings of the National Academy of Sciences of the USA* **93** 15508–15511) and Logothetis, Leopold, and Sheinberg [1996 *Nature (London)* **380** 621–624]. Kovács et al showed that observers can obtain one-colour percepts when presented with chromatically rivalrous stimuli, even when there are targets of two different colours in each eye. In this study we investigate whether other attributes, in addition to colour, can drive interocular grouping, and how they interact.

We extended the 'patchwork' rivalrous stimuli (Kovács et al) to study how colour, orientation, spatial frequency, and motion can group interocularly, and how they interact in grouping. Gabor patches are used, because they allow conjunctions of attributes to be formed systematically. To study the ability of an attribute (or a combination of attributes) to group interocularly, we induce rivalry by virtue of interocular differences in that attribute (or combination), and keep the other attributes fixed in both eyes' images. The main advantage of these stimuli is that they enable us to decorrelate the effects of eye competition and percept competition in binocular rivalry. The data show that colour is the most powerful attribute in grouping, and that combinations are stronger than single attributes. Overall, the results indicate that similarity in low-level attributes can drive interocular grouping, and that binocular rivalry follows complex rules of perceptual organisation that cannot be accounted for by eye suppression alone.

- ◆ **Memory and binocular visual direction**
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It has been shown by a number of investigators that perceived binocular direction (BD) could be changed by varying the contrast ratio between the left and right images of a target. In this and certain other cases, the former simple idea that BD is the average of the two monocular directions (MD) fails to predict BD correctly. As an alternative, Mansfield and Legge (1996 *Vision Research* **36** 27–41) suggested that a weighted average of modified MD signals be calculated

with weights depending on respective image contrasts. However, in experiments including not only ordinary (monocularly recognisable) but also cyclopean (monocularly imperceptible) targets, we have found that there exist (at least) two principally different mechanisms responsible for calculation of BD and that one of these mechanisms is contrast-dependent while the other one is contrast-independent (Rozhkova et al, 1995 *Sensory Systems* 9 46–57). The first one probably corresponds to the model of Mansfield and Legge but the second one (which determines perception of cyclopean targets) has other specific properties. In a new series of experiments based on the same paradigm (to align a test target with a control one under conditions of varying interocular contrast ratios for the test stimuli), we have found that perceived direction of a cyclopean target (coded by Julesz's random-dot stereogram) could be manipulated by memory. It appeared that if, in a given series of measurements, the random-dot patterns for the test targets were chosen at random from six samples, the results were independent of the contrast ratio, but if one and the same random-dot pattern was used many times throughout all the series of measurements, and the subject could memorise the texture of the target, perceived direction became dependent on contrast ratio as in the case of monocularly recognisable targets. One of the possible explanations of this effect is the secondary activation of the first BD mechanism, which usually does not process cyclopean targets.

◆ **Scaling of frontoparallel surfaces by vertical disparities: effects of field size, location, and eccentricity**

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Since the pattern of horizontal disparities created by a frontal surface depends on the distance of the surface from the observer, additional information about distance is needed in order to judge whether a surface lies in a frontal plane. Rogers and Bradshaw (1995 *Perception* 24 155–179) showed that both vertical disparities and vergence angle can be used to scale the curvature of surfaces in a horizontal direction. In the present experiments, we measured the extent of frontal plane scaling as a function of the location and eccentricity of the vertical disparity information. Observers were presented with a series of random-textured stereoscopic surfaces with vertical disparity information appropriate for surfaces located at distances between 28 cm and infinity. The observer's task was to vary the pattern of horizontal disparities until the surface appeared to lie in a frontal plane. The stereoscopic images were masked to reveal either a circular, or an annular, or a rectangular patch with dimensions between 10 deg and 70 deg. Maximum scaling was found for the 70 deg diameter circular patch; it decreased by 50% when the patch was masked down to 20 deg in diameter. Scaling remained at over 80% when the central 60 deg of the display were masked. Scaling was reduced more when the horizontal width of the rectangle was made smaller than when the vertical height was made smaller. Vertical disparities are most effective for frontal plane scaling when they are present in more eccentric regions of the visual field, especially in a horizontal direction.

◆ **Influence of peripheral on central stereopsis: an induced depth tilt effect**

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A large rotating black/white sector disk (58 deg diameter) viewed with a neutral density filter over one eye is perceived as tilted in depth according to the Pulfrich phenomenon. But with fixation on a centrally located vertical bar (7 deg in length), the disk is perceived as vertical while the central bar is perceived as tilted in the opposite direction. This effect remains even if the central 38 deg portion of the disk is occluded leaving a peripheral annulus 10 deg in width. At an optimal rotation speed of 45° s^{-1} and a filter of 2 log units, the inter-individual perceived tilt of the bar ranges between 5° and 10° as measured by nulling out the illusory tilt by adjustment with a joystick. Variable errors were extremely small and corresponded well with central stereoscopic resolution. The amount of illusory tilt depends on the speed of disk rotation and filter density, and its direction on the relation between the direction of motion and the filter-covered eye. The effect is not limited to Pulfrich-induced stereotilt: When the disk was stationary but physically tilted in depth, the induced tilt on the central bar corresponded to about 50% of the physical tilt. This effect, in turn, could be cancelled or enhanced by rotating the tilted disk and inducing an appropriate Pulfrich effect. With monocular viewing no induced depth tilt occurs. The results are interpreted in terms of a stereoscopic induced effect operating beyond the known peripheral limits of stereopsis.

◆ Colour as input to stereopsis

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Neural structures carrying information concerning stereopsis belong to the magnocellular subsystem of the visual pathway. Regarding the magnocellular system as insensitive to colour, one would expect a high threshold for chromatic stimuli to evoke stereoscopic depth perception. In the present study, a stereogram together with an equiluminant background was generated on a colour monitor. The monitor was calibrated by a tristimulus colorimeter before each experimental session. The chromaticity coordinates of both stereogram and background could be varied in small steps. The author and two naive subjects participated in the experiments. Two patterns of three vertical bars formed the stereogram which was viewed through a stereoscope. With binocular fusion, the spatial arrangement of the bars gave rise to a horizontal, crossed or uncrossed, disparity of 10 min arc for one of the bars. Accordingly, this bar appeared to float either in front of, or behind, the other two, provided the colour difference between the stereo pair and the background was large enough. Under equiluminant conditions, the minimal colour difference necessary to evoke a depth perception exceeded the just noticeable colour difference at the chromaticity coordinates chosen ($x = 0.265$; $y = 0.499$) by a factor of only 3 to 4. In control experiments, the use of an optical system to compensate ocular chromatic aberrations did not measurably alter the results. These findings indicate that colour has an input to stereopsis which is stronger than a purely magnocellular system could provide.

◆ Why do some people take a long time to see complex random-dot stereograms?

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Some observers take a long time to see the appropriate surface shapes depicted in complex random-dot stereograms (RDSs) whereas others report seeing them quickly. We have hypothesised that this may be due in part to some observers being more affected than others by the cue conflicts that are typically present in RDSs, for which disparity is often at odds with accommodation, texture, and outline shape cues.

We report two experiments in which we investigated whether a measure of dominance of texture/outline cues over disparity cues in stereograms of ridges could predict latencies to see RDSs of 'wedding cakes' viewed from above. Latencies were measured for correctly reporting the number of layers in the wedding cakes. The ridge cue dominance index was obtained by using amplitude judgements of convex parabolic vertical and horizontal ridge stereograms embodying texture/outline vs disparity cue conflicts (Buckley and Frisby, 1993 *Vision Research* 33 919–934). In the first experiment ($N = 38$) disparity cues in the wedding cakes were depicted with inconsistent dot texture elements, ie the dots signalled flatness as there were no density differences between the cake layers. Observers giving greater weight to texture/outline in the vertical-ridge amplitude task showed significantly longer latencies to the wedding cakes. In a second experiment with different observers ($N = 35$), 18 were shown wedding cakes with textures consistent with disparity (diamonds drawn with correct perspective and density) and 17 saw the same disparity cues carried by inconsistent textures (diamonds signalling flatness). Large and significant correlations were found between the cue dominance index from vertical ridges and the latencies to wedding cakes depicted with inconsistent textures: observers with higher texture/outline cue dominance showed longer latencies. This result was remarkable given the lack of any readily apparent differences between the consistent and inconsistent textures in the wedding-cake stimuli. Equivalent correlations for wedding cakes depicted with consistent textures were small and nonsignificant. We conclude that individual differences in latencies to complex RDSs can be partly explained by differences in observers' susceptibility to texture/disparity cue conflicts embodied in those RDSs.

OBJECT AND FACE RECOGNITION

◆ Successive versus simultaneous processes in the recognition of visual patterns

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In earlier experiments with known nonverbal figures that subjects had to memorise, we found that, at the beginning of practice, recognition probability fell with increasing number of elements in a figure. Thus, the recognition process obeyed the principle of successiveness (Gurčiņienė, 1993

Perception 22 Supplement, 50–51). In order to localise the successiveness at the lower levels of visual information processing, we investigated how the recognition probability for unknown patterns depended on their complexity. Test patterns were nonverbal geometrical figures consisting of four, five, six, seven, or eight vertical and horizontal line-segments. The sequence of each trial was as follows: a sound signal for attention fixation; the test pattern (10 ms); an individually determined interstimulus interval (20–125 ms); the masking pattern (200 ms); a pause (0 s, 0.5 s, 1.5 s, 2.5 s, or 4.5 s); three sample patterns. Subjects were asked to identify which one of the three sample patterns presented was the test figure.

No dependence of the recognition probability of unknown figures on their complexity was found. We suppose that, in our experimental situation, the feature extraction from the stimulus is a simultaneous process, but the matching of extracted features with information from long-term memory is carried out successively.

◆ **Thresholds for identification of shape**

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Shape thresholds of geometrical figures have been found equal in cases when both the shortest and the longest linear dimensions of different stimuli were the same [Gutasukas et al, 1994 *Perception* 23 Supplement, 43]. The regularity depended neither on colour, nor on size, nor on spatial orientation of the stimuli. In the present study we have checked this result with five different stimuli, which had a central symmetry. Circles, squares, equilateral triangles, pentagons, and hexagons were taken for the psychophysical measurements of the increment shape thresholds. The stimuli, as bright filled objects, were shown on the dark screen of the optical stimulator. Monochromatic light (wavelength 552 nm) was used for the stimuli. As the area of the stimuli increased [from 8 to 1157 (min arc)²], the threshold decreased gradually. Five curves, running in parallel, were obtained in a certain order: squares, hexagons, circles, pentagons, and triangles, if seen from top to bottom. The data obtained demonstrate that the thresholds for identification of shape are different if various figures are of equal area, and they are the same if the figures are of equal height. This supports the idea that certain spatial frequencies of the two-dimensional spectra of the stimuli and the shape thresholds may be interrelated variables.

◆ **A model of shape recognition and categorisation**

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To recognise a previously seen object, the visual system must overcome the variability in the object's appearance caused by factors such as illumination and pose. It is possible to counter the influence of these factors, by learning to interpolate between stored views of the target object, taken under representative combinations of viewing conditions. Routine visual tasks, however, typically require not so much recognition as categorisation, that is making sense of objects not seen before. Despite persistent practical difficulties, theorists in computer vision and visual perception traditionally favour the structural route to categorisation, according to which forming a description of a novel shape in terms of its parts and their spatial relationships is a prerequisite to the ability to categorise it. In comparison, we demonstrate that knowledge of instances of each of several representative categories can provide the necessary computational substrate for the categorisation of their new instances, as well as for representation and processing of radically novel shapes, not belonging to any of the familiar categories. The representational scheme underlying this approach, according to which objects are encoded by their similarities to entire reference shapes (S Edelman, 1997 *Behavioral and Brain Sciences* in press), is computationally viable, and is readily mapped onto the mechanisms of biological vision revealed by recent psychophysical and physiological studies.

◆ **Temporal correlations in presentation order during learning affects human object recognition**

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The view-based approach to object recognition supposes that objects are stored as a series of associated views. Although representation of these views as combinations of 2-D features allows generalisation to similar views, it remains unclear how very different views might be associated together to allow recognition from any viewpoint. One cue present in the real world other than

spatial similarity, is that we usually experience different objects in temporally constrained, coherent order, and not as randomly ordered snapshots. In a series of recent neural-network simulations, Wallis and Baddeley (1997 *Neural Computation* 9 883–894) describe how the association of views on the basis of temporal as well as spatial correlations is both theoretically advantageous and biologically plausible. We describe an experiment aimed at testing their hypothesis in human object-recognition learning.

We investigated recognition performance of faces previously presented in sequences. These sequences consisted of five views of five different people's faces, presented in orderly sequence from left to right profile in 45° steps. According to the temporal-association hypothesis, the visual system should associate the images together and represent them as different views of the same person's face, although in truth they are images of different people's faces. In a same/different task, subjects were asked to say whether two faces seen from different viewpoints were views of the same person or not. In accordance with theory, discrimination errors increased for those faces seen earlier in the same sequence as compared with those faces which were not ($p < 0.05$).

◆ **Scene recognition after active and passive learning**

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Most research on visual recognition has been carried out on isolated objects with the main finding being that for certain classes of objects recognition strongly depends on the views learned during training. Recognition of scenes, ie structured environments, is rarely studied, possibly because of the difficulty involved in isolation and control of pertinent cues. We can overcome such problems by using computer graphics to model structured environments where training or learning is facilitated by active explorations with the use of VR technology.

We are trying to determine whether there exists the same degree of view-dependence in scenes as has been found for objects. We do this by using a single, sparsely decorated, yet structured room with which subjects familiarise themselves. This learning process can take two forms: either active or passive. In the active case, subjects can manoeuvre in a restricted set of directions in order to find 'hidden' coded targets. In the passive case, fifty 2-D views of the room are presented to them in random sequence with some views containing embedded targets which they have to acknowledge. Correct responses and response latencies of eighteen subjects in each condition were recorded in subsequent (old/new) recognition tests. Performance for recognition from familiar directions was similar after active and passive learning (eg approx. 80% hits). However, we found that active learning facilitates recognition from unfamiliar directions (d' active = 0.96; passive = 0.22). This superior performance after active learning could be due to the increased availability of 3-D information (eg from motion parallax during movement). We are therefore testing this using binocular disparity as a depth cue during passive learning.

◆ **Going beyond the information given: seeing versus seeing as**

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Variations in how we interpret ambiguous figures indicate that how a visual stimulus is perceived is determined by both its 'objective' visual pattern and the particular attitude we adopt towards it, ie what we see the stimulus as (Chambers and Reisberg, 1992 *Cognitive Psychology* 24 145–174). We report two experiments in which (i) ambiguous figures and (ii) natural scenes have been used to examine the relationship between how an image is perceived and what that image means to an observer.

In experiment 1 we used 'invertible figures' (images which when inverted portray different objects) to test two groups, (i) upright, and (ii) inverted orientation, on a recognition task involving distorted versions of the original stimulus. We found systematic differences between the two groups such that the meaning attributed to the original image determined how it was remembered. In experiment 2 we asked how prior experience affects perception. We measured rock-climbers' and non-rock-climbers' thresholds for detecting (i) non-meaningful visual pattern changes (surface changes), and (ii) meaningful changes in terms of climber affordances (deep changes). We found that climbers had lower thresholds for detecting deep changes and higher thresholds for detecting surface changes, compared with non-climbers. In contrast with the explanation based on the incomplete mental image (Chambers and Reisberg, loc. cit.), we propose that such differences are due to differences in attitude adopted towards the original stimulus, and these in turn determine what types of change can be discerned. In other words, what is important is not what is seen but how it is seen.

◆ **The role of visual field position in object recognition**

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Visual recognition of objects is generally assumed to be independent of the location in the field of view. Experiments have shown, however, that for stimuli such as random-dot clouds recognition can be severely affected by retinal displacement (Foster and Kahn, 1985 *Biological Cybernetics* 51 305–312; Nazir and O'Regan, 1990 *Spatial Vision* 5 81–100; Dill and Fahle, *Perception & Psychophysics* in press). In a series of new experiments, we tested whether similar shortcomings of translation invariance can be obtained also with more natural-looking objects. For that purpose, we tested human subjects with 3-D animal-like shapes that had been employed previously in studies of rotation invariance (Edelman, 1995 *Biological Cybernetics* 72 207–220). Some of our experiments included same–different discrimination, while in others the subjects had to label the briefly displayed stimulus with one of two possible labels. In both tasks, translation invariance was found to be incomplete: performance was significantly reduced when object memory had to be transferred to new locations. This positional specificity parallels the imperfect generalisation of recognition over rotation in depth, reported in the past years by many research groups. Similar to those findings, our present results suggest that the mechanisms of visual object recognition may be view-based rather than object-based. As before, these results have implications concerning the various theoretical approaches to the understanding of recognition currently under consideration.

◆ **Detecting and identifying mirror-symmetric letters in the periphery: A test of the equivalent-size hypothesis**

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If the visual mechanisms underlying form perception scale similarly with eccentricity, then performance in regions of different eccentricity should be characterised by a single function of the form $f(s/e)$ where s is a spatial variable, like size or spatial frequency, and e is a parameter that represents the local scale at that eccentricity. This formulation implies that performance at a given size s_0 and eccentricity should be identical to that at a size $s_1 = s_0 e_1 / e_0$, at a different eccentricity, where e_0 and e_1 are the local scale parameters for the two eccentricities. We refer to this as the equivalent-size hypothesis. We tested the equivalent-size hypothesis by measuring contrast thresholds for detection and identification of four mirror symmetric letters (b, p, d, q) for a series of sizes at each of three eccentricities (2, 4, and 8 deg). Psychometric functions were obtained for each size and eccentricity with the use of a spatial, 4-alternative forced-choice, double-judgment technique. First, observers specified at which of four positions around the fovea the stimulus appeared. Then they responded with the letter name. At each eccentricity, contrast thresholds for detection and identification as a function of size were described well by a power function. A single power function scaled for eccentricity was able to account for either the detection or the identification behaviour, and a single scaling parameter for the two tasks would not suffice.

◆ **Identifying facial images in the visual periphery**

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Identification sensitivity for four different faces was measured at the fovea and in the periphery to find out whether foveal and peripheral visual performance in this complex spatial task can be made equivalent simply by changing image magnification. Identification sensitivity was measured as a function of image magnification. The lowest contrast for identification was determined by a 4AFC method. Observers indicated via the keyboard which of the four faces was presented on the CRT screen. The images were shown monocularly at the fovea and at 2.5, 5, and 10 deg eccentricities in the nasal visual field of the right eye (eccentricity measured from the right-hand edge of the image).

If scaling is successful, the foveal and peripheral sensitivity vs size functions collapse together when shifted along the size dimension only (Watson, 1987 *Journal of the Optical Society of America A* 4 1579). Although the foveal and peripheral sensitivity functions could be superimposed, they

did not fully superimpose without also shifting them in vertical direction, as foveal sensitivity at largest sizes was slightly superior to that of any eccentric location. Thus, size scaling alone was not adequate for this task, in agreement with the contrast sensitivity results of Valeton and Watson (1990 *Perception* 19 Supplement, 393). In this identification task, performance deteriorated towards the periphery at approximately the same rate as visual acuity, when the size corresponding to half-maximal sensitivity at each eccentricity was used as a measure.

◆ **Different spatial scales for different face categorisations**

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When people categorise complex stimuli such as faces, they might flexibly use the perceptual information available from the visual input. Three experiments were run to test this hypothesis with two different categorisations (gender and expression) of identical face stimuli. Stimuli were hybrids (Schyns and Oliva, 1994 *Psychological Science* 5 195–200): they 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 the fine spatial scale. In experiment 1 we tested whether a gender vs an expression categorisation task tapped preferentially into a different spatial scale of the hybrids. Results showed that expression was biased to the fine scale, but that gender was not biased. In experiment 2 the same task was replicated, following a learning of the identity of the faces. It was then found that gender also became biased to the fine scale. In experiment 3 the expression task was changed to an identification of each expression to establish whether this could revert the scale biases observed in experiments 1 and 2. Results suggest that different categorisations of identical faces use different perceptual cues. This suggests that the nature of a task changes the representation of a stimulus.

◆ **Categorical effects in the perception of familiar faces**

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Photographs of morphed faces were shown to close friends of portrayed individuals. Three tasks were used: localisation of a morphed target on the continuum between the two original faces, simultaneous same–different discrimination of face pairs separated by a 20% morphing step (AB task), and sequential classification of the same pairs (ABX task). Localisation data were plotted against morph coefficients. Evidence of categorical processing was provided by steeper functions for upright vs upside-down faces.

In the AB task, intermediate faces were discriminated better than faces separated by the same morphing step but closer to one original. This was confirmed in a control experiment where the participants were unfamiliar with portrayed individuals and were unlikely to process our stimuli categorically. The superiority of intermediate faces in the AB task was attributed to a nonlinearity of continua generated by the morphing procedure, and used as a baseline to evaluate ABX classification data. Also in the ABX task, intermediate faces, those straddling the categorical boundary, were classified more accurately than faces located on the same side of the boundary. However, the superiority in classification accuracy was larger than the superiority in discrimination accuracy operationalised by the AB task, as predicted by the categorical perception hypothesis.

◆ **One eye is usually centred horizontally (and near the golden section vertically) in portraits over the past 500 years**

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Although the eyes are a key feature of facial portraits, compositional rules for the placement of the eyes relative to the frame are obscure. Two hypotheses of eye position in the portrait frame were compared: that the pair of eyes were symmetrically placed or that one eye was centred in the frame. Portraits were defined as paintings of a single person from the waist up without other dominant objects or animals in the scene. From all artists represented in seven source-books on portraiture over the past five centuries (eg from van Eyck to Picasso), the first portrait in which both eyes were visible was analysed (170 portraits). Horizontal and vertical eye and mouth positions were measured as a proportion of frame width and height.

The eyes in portraits tend to cluster horizontally around the centre vertical, with one eye centred in a normal distribution with a σ of only $\pm 5\%$ of the frame width. The binocular mean had a bimodal distribution implying that one or other eye was usually centred. Conversely, the eye height distribution was not centred vertically but peaked close to the classic golden ratio of 0.618 (where the smaller portion has the same ratio to the larger as does the larger to the

whole), with virtually no eyes below the vertical centre. The mouth distribution was much broader than that of the centred eye. The eye centring with an accuracy of ~ 1 eye width seems not to be mentioned in art criticism, which suggests that unconscious functions operate in our aesthetic judgements.

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READING

◆ Complexity of Chinese ideograms is related to the number of sampling elements

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Two sets of psychophysical experiments were carried out to find a qualitative measure of the complexity of visual images. The stimuli were 15 Chinese ideograms of the same size. In experiment 1, observers were asked to rate the complexity of images. In experiment 2, for each stimulus the threshold size was determined, defined as the smallest size for which the perceived quality of the image was the same as for large (2 deg) stimuli, ie all details were clearly seen and the stimuli had the same contrast. The measured threshold sizes were in the range 7.9–27.6 min arc. Analysing the data further, we found that for some ideograms the sizes of the minimal details (strokes, dots) corresponded to the resolution limit (1 min arc). Some ideograms contained parts with parallel stripes forming quasi-gratings. The distances between stripes at threshold were 1.8 min arc which corresponds to the tuning frequency of the highest spatial frequency channel (Wilson et al, 1983 *Vision Research* 23 873–882).

The average order of ideograms sorted by degree of complexity was similar to the order according to threshold size. Thus we found a direct correspondence between the complexity of an object and a description in terms of the minimal number of elements needed to preserve the quality of a reduced image. Our results are in agreement with concepts of complexity expressed as a number of details in objects as suggested by Landolt and Snellen, or as a number of spatial-frequency channels as suggested by Ginsburg (1971 *IEEE Proceedings* 283–290).

◆ Text font affects reading speed at a low luminance but not at a high luminance

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We are beginning a series of studies in which we shall investigate which characteristics of text fonts may be successful in allowing text to be read with different kinds of degradations that may be experienced by low-vision patients. As a first attempt to simulate one of the problems that certain patients might have, we measured reading speeds with two proportionally spaced fonts at a high photopic luminance (146 cd m^{-2}) and at a very low luminance (0.146 cd m^{-2}). We used the RSVP (rapid serial visual presentation) reading method, which eliminates the need for scanning eye movements. The two fonts were 'Swiss', a simple sans-serif font, and 'Dutch', a serif font similar to Times Roman, both presented at the 20/80 size; letters were white on black, with a contrast of 0.94. Subjects were young, normally sighted high-school and optometry-college students. The reading speed results from 47 subjects were as follows, for four conditions: high luminance, Swiss 531 and Dutch 540 words min^{-1} ; low luminance, Swiss 479 and Dutch 429 words min^{-1} .

At the high luminance, there is no significant difference between reading rates. There is a significant advantage for the Swiss font at the low luminance: $p = 0.005$.

There may be a significant difference in reading speed with different fonts when the patient's perceptions are degraded by disease and/or aging processes. Other parameters to be investigated with this method include contrast, size, blur, and visual field position. The simulation results will suggest parameter values to test on low-vision patients.

◆ In congenital nystagmus, reading text with rapid serial visual presentation (RSVP) reduces mean eye velocity

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Most low-vision subjects read text faster from an RSVP display than they do with full PAGE reading. This result has been confirmed with a group of subjects with congenital nystagmus (Plass and Yager, 1995, paper presented at ARVO). The present experiment was intended to determine whether reading with RSVP also reduced the severity of the nystagmus, which may have contributed to the faster reading rates.

Eye position and velocity of congenital nystagmats were recorded with an infrared reflection technique, sampled at 40 s^{-1} . Recordings were made in three conditions: (1) passively viewing a blank computer monitor; (2) silently reading full PAGE text at a size of approximately four times Snellen acuity; (3) silently reading RSVP text at the same size, at about $200 \text{ words min}^{-1}$. We found that: (1) in frequency histograms of instantaneous eye velocities at 25 ms intervals, the full width at half height was an average of 60% smaller for RSVP reading compared to PAGE; (2) with a window of ± 5 to 20 deg s^{-1} , depending on the subject's baseline eye velocity, the number of epochs that were at least 75 ms in length, and the total time in these epochs, were significantly greater during RSVP reading than during PAGE reading or viewing a blank screen. We conclude that reading with RSVP reduces nystagmus, and may contribute to greater reading speed. [Supported by a grant from the Schnurmacher Institute for Vision Research.]

◆ **The LEO-reading test: A set of nine reading charts with M-units**

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Visual acuity, near-distance visual acuity, and reading ability all depend on the minimal angle of resolution. Visual acuity is defined as the inverse of the minimal angle of resolution, measured at a distance of 4–6 m, and expressed in units of $(\text{min arc})^{-1}$. Near visual acuity and reading ability are measured at reading distance. The preferred reading distance is not the same for every subject. A practical way to combine character size and reading distance is to use the 'M-unit' for text size and 'Dioptre' for the reading distance. For example, a character size of 1 M at a viewing distance of 1 m corresponds to a visual acuity of 1. A character size of 0.20 M at a viewing distance of 25 cm ($= 4 \text{ D}$) corresponds to a visual acuity of $1/(0.2 \times 4) = 1.25$.

In the rehabilitation institute we had a need for reading charts with different text blocks for repeated testing (OD, OS, OU, and at various illumination levels). Furthermore we wanted text blocks with a comparable layout and reading difficulty. Such reading charts exist in other languages and we preferred to adopt a similar design, together with the M-unit and Dioptre notation. We composed the text and tested the equivalence of text blocks by measuring the reading speed of young (aged 18–27 years) and old (aged 60–69 years) subjects. We present the resulting set of nine reading charts with a plea for general use of the M-unit and Dioptre notation for near-distance visual acuity and reading ability assessment in visually impaired people.

SYMPOSIUM

LOW VISION

◆ **Vision with age-related macular degeneration**

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Visual Science at the Norwegian University of Science and Technology (NUST) includes activities in visual psychophysics and electrophysiology, clinical tests of vision, and low vision. In recent years the Tambartun National Resource Centre for the Visually Impaired, in cooperation with NUST, has been encouraging applied projects aimed at improving the quality of life of people with low vision. One such project, headed by Per Fosse, is devoted to the study of the visual capacity of elderly with age-related macular degeneration. Systematic assessments are made of acuity, contrast sensitivity (CS), colour vision, visual field, dark adaptation, and optimal illumination levels for reading and orientation. We report on some preliminary results for ten clients, which is about half the number of anticipated participants in the project. The differences in performance of the individuals that we have seen so far are large, particularly concerning their lighting requirements. Some clients preferred a relatively restricted optimum range of illumination, while others required very high levels. All clients profited from these extensive tests in orientation in real-life settings and in reading. Different CS tests and acuity measures have been compared in the course of the study, and some of these data are also presented.

◆ **Head-mounted video camera system in testing multihandicapped children with low vision**

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Vision testing with multihandicapped children is more difficult than with normally developed children: the child's ability to concentrate in the test situation is often markedly reduced, or

the child is not capable of communicating with the examiner in the normal way owing to deficiencies in motor skills, hearing, or speech. Often observation of the eyes and face is difficult because of bent-down sitting position caused by poor control of head and neck.

By recording the test situation on a video tape it is possible to analyse the child's reactions afterwards more accurately. Our video system consists of a miniature video camera attached to the head of the child with a small mirror in front of the camera to provide a picture of the eyes. Simultaneous recording of the eye movements and the fixation target is possible by adjusting the position of the mirror so that it covers the view of the camera only partially. With the aid of a second, conventional video camera, we get an overview picture of the test situation. This picture is combined with the image of the miniature camera on the child's head and recorded on a video tape.

With our video system it is possible to see the eye movements even when the child's head is bent-down or the child is moving in the examination room. It also allows the use of full-field stimuli covering the eyes as in examination of the optokinetic nystagmus. The eye-hand coordination can also be monitored on the video tape.

◆ **Visual consequences for children with early acquired lesions to the optic radiation—vision 'without seeing'**

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The brain lesion caused by perinatal hypoxic-ischemic events at gestational age 24–34 weeks has a typical anatomical pattern known as periventricular leukomalacia (PVL). PVL affects the corticospinal tracts, causing spastic diplegia and/or the geniculocalcarine tract, causing visual impairment. Computer tomography or magnetic resonance imaging are the methods of choice for diagnosing PVL. This lesion is the cause of visual impairment in 20% of all visually impaired children in a Swedish population of children born in 1989–1995.

The visual deficit in PVL is characterised by decreased vision with crowding (an inability to resolve linear optotypes, while single optotypes of the same size may be identified) and visual field defects, further complicated by perceptual and cognitive problems. A relatively high single optotype acuity may lead to overestimation of visual function. Oculomotor impairments with strabismus and nystagmus are common findings. Colour vision is often preserved and used by the children as one of many strategies to sort out an otherwise chaotic visual world. Instead of looking, these children listen carefully, talk a lot and remember well, and sometimes use tactile information to solve visual tasks. They easily get lost in new surroundings and they recognise known faces among others only by the voice and the colour of the clothes. Reading is often difficult. This group of visually impaired children call for adaptation of education and habilitation to manage daily life, mobility, and reading.

◆ **Reading with visual field defects**

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The influence of different visual field defects on the reading performance was examined with potential adaptive strategies to improve the reading process in mind. By means of an SLO, the retinal fixation locus (RFL) was determined with the use of single targets and text, and eye movements scanning the text were recorded on video tape. Additionally, eye movements were monitored by an Infrared Limbus Tracker. Visual fields were assessed by the Tübingen Manual and/or automatic perimetry. Normal subjects, and patients with central scotomata, ring scotomata, and hemianopic field defects (HFD) were examined.

The main pathological reading parameters were an increase of saccade frequency and regressions per line, and a decrease of reading speed. In patients with field defects involving the visual field centre, fixation behaviour is significant for regaining reading ability. In absolute central scotoma, the lost foveal function promotes eccentric fixation. The remaining problem is insufficient resolution of the RFL, which can be compensated for by magnification of the text. In patients with insufficient size of their reading visual field, due to HFD and ring scotoma, it is crucial that they learn to use a new RFL despite intact foveolar function.

Preconditions for reading have been found to be: (1) sufficient resolution of the RFL, (2) a reading visual field of a minimum extent, and (3) intact basic oculomotor function. In patients with visual field defects involving the centre, a sensory-motor adaptation process is required: the use of a new RFL as the new centre of the visual field and as the new zero point for eye-movement coordinates.

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POSTERS

BINOCULARITY

◆ **Computation of binocular eye position from vertical disparities with the use of probabilistic place coding**

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Stereoscopic vision exploits the fact that points in a 3-D scene will in general project to different locations in the images in the left and the right eye. The differences in retinal locations, measured horizontally and vertically, are called horizontal (H) and vertical (V) disparities respectively. Their size is affected by the positions of the eyes which determine the viewing geometry parameters, that is distance to the fixation point (d) and the angle of gaze (g). H is also affected by the depth of the scene point relative to fixation distance, which is why one can recover 3-D scene structure using binocular vision. Achieving metric reconstruction requires knowledge of d and g to allow for their influence on H . Computational analyses have shown that d and g can in principle be recovered from V because of its relative insensitivity to scene depth variations. As d and g are the only two unknowns in the equation for V , in theory only two measurements of V (at suitable retinal locations) are needed. A practical system, however, dealing with noisy images composed of many points, needs to pool information from measurements of V at numerous retinal locations. A place-coding algorithm of the Hough transform type is well suited to this purpose (S A Peek, J E W Mayhew, J P Frisby, 1984 *Image and Vision Computing* 2 180–190), but it has not hitherto been used in a way which deals appropriately with measurement noise. We describe how this can be done and demonstrate with computer simulations greatly improved estimation of d and g as well as improved robustness to noise. The new method also permits the solution of an important aspect of the stereo correspondence problem—that of finding epipolar lines.

◆ **Suprathreshold motion sensitivity and ocular dominance**

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Sensitivity to visual motion was investigated by measuring the time required to deflect a joystick in the direction of movement. The stimulus was a small light spot that moved at 2 deg s^{-1} for 1 s to the left or right; observation was binocular. Two conditions were tested: (A) a single moving stimulus suddenly appeared 5 deg left or right of fixation; (B) two stimuli were constantly visible at 5 deg left and 5 deg right of fixation before one of them began to move. Walls' (1951 *A.M.A. Archives of Ophthalmology* 45 387–412) pointing test and a subset of Coren's (1993 *Bulletin of the Psychonomic Society* 31 1–3) laterality questionnaire were used to identify two groups of eight subjects (matched for age, handedness, and gender) with pronounced dominance of their left or right eyes, respectively. The data suggest a higher suprathreshold motion sensitivity (better visuomotor performance) for right-eyed persons who were, on average, faster by 11 ms (A) and by 32 ms (B) than left-eyed persons. Although a similar effect of ocular dominance on suprathreshold motion sensitivity had been shown before [Schlykova and Ehrenstein, 1993, in *Gene–Brain–Behaviour* Eds N Elsner, M Heisenberg (Stuttgart: Thieme) page 439], this was for monocular comparison of the dominant versus non-dominant eye. Here, however, eye-dominance effects still occur with binocular vision, especially in condition B where motion has to be detected from two mirror-symmetric stimulus locations.

◆ **Measurements of the relative tilt of corresponding vertical and horizontal meridians in the two eyes as a function of elevation and eccentricity in the visual field**

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Helmholtz first reported that when the horizontal meridians of the two eyes are aligned, the vertical meridians of the two eyes are tilted outwards (with respect to each other) by approximately 2° . We adapted Nakayama's technique (1977 *Proceedings of the Society of Photo-Optical Instrument Engineers* 120 2–9) using the minimal apparent motion of alternating dichoptic images to measure the relative tilt of corresponding vertical and horizontal meridians located up to 20 deg away from the fovea. Observers were presented with the alternating dichoptic images of a pair of dots or a pair of extended lines which had a relative tilt (binocular orientation difference) of between -5° and $+5^\circ$. The images were alternated at a rate of 0.2 Hz . Observers were asked to select the pair of images which produced the smallest amount of apparent orientation change. The vergence angle of the binocularly visible fixation point was varied between 28 cm and infinity. On the assumption that minimal apparent motion is a valid indicator of binocular correspondence, the corresponding vertical meridians of the two eyes remained offset

by around 2 deg even when they were located 20 deg eccentrically. The corresponding horizontal meridians remained approximately aligned even when they were elevated by up to 20 deg. Corresponding horizontal meridians were altered when the vergence angle was changed but corresponding vertical meridians were unaffected for most individuals. With the eyes held in an elevated position, both vertical and horizontal meridians were altered by a similar amount when the vergence angle was altered, indicating a change in cyclovergence.

◆ **Does the gamma distribution refer to an underlying mechanism in binocular rivalry?**

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Thirty years ago, Levelt (1967 *British Journal of Psychology* 58 143–145) fitted the distribution of dominance times in binocular rivalry with the gamma distribution (the distribution function of waiting times for N random events with process speed λ). Ever since, the gamma distribution has been used to describe the rivalry phase durations, without an explanatory underlying mechanism being given. Although Levelt suggested λ to be proportional to the stimulus strength (eg contrast, luminance, blur, amount of contour) and N to be 'successive neural spikes', this suggestion has never been tested. The purpose of this study was to test whether or not N and λ represent characteristics of the observer and the stimulus, respectively.

To collect the data as accurately as possible, we performed a large number of measurements involving different designs and stimuli. In contrast to previous experiments, collected data were not pooled but were compared within each subject. We tested the hypothesis by collecting time intervals from subjects responding to numerous conditions in which disk–ring stimuli were varied in contrast, blur, or amount of contour in one eye.

◆ **Binocular rivalry in half-occluded regions of coloured stereograms where the background is a drifting grating**

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Binocular rivalry in half-occluded (HO) regions was studied with coloured stereograms where the background was a drifting grating. The coloured stereograms consisted of a central square-shaped region, a background, and HO regions. The central square-shaped region was coloured green, and was presented in either crossed or uncrossed disparity. The background was a stationary or drifting vertical grating consisting of white and grey bars. The HO regions were coloured blue, and the luminance was fixed or was changed consistently with the drifting grating in the background. Subjects judged the disappearance of the HO regions, and the cumulative time of disappearance was measured during a 30 s period. When the luminance of the HO regions was fixed against the background of a drifting grating, the disappearance time was the same as for the static grating background. However, when the luminance of the HO regions was modulated consistently with the drifting background grating, the cumulative disappearance time was significantly less than when the background was a static grating. These results suggest that the HO regions escape binocular rivalry when they correlate with the background.

◆ **Volume perception with binocular viewing**

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We reported earlier that the binocularly unpaired region plays an essential role in the perception of the volume of a solid object (Idesawa, 1991 *Japanese Journal of Applied Physics* 30-4B L751–L754). We have investigated this volume perception using both illusory and physical objects. The illusory objects used in the tests were of two types, either with or without binocularly unpaired contours. The physical objects used as stimuli in the present experiments were half-moon-shaped textured cylindrical objects, one with and one without a binocularly unpaired region. A rectangular probe was placed beyond the object, and subjects were asked to adjust its position in depth until they felt that the probe just touched the object.

We found that the chosen depth settings were systematically 'behind' the objects with unpaired parts, while they were almost 'correct' for the objects without unpaired parts. In the former case, subjects thus had the impression that the volume extended further back. We also found that the rim of an object is important for volume perception, especially for objects without textures. A typical example is an imaginary cone occluding two disks, one a little larger than the bottom surface and placed near the bottom, the other a small one located just beyond the top. A complete illusory cone with volume (just like a 'Santa cap') could be seen!

STEREOPSIS, DEPTH, AND 3-D◆ **Disparity information in the peripheral visual field for pattern perception**

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Although it is known that stereo-acuity declines with increasing eccentricity of the targets, it is not clear how we use disparity information in the peripheral visual field for pattern perception. To examine this question, we investigated pattern perception by restricting the area that presented stereo or luminance information in the periphery.

We measured the reaction time for recognising a letter defined by binocular disparity or by luminance in a random-dot display. We restricted the area containing the specific information (disparity or luminance) using an eye-contingent window technique. Disparity or luminance information was thus present only inside a window centred on the fixation point. Observers viewed the display with free eye movement. The magnitudes of the disparity and luminance contrast were chosen so as to give the same reaction times when the area containing the pattern information was not restricted. Eye movements were measured by a limbus-tracking system and the signal was fed into a computer for real-time control of the window position.

The reaction time increased as the window size decreased. The increase in reaction time, however, was steeper for the stimuli defined by disparity than for the stimuli defined by luminance. We conclude that disparity information in the periphery is used for recognising a pattern and is more effective than luminance information for a given window size.

◆ **Estimation of lengths and angles of kinematically induced amodal rods**

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In previous experiments computer-generated stimuli consisting of two dots moving on semi-elliptical paths, either on inner or on outer halves of ellipses, induced percepts of amodal rods rotating or oscillating in 3-D space, with the two stimulus dots as the visible endpoints. The task was to estimate the length and the angle of inclination of the perceived rod in a specified position. Results of the experiments were only in partial accord with the frontoparallel principle (Johansson and Jansson, 1968 *Perception & Psychophysics* 4 165-170). A geometrical model was proposed to explain the perceived characteristics of the rod. The model was tested in two experiments. In the first experiment the length and the angle of inclination of the perceived rod were varied. Subjects were sensitive to changes of length and angle. Furthermore, when they overestimated the length, they underestimated the angle. In the second experiment the curvature of the semi-elliptical paths was increased. Compared to the first experiment, estimations of lengths increased but estimation of angles were not significantly different.

◆ **Relevant perceptual factors in stereoscopic displays: Image disparity, convergence distance, and focus length**

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Traditionally, visually relevant factors in stereoscopic displays have been investigated within a performance-oriented framework, focusing on the veridicality of depth perception. However, for some applications, most notably in the areas of broadcasting and entertainment, an appreciation-oriented approach seems to be more relevant. Within this framework, we investigated the influence of image disparity, convergence distance, and focus length on the subjective assessment of depth, naturalness of depth, and quality of depth (or preference).

Twelve observers with normal or corrected-to-normal vision and good stereopsis viewed a fully randomised presentation of stereoscopic still images that varied systematically in image disparity (six levels of camera base difference: 0, 4, 8, 12, 16, and 24 cm), convergence distance (two levels: 1.30 m and 2.60 m) and focus length (two levels: 10 mm and 20 mm). Each observer was asked to rate, in separate counterbalanced sessions, his/her impression of depth, naturalness of depth, and quality of depth.

The results indicate that observers prefer a stereoscopic presentation of images over a monoscopic presentation. A clear optimum was found at 4 cm image disparity for subjective judgments of naturalness and of quality. Depth judgements increased up to an image disparity of 12 cm, a result that is in line with earlier psychophysical literature. There was an effect of focus length only at extreme image disparities. An effect of convergence distance was also found that can be

adequately explained by rescaling to match the effective visual disparities. Although there was a strong linear correlation between naturalness and quality ($r = 0.96$), a small but systematic deviation could be observed. This deviation was best modelled by a linear quality model that incorporates both naturalness and depth.

◆ **Illusory contours do not capture stereopsis—they just constrain the depth spreading**

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If vertical cut-out sectors defining a Kanizsa square are given crossed disparity, the illusory figure appears in depth. Such an illusory figure can pull the background pattern inside the illusory figure to the same depth. It has been assumed that illusory contours are necessary for this phenomenon, which is called stereo capture (Ramachandran, 1986 *Perception & Psychophysics* 39 361–373). However, we noticed that the vertical cut-out sectors of the inducing figures ('pacmen') are not the only structures that can capture the background texture. The rows of background dots that are enclosed between the disparate vertical cut-out sectors also have unambiguous stereoscopic depth. Thus it might be possible that the disparate rows alone capture the background texture. To investigate our hypothesis we created a stereogram in which the inducing figures were removed. It consisted of a dotted background texture and four areas devoid of dots. The dotless areas corresponded to the areas which were occluded by the original inducing figures. Because of this, the top and bottom rows inside the central area were in crossed disparity.

According to our results (a) depth capture also occurred without illusory contours; (b) when illusory contours were not present, the depth of the disparate rows spread more often to other areas. Usually the depth spread first to the central area of the figure and after that horizontally to other areas of the figure. Therefore, we conclude that illusory contours do not capture stereopsis—they just constrain the depth spreading.

◆ **Effects of stereo and motion manipulations on measured presence in stereoscopic displays**

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Methods of assessing presence, a sense of 'being there' within a displayed virtual environment, include post-test subjective measures, discrimination tests, and monitoring reflexive responses. Each is limited—either they do not provide a measure of temporal variation, are not feasible with current display technology or are overly content-specific.

A measure of presence derived from the method of continuous evaluation (ITU-R, Recommendation BT.500-7, revised, "Methodology for the subjective assessment of the quality of television pictures", 1995) has been used to overcome these limitations. The results of two experiments are presented. Those of the first experiment established that the methodology is usable under the optimal viewing conditions for the 20 inch stereoscopic TV display upon which our stimuli were presented. It compares within-subject variation on continuous TV picture quality ratings under two viewing conditions—at six picture heights in the light (standard for quality evaluations) and at two picture heights in the dark (optimal stereo TV viewing). The second experiment investigated the effects of manipulations of the visual parameters of stereo, scene motion, and observer-based motion on participants' presence evaluations within edited sections of a stereoscopic film. The results provide support for theories predicting that the extent of sensory information available to a participant is one of the factors determining presence.

◆ **Continuous assessment of presence in stereoscopic displays**

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Presence, a sense of 'being there' evoked by a display, can be regarded as a concept of central importance in the evaluation of broadcasting and entertainment services in general and virtual reality applications in particular. Subjective methods of assessing presence that have either been used or proposed to date do not provide a measure of temporal variation in observers' presence. To overcome this limitation, we have applied the method of continuous assessment (ITU-R, BT 500-7) to the measurement of presence. Thirty observers (twelve at IPO, eighteen at UoE) with normal

or corrected-to-normal vision and good stereo-acuity viewed a stereoscopic film. While watching, observers were asked to continuously rate their perceptions of depth, naturalness and presence. The stimulus material varied considerably in the amount and strength of the visual cues presented over time. This enabled us to investigate whether the extent of sensory information presented to an observer was a determinant of presence, as proposed by Sheridan [1992 *Presence: Teleoperators and Virtual Environments* 1(1) 120–125].

The results, which were very similar across two independent laboratories, suggested that continuous assessment provides a promising methodology for the subjective assessment of temporal variation in the observer's sense of presence. Further, increasing the extent of sensory information presented to an observer may enhance the sense of presence, provided the depth cues introduced are consistent and within natural bounds. [Note: First and second author in arbitrary order.]

◆ **Completion under isoluminance**

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It is known that monocular depth cues become much less effective under isoluminance. One of these depth cues, occlusion, gives rise to surface completion. A study is reported in which the loss of completion under isoluminance was tested.

A pair of horizontally aligned bars of different lengths is detected automatically in a display filled with pairs of bars of the same length. The pair is detected serially, when vertical bars are placed over the gaps between the pairs. Because the vertical bars are occluders, and the pairs of horizontal bars are aligned, completion behind the vertical bars takes place and the two parts together behave perceptually as a single bar.

We used this knowledge to measure completion under isoluminance. When occlusion is lost under isoluminance, we expect that an occluding surface, isoluminant with the background, will not lead to object completion and as a consequence, the pair with unequal lengths of the parts will pop out. Using this procedure we have demonstrated that completion is lost under isoluminance.

◆ **The impact of 3-D video endoscopy on binocular perception and visually guided manipulation**

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Monocular video endoscopic systems are established in the clinical routine of surgical endoscopy. The introduction of 3-D video systems could improve visualisation of the intracorporeal operating site because of the stereoscopic depth information. The goal of our investigations has been to quantify the influence of this visualisation technology on visual perception, on visually controlled endoscopic manipulations, and on the intraoperative performance, including ergonomic and psychophysical aspects. These results are used to define guidelines for improvement and for the integration of such systems into clinical routine so as to achieve optimal support of the medical team.

The comparison of 2-D and 3-D video endoscopic systems showed a general improvement in the performance of endoscopic procedures. However, 30%–50% of the users had perceptive problems with 3-D endoscopy. To study the problems quantitatively, we compared the case of stereoscopic visualisation with the real situation of direct view onto the specific objects. The users with problems had insufficient binocular depth perception of stereoscopic images for visual discrimination tasks, although their depth perception of real objects was good. Analysis of their eye movements showed significant differences compared with those of users with good binocular depth perception of stereo images. In particular, there were differences in the relation of vergence movements and accommodation. When we compared visually guided manipulations under stereoscopic video sight and direct view, we found the overall manipulative performance of all users to be the same, but the users with problems showed a lower performance in general.

The experimental design and the results are discussed in detail.

◆ **Effects of position and contour blurring of cast shadow on depth perception**

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Shadows are known as a qualitative depth cue. Moreover, dynamic changes of shadow position were recently reported to lead to the perception of a looming object, suggesting that shadows

can be a quantitative depth cue as well. If this is the case, the position and/or contour blurring of shadows would contain quantitative depth information; however, the visual system needs to assume a direction and/or size of a light source to use this information. To examine this idea, we measured perceived depth between a target object and a background for different positions and different contour blurrings of the shadow of the object on the background. The displays were 2-D drawings (18 deg $\times$ 18 deg) produced by computer software on a CRT screen and seen through a 3 cm $\times$ 3 cm aperture in a sheet of black cardboard. The position of the shadow to the lower right of the object was varied in terms of angular distance between the two. The contour of the shadow was blurred by Gaussian filters of different diameters. We found that perceived depth increased with angular distance, but was independent of contour blurring. This result indicates that the visual system makes an assumption on the direction of the light source, but not the size of it, to derive the amount of depth from the object's shadow.

◆ **Convex grouping impedes detection of stereoscopic depth**

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When two image regions are separated by an occluder, the strength of their perceptual grouping behind the occluder depends in part on the possible smoothness of the hidden contour completions (ie, Gestalt 'good continuation'). We consider if grouping strength also depends on whether the contour completion is convex or concave.

We hypothesised that the stronger the grouping between two such regions, the harder it is to resolve their relative stereoscopic depth; and employed accordingly an objective method of relative depth discrimination. The stimulus was in stereo. A horizontal bar in the centre of the image occluded two pairs of planar regions parallel with the image plane. One pair assumed a convex (oval) shape behind the occluder, the other pair a concave (hourglass) shape. The regions in one pair had a slight depth difference. The task was to detect which pair was not coplanar.

The convex grouping impeded detection of stereoscopic relative depth (73% vs 86%, $F_{1,10} = 8.66$, $p < 0.02$). This held even when the convex completion boundaries were less smooth than the concave ones, a result opposite to predictions by Gestalt 'good continuation'. In a control experiment, the stimulus was viewed with the 'occluder' in the background, so grouping was no longer possible. No difference between the two pairs was found.

Our results suggest that convexity, known to play a role in figure/ground segmentation, is also significant in perceptual grouping, and can even win out over 'good continuation'. We also propose an objective method of depth discrimination to study perceptual grouping in general.

◆ **2-D affine transformations cannot account for human 3-D object classification**

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Converging evidence in object recognition has shown that the performance of human observers depends on their familiarity with the appearance of the objects. The degree of this dependence is a function of the inter-object similarity in the object set. The more similar the objects are, the stronger is this dependence, and the more dominant is two-dimensional (2-D) image information. However, the extent to which 3-D structural information is used still remains an area of strong debate. Previously, we showed that all models that allowed 2-D rotations in the image plane of independent 2-D templates were unable to account for human performance in recognising novel object views. Here we derive a closed-form Bayesian ideal observer that gives rise to probably the best possible performance when applying 2-D affine transformations (translation, rotation, scaling, stretching, and other linear transformations) to stored 2-D templates. In addition, we compare human performance with a closed-form derivation that finds the best match between a 2-D template and a 2-D image under 2-D affine transformations. We also compare human performance with a generalised radial basis functions model. This model establishes optimal performance for learned 2-D templates, and then adjusts the variance of its radial basis (Gaussian) functions to achieve best possible performance for novel views of individual objects. We demonstrate that none of these models can account for human performance in 3-D object recognition. Human statistical efficiency for novel views is higher than for learned views, which suggests that 3-D structural information is used by human observers.

◆ **Sequential stereopsis demonstrated with high-bandpass spatial-frequency filtered textures**

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Enright (1995 *Vision Research* 36 307–312; 1995 *Perception* 24 Supplement, 32–33) described a simple piece of equipment for demonstrating a highly sensitive perceptual mechanism that he called sequential stereopsis. The apparatus prevents 'conventional' stereopsis mechanisms from operating as it prevents the comparisons of disparities of targets seen at the same time. Enright suggested that the mechanism of sequential stereopsis relies on a comparison of disparities before and after isovergent saccades between fixations of the two targets. In his apparatus, the observer makes fixations between two textured targets seen behind a pair of viewing ports and the task is to adjust these to appear equidistant. The principle upon which the apparatus depends is the use of textures whose elements cannot be resolved in peripheral vision at the eccentricity determined by the target separation. Enright used a fine sandpaper for this purpose. We describe two similar experiments ($N = 3$ in both) with high-bandpass filtered textures which eliminate any possibility of the low-spatial-frequency content of sandpaper textures playing a role. Our results corroborate Enright's general conclusions on sequential stereopsis while at the same time showing that high-bandpass textures do not give wholly similar results to sandpaper. Possible reasons for this are discussed.

◆ **The assignment of absolute and relative depth in constructing a 3-D mental model from viewed orthographic displays**

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Constructing the 3-D mental structure from viewed 2-D orthographic displays may require establishing both the relative depth relation (RD) between adjacent areas in the orthographic displays and the exact magnitude of absolute depth (AD) for a given area. We examined the processes of depth assignment involved in 3-D model construction by asking subjects to mentally imagine the 3-D object portrayed by a pair of orthographic projections, and then choose among four alternative isometrics the one that matched the imagined 3-D model. One alternative corresponded to the previously shown orthographic views (ie, target). The other alternatives were distractors that differed from the target in terms of RD, AD, or both.

Results from four experiments show that (a) when subjects mistook a distractor for target, they were more likely to misidentify the distractor sharing the same RD with target but with different AD, than to misidentify the distractor sharing the same AD but with different RD; (b) subjects could shorten their solution time by 40% without greatly compromising their performances when times available for imagining 3-D models were reduced in proportion to those consumed in a self-pacing condition. The implications of these results are discussed in terms of a model in which an observer may try to decide the relative depth prior to figuring out the exact absolute depth, although it is necessary to consider both aspects of depth assignment in the construction of 3-D mental models.

◆ **Curvature biases in stereoscopic vision**

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The reliability of in-depth curvature judgements for linear elements was studied with stereograms that contained two linear targets and a background representing a hemisphere. The targets were arcs facing to the left or to the right, like parentheses. Some formed binocular pairs with (type 1) or without (type 2) in-depth curvature. The others were monocular (type 3). The hemisphere in the background was generated by a random curve (Ninio, 1981 *Perception* 10 403–410); it was either concave (hollow) or convex. The arcs had their binocular centre in the plane of the centre of the hemisphere. Each stereogram contained a type 1, and either a type 2 or a type 3 target. Subjects had to judge the hemisphere curvature, then the in-depth curvature of the targets in 32 different stereograms covering all curvature combinations. There were about 15% errors on type 1 targets, and 80% of these occurred when both the hemisphere and the target were convex, the target being perceived as concave, by transparency through the hemisphere. There were also about 15% errors on type 2 targets, but spread among all situations, the trend being to perceive them as slightly concave. The monocular stimuli (type 3) were judged to be frontoparallel in 70% of the cases. Otherwise, there was no directional bias except for monocular arcs on the

nasal side, in conjunction with a concave background. Then, the perceived in-depth curvature was in the 'generic' direction predicted by associating the monocular arc in one image with a straight vertical segment in the other image.

◆ **Temporal integration of alternately exposed monocular images of a random-dot stereogram**

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J R Ewald and O Gross (1906 *Pflügers Archiv* CXV 514–521) reported that monocular half-images presented alternately can be fused to a stereoscopic percept. The situation is like looking through a fence close to the eyes, with picket and gap widths being identical to the interpupillary distance. Though vision is monocular, an observer moving fast enough parallel to the fence will have stereoscopic vision of the scenery behind it. Little is known about the limits of this integrating mechanism.

In two experiments, LCD shutter glasses were used to control the viewing conditions of the anaglyphs of a random-dot stereogram. Binocular fusion was supported by a visible binocular fixation mark and a frame around the display. Subjects were eight male and three female students with normal stereoscopic acuity. They were instructed to press a key as long as they could perceive a global figure portrayed in the stereogram (25 min arc disparity). In experiment 1, monocular exposures to the right and the left eye followed each other without pauses. Psychophysical procedures were used to determine the frequency threshold for stereopsis. A breakdown frequency of 2.5 Hz was found, for descending as well as ascending series. Transferred to the concrete example of a fence, the result corresponds to a pace of 0.32 m s^{-1} , with an interocular distance and a fence measure of 63 mm. In experiment 2, alternating monocular exposures of 100 ms duration were separated by variable pauses. Stereopsis disappeared with 8 ms pauses (ascending), and 17 ms pauses (descending). Results may be attributed to integrating mechanisms of binocular cortical cells, rather than to retinal processes (afterimages).

◆ **Stereo depth perception uses first-order phase and second-order position disparities**

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We examined the nature and variety of cues underlying the use of binocular disparity in depth perception. Stimuli were Gabor patches (Gaussian-windowed sine-wave gratings, $2 \text{ cycles deg}^{-1}$) and horizontal disparities were produced by varying the phase of the carrier grating or the position of the Gaussian envelope ($\text{SD} = 24 \text{ min arc}$), or both. Disparity varied from -180° to $+180^\circ$ of carrier phase (or the positional equivalent) at carrier orientations 0° , 30° , 60° or 90° from vertical. Direction and magnitude of perceived depth were reported in a 2IFC procedure where the comparison interval contained a zero disparity vertical patch. Use of different orientations allowed phase disparity to be distinguished from horizontal position disparity.

Two main conditions were tested. (1) In the 'patch' condition carrier and envelope disparity varied together, and perceived depth was found to vary monotonically with positional disparity. When carrier disparity was ambivalent (at $\pm 180^\circ$ phase disparity) or zero (with horizontal orientation) perceived depth followed envelope disparity, showing that 2nd-order (envelope) disparity alone can produce depth. (2) When carrier disparity was varied with the envelope held fixed, perceived depth and discrimination thresholds depended on phase disparity rather than horizontal position disparity, lending support to the phase-based theory of De Angelis, Ohzawa, and Freeman (1995 *Perception* 24 3–31). At the larger crossed disparities (-90° to -180°) depth reversed sign, suggesting a role for occlusion cues as well as phase and envelope disparity in stereo depth coding.

◆ **Conflicts with extraretinal and monocular cues cause the small range of the induced effect**

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A vertical magnifier before one eye causes the induced effect: an apparent rotation of frontal surfaces toward that eye. The rotation required to restore apparent frontoparallelism grows linearly up to $\sim 4\%$ magnification, but plateaus at 8% . We examined the cause of the plateau.

Horizontal disparities (quantified by horizontal size ratios, HSRs) are ambiguous indicators of surface slant. Various retinal and nonretinal signals can allow veridical slant estimation from HSR, sensed eye position, vertical disparities (vertical size ratios, VSRs), and monocular cues. Vertical or horizontal magnification of one eye's image alters the natural relationships among HSR, VSR, eye position, and monocular cues. We argue that the induced-effect plateau is caused

by conflicts between these means of estimating slant. A plateau is not observed in the geometric effect because some of the conflicts do not occur with horizontal magnification. Two experiments were designed to test this hypothesis. When strong monocular cues were present, plateaux occurred at $\sim 8\%$ magnification in the induced, but not the geometric effect. When monocular slant cues were made useless, induced-effect plateaux were abolished. Even with strong monocular cues present, plateaux in the induced effect were eliminated when eye position was consistent with the vertical magnification in the retinal images. The smaller range of the induced effect can only be understood from consideration of all the signals involved in slant estimation.

◆ **When stereopsis does NOT improve with increased contrast**

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It is well established that stereoacuity for conventional (1st-order) stimuli improves with increasing contrast, with slopes ranging from -0.5 to -1.0 on log-log axes (Halpern and Blake, 1988 *Perception* 17 483–495; Legge and Gu, 1989 *Vision Research* 29 989–1004). In the experiments reported here we used a variety of stimuli (Gabor patches, amplitude-modulated gratings, and 1-D noise patches) and tasks (stereoacuity and D_{max}) to determine if 2nd-order stereopsis shows a similar square-root dependence, or if the contrast relationship is relatively flat as observed for monocular localisation tasks (Hess and Holliday, 1992 *Vision Research* 32 1085–1097). Where possible, stereopsis was assessed with the use of the same stimuli for both 1st-order and 2nd-order stereopsis to ensure that the resulting data would be comparable. In all cases where stereopsis was based on 2nd-order processing there was little or no influence of contrast on performance; the average slope was approximately -0.15 . In comparison, more typical slopes near -0.75 were obtained under 1st-order test conditions.

The indifference of 2nd-order depth perception to changes in stimulus contrast not only supports the proposed distinctiveness of the two types of processing but places constraints on theoretical and computational models of 1st-order and 2nd-order stereopsis. Further, these data support the proposal that the same nonlinear position estimate is used for monocular localisation of nonabutting targets, and for 2nd-order stereopsis.

◆ **Anisotropic temporal integration in the perception of stereoscopic corrugations**

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Disparity sensitivity for horizontal depth corrugations increases with exposure duration for presentations of up to 1 s (Tyler, 1990 *Vision Research* 30 1877–1895). To extend the work of Parton et al (1996 *Perception* 25 67) we investigated whether differences existed in the effects of exposure for corrugations at different orientations. Disparity thresholds were measured for horizontal, vertical, and diagonal gratings with spatial frequencies ranging between $0.1 \text{ cycle deg}^{-1}$ and $0.8 \text{ cycle deg}^{-1}$, as a function of stimulus duration. Stimuli were presented for exposures of between 50 ms and 32 s, and were followed by a random disparity mask, which served the important function of disrupting further processing of stimulus disparity. Thresholds were greatest for vertical gratings. This effect was particularly pronounced for the lowest frequencies. In all conditions, disparity sensitivity improved as exposure duration increased, and continued to do so for all durations tested. For vertical and diagonal gratings, log-log plots of threshold against time showed a linear relationship with a slope of -1 up to 1.0 s, after which time improvements in sensitivity reduced. Horizontal gratings showed a similar relationship, but with thresholds ceasing to decrease significantly after 0.5 s. Temporal integration limits differ with surface orientation, and represent another important difference in our ability to detect and encode depth in stereoscopic surfaces.

◆ **Differences in processing time for stereoscopic inclination and slant**

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Howard and Kaneko (1994 *Vision Research* 34 2505–2517) suggested that stereoscopic slant and inclination may be encoded on the basis of relative expansion and shear, respectively. We investigated the perception of surfaces with diagonal axes of tilt, having components of both inclination and slant. Latencies for the perceptual resolution of slant can be several times those for inclination (Gillam et al, 1988 *Journal of Experimental Psychology* 14 163–175). Using a forced choice methodology, we measured the time required to discriminate surfaces with horizontal, vertical, and

diagonal axes. Subjects were presented with random-dot stereograms of planar surfaces, with or without a visual reference. Stimuli were followed by a random-disparity mask. In the first experiment, subjects discriminated the direction of slant or inclination of surfaces rotated in depth by 45° from frontoparallel. A staircase procedure was used to find the shortest presentation time for which surfaces could be correctly discriminated. With a visual reference, both surface types could be discriminated with brief presentations. Without a reference, mean thresholds were 300 ms for inclined surfaces, and 2.5 s for slanted surfaces. In a second experiment, temporal thresholds were measured for surfaces with diagonal axes. In one condition, subjects discriminated between surfaces with equal inclination, but opposite slant. In the second condition, surfaces had equal slant, but opposite inclination. Surfaces differing in inclination could be discriminated with shorter presentations than surfaces differing in slant. These results support the notion that surfaces are encoded in terms of components of inclination and slant.

◆ **The task-dependent use of binocular disparity and motion parallax under natural viewing conditions**

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The use of binocular disparity and motion parallax information was compared in three different psychophysical tasks for which natural viewing and physical stimuli were used. Natural viewing may be an important factor in interpreting experiments which have addressed the ability to use disparity and parallax both separately and in combination (see Frisby et al, 1996 *Perception* **25** 129–154). The stimuli consisted of configurations of three bright LEDs carefully aligned in the horizontal meridian and presented in darkness. The distance of the middle LED (flashing at 5 Hz) could be adjusted along the midline in accordance with the tasks which included: (i) a depth nulling task, (ii) a depth matching task, and (iii) a shape task—match base/height of triangle. Each task was performed at two viewing distances (1.5 and 3.0 m) and under four different viewing conditions: (i) monocular-static, (ii) monocular-moving, (iii) binocular-static, and (iv) binocular-moving. Note that the different tasks differ in their dependence on viewing distance, and the available cues for viewing distance differ between viewing conditions. Four observers made ten settings in each condition at each distance. Observers, as expected, performed badly (bias and accuracy) in all tasks in the monocular-static condition. Nulling was accurate in the other viewing conditions (no estimate of viewing distance required). Performance was best in the matching task (ratio of viewing distances) but although binocular-static was significantly better than monocular-moving performance in this and in the shape task (absolute distance required), there was no additional improvement in the binocular-moving condition. Results show that observers can recover structure accurately from parallax or disparity information in real-world stimuli.

◆ **Poor recovery of surface orientation from VDU images predicts poor performance in laparoscopic surgery**

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There are large, and vitally important individual differences in aptitude for laparoscopic ('keyhole') surgery. Intuitively it seems likely that an important component is ability to recover the shape of 3-D structures (patients' internal organs) from displays on a video monitor. The issue was studied empirically with PICSOR, a test based on research reported by Cowie and Byth (1995 *Perception* **24** 118–119). Subjects adjust a probe, which consists of a rotating arrowhead, until it appears perpendicular to a specified surface in a simple object (a sphere or a cube). Both probe and surface are depicted on a VDU screen. Measures of apparent slope are derived and related to the theoretical slope. Eight trainee surgeons were studied. They completed a battery of simulated laparoscopic tasks and the PICSOR tests. Two measures of performance on PICSOR were derived from simple regressions relating apparent and theoretical slope, R , and the slope of the fitted line. These were used in multiple regressions to predict performance in the simulated laparoscopic tasks. Performance on the PICSOR cubes task predicted performance in simulated surgery ($F_{2,7} = 29.5$, $p = 0.0017$). Both measures (R and slope) contributed significantly. Relationships are probably not linear. One subject performed very badly on both PICSOR and simulated operations. If his data are excluded, both low R and high slope would appear to be related to poor laparoscopic performance. The nature of the area makes large-scale studies difficult, but the data suggest that they ought to be conducted.

ILLUSIONS

◆ Phenomenal shrinkage and expansion of visual surfaces: Is amodal completion a factor?

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When two figures intersect, two apparently paradoxical size effects take place (Kanizsa, 1979 *Organization in Vision* chapter 11): (1) the partly occluded figure looks shorter than an identical unoccluded figure, and (2) the modally visible parts of the occluded figure look larger than identical isolated parts. Kanizsa explains such effects as due to amodal completion.

Three experiments were carried out by the method of adjustment to test this explanation: two were devoted to the shrinkage effect, and the third one was devoted to the expansion effect. The first experiment exploited the properties of the so-called Helmholtz–Ratoosh law (T-shaped vs Y-shaped junctions) to test whether a figural shrinkage is also present in a pattern in which amodal completion should not occur. The second experiment was aimed at checking whether stereoscopic displacement of the ‘occluded’ figure ‘behind’ or ‘in front of’ the ‘occluding’ one is capable of affecting the amount of shrinkage. In the third experiment the Helmholtz–Ratoosh law was again applied to the expansion. The results of all three experiments converge in showing that the amount of shrinkage of the ‘occluded’ figure as well as the amount of expansion of the ‘modally visible’ parts are not affected by the presence or the absence of amodal completion. We conclude that both the shrinkage and the expansion effects are due to other factors, probably the same factors as those that affect classical optical-geometrical illusions, such as the Oppel–Kundt or the horizontal–vertical illusions.

◆ Can illusory figures be transparent and opaque at the same time?

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A simple and convincing way of explaining illusory figures is based upon the idea that the visual system would infer the presence of an occluding object when the inducing pattern shows features, such as indentations or interruptions, that can be logically explained as due to an occlusion. This kind of explanation implies (a) that an illusory figure should be prevented from occurring if there is no logical need for it, and (b) that the illusory figure must be opaque to be effective as an occluding object. It can be shown, however, that illusory figures can emerge even when there is contrary evidence to occlusion. A special kind of stereoscopic Kanizsa-like pattern superimposed onto a picture (an Escher engraving) is capable of inducing clear illusory figures (two rectangles). In this pattern, the illusory figures seem to be transparent with respect to the picture on the background, which remains fully visible through them, but act as opaque surfaces with respect to the inducers. The inducers are parts of a Necker cube which can be clearly seen only when its fragments induce the illusory rectangles, but disappears if the same fragments, being only outlined, are not able to induce them. If this outcome can be regarded as a demonstration that the Necker cube can be seen as an amodally completed object only when it virtually completes itself ‘behind’ the illusory rectangles, one would have to conclude that the same illusory surfaces can be transparent and opaque at the same time. This paradoxical result seems to challenge any interpretation of illusory figures as being due to an intelligent solution to a cognitive problem.

◆ Zooming diamonds: a new illusion, and a warning on the biological relevance of parallel projection

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A new illusion is described. Observers watch parallel projections of ‘diamonds’ (rhombi) tumbling in 3-D. The displays are generated by moving a viewpoint round a fixed rhombus on a trajectory with two components—a circle parallel to the plane of the diamond, and a superimposed change in elevation which varies sinusoidally. To a greater or lesser extent, depending on the phase of the sinusoid, elevation change is misinterpreted as ‘zooming’ in and out—though in fact the projection always corresponds to an object at a fixed distance. The illusion was devised to underline the questions surrounding the treatment of parallel projection in biological systems. The standard formulations considered in computational vision preclude the kind of size–distance trade-off that the illusion demonstrates, but they do imply that observers should be able to register the shape of an object from this kind of display. A less familiar formulation, ‘paraperspective projection’, allows size–distance trade-off as in perspective projection, but it suggests the shape of a lamina should be impossible to recover from motion. Stimuli which promote ‘zooming’ do weaken shape discrimination, but the trade-off is incomplete. A possible solution is that human vision picks out size change in a way that is appropriate when either object or motion path is

'friendly', but that misleads when awkward combinations occur. Certainly vision research should avoid assuming that the attractively simple consequences associated with standard parallel projection govern the way biological systems operate.

◆ **Categorical perception of illusory contour defined shapes**

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Categorical perception (CP) is the phenomenon when people are better able to distinguish between stimuli of different categories than between stimuli of the same category and it appears for innate and learned stimuli of various sensory modalities. We tested if CP occurs also for illusory contour stimuli. First, in an ABX paradigm the shape discrimination capacity of subjects was tested for convex ('fat') or concave ('thin') Kanizsa-square-like shapes (cf Rubin, 1996 *Perception* 25 Supplement, 3; pre-category-learning test). The proportion of correct responses and response latency were measured. Second, subjects were instructed that every stimulus belongs to either the 'fat' or the 'thin' category, and they were trained to categorise the individual stimuli using a 2AFC paradigm with corrective feedback until 90% of correct responses. Third, we measured the shape discrimination capacity of subjects, by repeating the first ABX paradigm (post-category-learning test). Comparison of the ratio of correct responses in the post/pre discrimination tests showed that discrimination of illusory shapes of different categories is enhanced but discrimination of members of the same category is made more difficult by category training. In a second experiment, by increasing the physical differences between the extreme 'fat' and extreme 'thin' stimuli (increased range of the opening-angle of the Kanizsa-square inducer pacmen), we made the categorisation task easier for the subjects and tested if discrimination capacity is altered by the modified difficulty of the categorisation task. We discuss the effect of difficulty on CP and the relation of illusory CP to that of real luminance contour stimuli.

◆ **Role of inducer length in the formation of the Ehrenstein illusion**

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We wanted to study the role of the length of the inducers in the Ehrenstein illusion and, particularly, the possible interdependence of inducer length and gap size in sustaining the illusion.

We used a subthreshold summation paradigm. As described previously (Tassi et al, 1995 *Perception* 24 127), the presence of an illusory contour reduces the threshold for detection of a real line superimposed on it. In agreement with the model of Grossberg and Mingolla (Grossberg and Mingolla, 1985 *Psychological Review* 92 173–211; Grossberg, 1994 *Perception & Psychophysics* 55 48–120), these authors suggested that the Ehrenstein illusion was generated by a bipole operator joining two line ends. In an Ehrenstein figure induced by four white lines, we varied the size of the central gap from 1.6 to 4 deg. The threshold of a white line joining the ends of two inducers was measured with a spatial alternative (left–right). The Ehrenstein figures involved either long (2.5 deg), or short (0.58 deg) inducers.

The result shows that whatever the length of the inducers, the threshold for detecting the real line increases with increasing gap size. The results obtained with short and long inducers were very similar. Moreover, in this experiment, the spatial limit of integration of the illusion occurs for a gap size of 2.4 deg: the detection threshold for the real line was significantly higher from this value. This result, consistent with previous research (Salvano-Pardieu and Bonnet, 1994 *Perception* 23 104), suggests that the length of the inducer is a factor less important than the gap size in the formation of the illusion.

◆ **Oppel–Kundt illusion and visual field anisotropy**

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Psychophysiological experiments are reported in which a combined influence of visual field anisotropy and the Oppel–Kundt illusion on length judgement was tested. The subjects adjusted the test interval of a stimulus to be equal with the reference interval in length. The stimuli—three dots or the Oppel–Kundt figure with ten dots within the filled half—were generated on the monitor. In the Oppel–Kundt figure, the filled half was considered as the reference interval, and the empty half as the test one. In sessions of the experiments, values of errors as functions of the size and orientation of the stimulus were measured. The reference interval varied within 14–150 min arc range, and the orientation was fixed in the 0°, 90°, 180°, or 270° position. The orientation of the test

interval varied from 0° to 360°, in 7° steps. The experiments with the three-dot stimuli yielded pure characteristics of visual field anisotropy, and the experiments with the Oppel – Kundt figure showed combined appearance of both the anisotropy and the illusion. The data demonstrate an algebraic summation of the two factors in a simultaneous manifestation. It is assumed that estimation of symmetry of the stimulus, in accordance to the bisector of its internal angle, provides discrimination of the length. Calculations have shown a satisfying confirmation of this assumption.

OBJECT AND FACE RECOGNITION

◆ Differential effect of object complexity on 2-D and 3-D matching processes

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Previously, we found that two matching processes work in parallel when an object is recognised from unknown viewpoints: the 2-dimensional (2-D) and the 3-dimensional (3-D) matching process. These processes were shown to differ in several respects, including recognition speed, generalisation range, and learning ability. We have now examined the effect of the complexity of an object on these two matching processes. We performed a recognition experiment where the subjects had to compare two sequentially presented images. The stimuli were objects that had different numbers of segments, presented for either 1.5 s (short condition) or 3.0 s (long condition). The different presentation times enabled us to separate the two processes, as 3-D matching requires a longer processing time.

We adopted the ability to generalise from a known view as a measure of the performance of each process. Under the 'short' condition, the generalisation range for objects of high complexity was almost the same as that for objects of low complexity. Under the 'long' condition, however, the ranges for objects differing in complexity were significantly different. Our interpretation is that the effect of complexity was mainly associated with the 3-D matching process. The matching performed by the 2-D process under a shorter duration may be a simple image-to-image matching without recourse to the 3-D structure of the object.

◆ Illuminant and viewpoint biases from embossed surfaces

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The human visual system uses a-priori constraints for the estimation of surface shape from images. We propose here a robust paradigm to study individual observers' assumptions about the illuminant and viewpoint positions.

In the study of illumination, the stimuli consisted of parallel, sinusoidally shaped, striped regions, alternating between wide and narrow. Narrow stripes alternating between white and black separated the uniform grey stripes, representing slanted edges in light and in shadow. The stimulus had the shape-from-shading ambiguity: either the wide or the narrow stripes could be seen as 'in-front', consistent with different assumed tilts of the illuminant. In a brief flash of a randomly oriented stimulus, observers stated whether the narrow or wide stripes appeared in the foreground. The results showed a strong bias for a light-from-above-left assumption (as in Howard et al, 1990 *Perception* 19 523–530; Sun and Perona, 1996 *Investigative Ophthalmology and Visual Science* 37 935). This bias was 20 to 30 deg to the left of vertical. Slower reaction times were obtained for more ambiguous figures.

The same shape judgment task was used with an unshaded stimulus where the only depth cue was image contour. The same curvy, striped figure was portrayed with image contours at the edges of the stripes, as well as surface markings orthogonal to the depth variation, resulting in a shape-from-contour cue. We have previously reported indirect evidence for a bias of viewpoint above the object, that is observers interpret surface normals as pointing upward (Mamassian, 1995 *Perception* 24 Supplement, 35). Our observers' shape judgments were consistent with this bias. [Supported by NIH grant EY08266.]

◆ From simple to complex or vice versa: Sequence effects on the detection of embedded figures

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In a series of studies concerning part – whole perception we have investigated effects of perceptual learning, and of systematically varied presentation orders on the detection of embedded figures. In the present study the effects of increasing and decreasing complexity orders on detection performance are reported.

Stimuli were 170 pairs of whole and part figures. Half of them were positive items, ie the searched part was contained in the (simultaneously presented) whole. The other half were negative items, ie the searched part was not contained in the whole. The difficulty of all figure pairs was determined from earlier data. On the basis of these difficulty parameters three presentation orders were created: (1) increasing difficulty (from simple to complex), (2) decreasing difficulty (from complex to simple), and (3) randomised order. Sixty subjects performed each of these tasks in three sessions separated by one week. Effects of practice and samples were balanced by permutating the order of the three tasks. The reaction times and error rates for all presentations were registered.

The results showed marked differences between the three tasks: The lowest mean reaction time was obtained in the presentation order with increasing difficulty. Error rate, on the other hand, was lowest in the decreasing-difficulty presentation order. For the random-order presentation error rate and reaction time was in between the other orders. Furthermore, differences in benefit from practice were observed between the three orders of difficulty. Results are discussed with respect to the question of how efficient search strategies may be learned and whether one can learn to bend the rules of Gestalt organisation if required.

◆ **Functional 'tunnel vision' in pattern classification learning**

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Visual pattern recognition has been defined in cognitive science as the ability to relate a perceived object to a learned categorical concept (see Rosch and Lloyd, 1978 *Cognition and Categorization* Hillsdale, NJ: Lawrence Erlbaum). In contrast, physiologists and clinical practitioners often prefer a low-level functional approach, where visual performance is characterised in terms of acuity, visual field, and contrast sensitivity. From a paradigmatic viewpoint, the former definition can be related to tasks of pattern classification, whereas the latter involves tasks of discrimination. We show that this dichotomy concerning perceptual tasks corresponds to dichotomous internal representations that observers develop in such tasks. For a common set of grey-level patterns (compound Gabor signals), we compared performance in classification and discrimination learning in foveal and extrafoveal vision. Learning speed for classification learning was found to be drastically reduced in extrafoveal relative to foveal vision. Discrimination learning of the same signals remained unaffected by viewing condition. Further analysis of the data in terms of a probabilistic prototype model (Rentschler, Jüttner, and Caelli, 1994 *Vision Research* 34 669–687) showed that internal representations acquired in extrafoveal classification learning are characterised by a distinct reduced perceptual dimensionality. The results suggest that internal representations underlying pattern classification and discrimination arise at distinct cortical levels, and that the former are developed within an extremely narrow visual field essentially restricted to the fovea.

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◆ **Psychophysiological basis for errors in identification of degraded geometric forms under conditions of high information uncertainty**

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Identification of ambiguous geometric forms by human subjects with brief experience or pre-knowledge of the stimulus may call upon Bayesian specialised mechanisms. Subjects were presented with a 2-alternative forced choice between a pair of incomplete geometric figures in conditions with common and varying components. Stimuli of 1, 3, 5, and 6 pixel acuity grades were displayed in iterative order in randomised blocks at 100, 200, 260, and 360 ms exposure times, rotated or upright, under local or global viewing. Analysis of probability of correct identification against stimulus intensity, acuity demand, and stimulus duration revealed: (i) sigmoid or dipper-shaped nonmonotonic psychometric functions; (ii) Poisson-like skewed binomial distributions of errors; and (iii) category-based dependence on the stimulus and its ambiguity. This is attributable to the high uncertainty constraints imposed on tasks sharing and also varying in their stimulus parameters and dimensions. Nonlinearities shown reflect category-based strategies and attention allocation, interactions as a drive for performance stability manifested in equalisation across sub-categories and invariances of errors, with acuity demand accounted for perhaps by mechanisms of differential attention allocation. Two sources of error are apparent: (i) possibly 'bottleneck of attention'-related and individually varying 'blink of attention', with small falls distributed across stimulus intensities, and (ii) 'lapse of attention' with large falls on easier tasks, and rightward-skewed deviations from normal Poisson-like binomial distributions ($p < 0.001$), the high correlation to performance effort suggesting an active process of pay-off.

◆ **The perception of transient structures**

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The phenomenon studied is the perception of well known structures, the elements of which are moving in the visual field and only briefly join together. Consider a horizontal bar traveling along the equator of the screen, and a capital letter F placed in the middle of the screen, with its foot in contact with the trajectory of the bar. There is a moment when the left end of the bar comes in contact with the foot of the F, producing a capital letter E. Preliminary observations show that an E is perceived only if the bar stops its motion for a considerable amount of time, some 120–150 ms. In this case a significant structure (the F) is transformed into another significant structure (the E). Other cases are under observation: a meaningless structure that becomes a significant one (an F completed by a bar that is traveling on its top), and a meaningless structure that remains meaningless (an upside down T constituted by a stationary vertical bar with its foot in contact with the trajectory of a moving horizontal bar). The phenomenon shows strong relations with other findings regarding the perception of a stop in the movement of an object, and the perception of a transition between two levels of brightness of the same object.

◆ **Symbolic meanings of computer-generated abstract forms**

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In experiment 1, symbolic meanings of 32 computer-generated abstract figures were rated by 27 subjects (undergraduates) on eleven semantic differential scales. The stimuli were basically generated by sine waves on a circular line. Random fluctuation was added to half of the stimuli. The stimuli varied in five physical parameters: sine-wave frequency, amplitude, linearity, regularity, and the height/width ratio of the whole figure. A factor analysis on the results of ratings on the semantic differential scales revealed four factors: evaluation, activity, lightness, and sharpness, which correlated with the physical parameters of the stimulus forms as follows: evaluation with regularity ($r = 0.830$), activity with frequency ($r = 0.806$), lightness with regularity ($r = 0.631$), and sharpness with linearity ($r = 0.782$). In experiment 2, another group (54 subjects) had to match ten abstract words: happiness, anger, surprise, fear, anxiety, creativeness, destruction, time, eternity, and loneliness, with sixteen abstract forms [half of the stimuli from experiment 1, with constant height/width ratio (1.00)]. These abstract words were also rated by a third group of 26 subjects on the semantic differential scales. The results indicated that forms and words that were matched with each other were rated similarly on the semantic differential scales, and indicated the validity of the symbolic meanings of the forms measured in experiment 1.

◆ **Recognition model with extension fields**

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A recognition model which defines a measure of shape similarity on the direct output of multi-scale and multiorientation Gabor filters does not manifest qualitative aspects of human object recognition of contour-deleted images in that: (a) it recognises recoverable and nonrecoverable contour-deleted images equally well, whereas humans recognise recoverable images much better; (b) it distinguishes complementary feature-deleted images whereas humans do not.

Adding some of the known connectivity patterns of the primary visual cortex to the model in the form of extension fields (connections between collinear and curvilinear units) among filters (a) increased the overall recognition performance of the model, (b) boosted the recognition rate of the recoverable images far more than of the nonrecoverable ones, (c) increased the similarity of complementary feature-deleted images, but not part-deleted ones. These correspond more closely to human psychophysical results. Interestingly, performance was approximately equivalent for narrow (± 15 deg) and broad (± 90 deg) extension fields.

◆ **Human efficiency in numeral recognition**

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Using a forced-choice method, we determined human contrast thresholds for recognising hand-written numerals. Digitised numerals were presented on a computer display with additive white static noise. The numerals were either unfiltered or were filtered to two-octave spatial-frequency bands of different centre frequencies varying from 1.2 to 17.7 cycles/object height. We had ten variations of each numeral representing the handwriting of different persons. Human performance

was compared with the performance of an ideal 'signals-known-exactly' (template matching) observer, and the results were presented in terms of efficiency. The highest efficiency for the band-pass filtered numerals was about 11% at centre frequencies of 3–5 cycles/object. The efficiency declined towards lower and higher centre frequencies so that at 1.2 cycles/object and 18 cycles/object the efficiency was about 4%. The efficiencies for unfiltered numerals were about 10%–14%, being thus slightly higher than or equal to the highest efficiency of the band-pass filtered numerals. If only a two-octave band of spatial frequencies contributed character recognition, as has been suggested previously, the unfiltered numerals would contain redundant low-frequency and high-frequency information. Band-pass filtered numerals of optimal centre frequency would contain less redundancy, and a larger proportion of contrast energy would be used. Therefore, efficiency for them should have been higher than for unfiltered numerals. Since this was not the case, it seems that human observers are able to use a relatively broad band of spatial frequencies in character recognition.

◆ **A comparative study of the spatial-frequency spectrum of different letter optotypes and its role in target recognition**

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We studied the contrast sensitivity functions (CSFs) in patients with different eye and brain diseases using a computerised sinusoidal grating test with a wide range of frequencies (0.4–19.0 cycles deg⁻¹), the Pelli–Robson chart and a new chart with frequency-filtered Snellen optotypes. The patients had different CSF curves with a decrease of contrast sensitivity in the low, middle, or high frequencies depending on their main disease (refraction anomalies, cataract, glaucoma, neuritis of optic nerve, brain tumours, etc).

Analysis showed that optotypes in the Pelli–Robson chart have a wide-range spatial-frequency spectrum, and optotype recognition is determined not only by low spatial frequencies. We find that the recognition of standard Sloan's optotypes is determined mostly by sensitivity in the range of 9.4–14.0 cycles deg⁻¹. At the same time we measured contrast sensitivity using the new filtered Snellen optotypes. Our calculations support our earlier suggestions that the new filtered optotypes have a narrow-band spatial-frequency spectrum, thus enabling selective measurement of contrast sensitivity in each narrow frequency band.

◆ **Gabor-based coding and facial similarity perception**

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Little is known about how facial representation in the face-selective areas of inferotemporal cortex is built up from the output of earlier visual areas such as primary visual cortex (area V1). We report work on a model of perceived facial similarity based on topographically ordered aggregates of localised, oriented, and spatial-frequency-selective receptive fields characteristic of V1 cells. The receptive fields are approximated with a set of Gabor filters. This Gabor-based code allows representation of the fine differences in texture and configuration needed for facial discrimination processes. Lyons and Morikawa (1996 *Investigative Ophthalmology and Visual Science* 37 910), showed that Gabor-based similarity is a good predictor of facial similarity for comparisons of fairly similar faces but not sufficient to model experience-dependent effects such as the 'other race effect'.

Here we report results of a study on the effects of image negation on facial similarity perception. Negation of image gray levels interferes with face recognition (Bruce and Lanton, 1994 *Perception* 23 803–822) while preserving 2-D facial-shape information. The Gabor similarity measure models non-endstopped complex cells of V1 and is not affected by image negation. One group of subjects judged similarity among a set of normal gray-scale facial images while another group judged similarity between negative images of the same stimuli. Agreement between the model and human subjects did not decrease with image negation. Moreover, human similarity ratings between negative faces were strongly correlated with those between positives. These results support Gabor-based similarity as a model for facial similarity perception.

◆ **Horizontal and vertical composite effects in novel faces**

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The composite effect, where the recognition of the upper half of a face is disrupted by a discrepant lower half relative to an isolated half-face, without a corresponding effect for vertical half-faces, provides a ready method of investigating configural information in face recognition. In previous studies purely photographic techniques have been used for composite construction. We investigated the effects of more face-like stimuli, constructed by morphing techniques.

Subjects were trained to identify frontal Japanese faces, and tested on recognition on marked upper, lower, left, and right halves, both as half-faces and with distractors. While response accuracy for the upper and lower composites was lower than those for the relevant halves, there was no such effect for the right-left composites. A familiarity design was used in the second experiment to replicate this result. In the third experiment quarter-faces (top left-bottom right facial quadrants) were used to control for the information present. We found a strong composite effect for the right-left composites, and weaker ones for the top-bottom and quarter composites. In the fourth experiment we examined whether this effect was dependent on the presence of the quarter-composites by presenting them in a second block but found no effect of this manipulation.

It thus appears that although there is a composite effect with faces composed in a shape-free manner, this effect is unstable. Under certain circumstances subjects may convert from a top-bottom relational processing strategy to a right-left strategy. The information used, even with a constant task, is dependent upon the variability of the images involved.

◆ **Judging the orientation of human faces: effects induced by varying the illumination**

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How do people estimate the orientation of other people's faces? We observed that two images of a face seen from the same orientation, but illuminated from different angles, appeared to have different orientations. The first experiment was designed to document and quantify this phenomenon with respect to the average orientation of the face. The images were rendered on a black background that made it impossible to discriminate the shadowed facial parts from the background. We determined the physical orientation shift necessary to compensate for the illumination-induced effect. Results showed that the measured illumination-induced apparent orientation shift (IAOS) correlates positively with the average orientation of the face and reaches values of up to 9°. This correlation implies that the mechanism is not based on local surface attitude judgements. We propose a model in which the symmetry plane of the face is detected, and then a comparison is made between the visible parts on both sides of this plane. The effect of the shadow occluding parts of the faces would then be responsible for the apparent orientation shift. To test this hypothesis we repeated the first experiment using a background colour that allowed subjects to perceive the true outline of the faces. We found that the IAOS was reduced to values of less than 2° and no longer depended on the average orientation of the faces. The results imply that orientation may be judged by comparing the size of the visible parts of the left and right halves of the face.

◆ **Chromatic cues for face detection in natural scenes**

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One of the challenging problems of human and machine vision is the detection of objects against complex backgrounds. Our research addresses the question of how faces can be very quickly detected in naturalistic scenes on the basis of luminance and chromatic cues. Although luminance information varies with pose and illumination differences, chromatic information is by and large invariant under these transformations. Hence, chromatic information might be a very powerful cue for segmentation and detection.

We compared faces of different pigmentation against background scenes of different colours. Specifically, colour histograms were computed in a perceptually uniform colour space ($L^*u^*v^*$). We computed the Euclidian distances between the averages of the colour histograms of faces and scenes in $L^*u^*v^*$. This metric was used to calibrate the contrast between face and scene colour in the experimental design. In a face detection task, subjects saw faces against scene

backgrounds at a different distance in colour space. Each combination face–scene was presented for 120 ms (to prevent saccadic explorations), and the subject's task was to indicate whether or not a face was present. Controls involved face–scene pairs on an isoluminant background. Results revealed that luminance information did not affect detection on the basis of chromatic cues. Importantly, the metric of detectability in $L^*u^*v^*$ space between scene and faces predicted reaction times to detection.

NATURAL SCENES

◆ Perception of slope in photographs

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Perceptions of characteristics of space such as slope, distance, and depth are frequently inaccurate, both in the real world and in pictures. We carried out experiments to study factors that influence the accuracy of perceived slope in photographs. Slopes varied in angle from 5° to 45° inclinations against the horizontal, and in the information available to the observer (outline shape and texture characteristics). We found that perceived slope is correlated with real slope ($r = 0.99$), but that observers consistently overestimate slope. The latter depends not only on the available information, but also on the focal length of the lens with which slopes were photographed. Overestimation is less pronounced for the wide-angle lens compared to the standard lens. A comparison of free viewing and viewing from the correct station-point showed that the latter leads to less overestimation of slope. Since the viewing distance was too far under free viewing, the results are compatible with geometrical optics. In a further experiment the effects of magnification and minification were studied by deliberately viewing the photographs from fixed points closer or further away than the station-point; this led to an increase and decrease in overestimation, respectively. Finally, results are frequently dependent on task characteristics: magnitude judgements of photographs without an anchoring point can only be accurate to a level of scale. Thus using an action-based matching task may lead to more accurate slope perception. We therefore carried out a comparison experiment using a matching task to check for the generality and action-dependence of our results. Practical implications for the use of photographs as surrogates for natural viewing are discussed.

◆ Global versus local cues for route finding in virtual environments

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Motivated by the results of Gillner and Mallot (1996 *Perception* 25 Supplement, 93) implying that local views are basic elements for a spatial representation, we studied the role of global versus local landmarks using a route-finding task. Our hypotheses were: (i) A global navigation strategy relying on allocentric movement decisions is used, eg “go from this place towards the chapel on the hill”, or (ii) a local navigation strategy based on view–movement associations is used, eg “at the red building go right”.

We performed an experiment in a computer graphics town based on a hexagonal grid structure. At each intersection we placed three different buildings. We also provided global direction information by placing six global landmarks distributed equally along a mountain range. Subjects had to learn the back and forth route between two buildings, not knowing that after a learning phase the location of buildings at a particular junction would be changed. These changes produced conflicting global and local information. In the test-phase, the subject approached individual junctions in both learned and novel directions and the movement decisions were recorded. In a control condition with unchanged places twenty subjects made correct decisions for 136 of 160 movements. In the experimental conflict condition 123 decisions were consistent with a local and 37 with a global strategy. This supports our previous finding that local views play a dominant role in making route judgements. Approaching a junction from a learned direction leads to more accurate movement decisions than approaching it from a novel direction, even if the global landmarks are available, which provides further support for the local-view hypothesis.

◆ **Brightness filling-in of natural images**

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There is both psychophysical and physiological evidence that the perception of brightness variations in an image may be the result of a filling-in process in which the luminance signal is encoded only at image contours and is then neurally diffused to form representations of surface brightness. Despite this evidence, the filling-in hypothesis remains controversial. One problem is that in previous experiments highly simplified synthetic stimuli have been used; it is unclear whether brightness filling-in is feasible for complex natural images containing shading, shadows, and focal blur.

To address this question, we present a computational model for brightness filling-in and results of experiments which test the model on a large and diverse set of natural images. The model is based on a scale-space method for edge detection which computes a contour code consisting of estimates of position, brightness, contrast, and blur at each edge point in an image (Elder and Zucker, 1996, paper presented at ECCV). This representation is then inverted by a diffusion-based filling-in algorithm which reconstructs an estimate of the original image. Psychophysical assessment of results shows that while filling-in of brightness alone leads to significant artifact, parallel filling-in of both brightness and blur produces perceptually accurate reconstructions. The temporal dynamics of blur reconstruction predicted by the model are consistent with psychophysical studies of blur perception (Westheimer, 1991 *Journal of the Optical Society of America A* 8 681–685). These results suggest that a scale-adaptive contour representation can in principle capture the information needed for the perceptually accurate filling-in of complex natural images.

◆ **Perceived stability of a scene depending on the gain of motion parallax**

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An observer moving in a natural environment is usually able to separate the constant changes of his retinal images in such a way that he perceives the environment and the changes of his observation point independently. The necessary and sufficient conditions to perceive a stable environment in spite of the retinal change produced by self-motion are, however, as yet unknown.

We found that under certain conditions a scene that changes during observer motion can appear more stable than a rigid one. In our experiment a scene consisting of a number of LEDs distributed in a dark room was visible through a window. A mechanical device controlled by a head-tracker was used to move the LEDs during head motion to either reduce or enhance motion parallax by a predefined gain factor. The subjects rated the scene with respect to different attributes including apparent deformation and degree of motion perceived. They were also asked to adjust the parallax gain to the value of greatest apparent stability of the scene. Monocular as well as binocular trials were conducted and different fixation points were employed. The result was a general tendency in all conditions to perceive scene motion when the scene was in fact rigid and to perceive the greatest stability when the scene was distorted in such a way as to produce reduced motion parallax.

◆ **Far distance perception**

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Determining how people perceive distance is a central issue in the study of visual perception. Whilst near-distance perception has been extensively researched, far-distance perception has received little attention. We review the literature and illustrate key points with new data, focusing on analysis of available information/cues, degree of accuracy, measurement procedures, perceptual/cognitive influences, and geometry of perceived space. Analysis of available cues suggests that under natural viewing there is sufficient information for veridical distance perception. However, distance judgements are inaccurate and vary with mode of measurement (eg absolute vs relative judgements). Inaccuracy includes compression of distance. This has been modelled with the use of different geometries—most commonly power functions. Exponents often average 1.0 but this conceals considerable individual variation (in our data individual exponents ranged from 0.5 to over 1.0). Further, even for averaged exponents values vary between 0.8 and 1.25, as a function of viewing conditions, experimental method, and of the relative contribution of cognitive and perceptual factors. Evidence suggests that distance is encoded at an ordinal level, but for many practical tasks the final judgement must be metric (eg range finding) and this transformation is

error-prone (in our data numerical estimates could be a factor of 10 out). Further, many natural judgements require perception of the full layout of the scene (including exocentric distances) rather than the more commonly investigated perception of egocentric distance. Evidence suggests that training based on practice with feedback produces some improvement in accuracy, but this is highly context-specific.

◆ **Curve perception by drivers: dependence of the critical viewing distance on planting structures and the driver's experience**

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The perception of road curves by car drivers was studied in a simulated driving situation. The purpose was to investigate how planting structures along the road would affect the distance at which the curve was clearly perceived by novices and by experienced subjects, respectively. Subjects rated the clarity of the curve percept in different situations on a nominal scale from 1 to 7. Estimations were made under static conditions at the distances 0 m, 100 m, and 200 m before the beginning of the curve. The critical point for a clear percept was found to be at 100 m for novices and at 200 m for experienced drivers. The planting conditions made no difference.

AGE AND DISORDERS

◆ **Stereoscopic vision deficiency in auditory-deprived children**

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There is a widespread opinion that in deaf persons, on average, the visual system should be more highly developed than in people with normal hearing. However, one could also argue that normally the auditory system promotes the development and refinement of visual spatial mechanisms since localisation of many objects in the environment can be accomplished by visual and auditory systems simultaneously and, hence, can be done faster and more reliably. Because such supporting interactions in auditory-deprived children are absent or are weaker, one could expect slower or imperfect development of their spatial vision. We tried to test this hypothesis with the aid of a special test software (CLASS) allowing generation of random-dot stereograms (RDSs) in anaglyphic form (red-blue images). The varying parameters of RDSs were dot sizes (1-8 pixels) and brightness contrast of the blue image. The judgement about a subject's stereo vision was based on the presence of a stereo effect per se and on the brightness contrast threshold for the recognition of 3-D objects. The group of auditory-deprived children consisted of 70 subjects aged 3-9 years, the whole control group included 131 schoolchildren aged 7-9 years, but 87 subjects were only tested for the presence of a stereo-effect. The monocular visual acuity of all children was normal or corrected-to-normal. The results of testing by CLASS revealed significant visual deficiencies in auditory-deprived children: 10 (14%) were found to be stereoblind, and 5 (7%) had markedly increased thresholds. In the control group, the percentage of stereo anomalies corresponded to the typical value of 2%-4%: stereo-blindness was found in only 2 of all 131 children (the cases of strabismus and ptosis) and elevated thresholds were found in 2 children (out of 44). [Supported by Malysh Ltd.]

◆ **Critical flicker frequency in auditory-deprived children**

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The visual system of auditory-deprived children deserves special attention since its development and functioning occur without the usual support of the auditory system which stimulates eye movements in response to sound producing objects, helps in their localisation, etc. Moreover, normally, the contributions of the visual and auditory systems to learning at school are comparable but, in the cases of complete or partial deafness, the visual system is the only or the main channel responsible for acquisition and processing of information. In a pilot study, we have found that such specific conditions of visual performance could affect some visual capabilities and indices of functioning, in particular, the critical flicker frequency (CFF). CFF was measured in 63 auditory-deprived children (aged 6-9 years) from special kindergartens and schools and in 92 children of the same ages from ordinary schools. The light source was a red-light-emitting diode in a dark plastic cone. Since it is known that CFF depends on the state of fatigue and other conditions, the measurements were performed at several different times of the day in each subject: in the morning before lessons, in the midday after lessons, and during the 2nd or the 3rd lesson before

and after a special visual exercise lasting 15–20 min. It was found that auditory-deprived children differed from the control group by much larger influence of school work on CFF ($p < 0.001$): in the control group, the average CFF after lessons was 17% lower than before lessons whereas in the test group, the corresponding lowering was equal to 34%, ie was twice as great. Other differences were less evident or insignificant.

◆ **Flicker fusion frequency in ophthalmic express-diagnosis**

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The critical flicker fusion frequency (CFF) for full-field illumination is an easily accessible measure for evaluating the functional state of the visual system. A decrease of the CFF is a symptom of some disorder and reason for medical care. Owing to the great number of components of the visual system (which includes the retina, neural pathways, and visual centres), however, diagnosis based on this single measure may be rather uncertain. This is possibly the reason why the diagnostic value of the CFF seems to be underestimated and why corresponding devices are not represented among everyday health evaluation procedures.

We suggest a simple and convenient (even though not precise) device for CFF testing, useful for express-diagnosis of (i) general visual fatigue due to visual strain and (ii) abnormalities related to ophthalmopathology, implying the need of medical care. The simplicity and convenience of the device make it appropriate for monitoring, for example, school pupils in classrooms. A toy-like modification of the device enables testing of pre-school children.

The diagnostic value of simple devices can be increased if the functional differences (relevant to the CFF: colour, movement, etc) of distinct parts of the human visual system are taken into account. Their deviations from the norm can be especially useful for selective diagnosis in some cases. This may be considered when developing further devices for simple express-diagnosis of ophthalmic diseases.

◆ **Estimation of visual performance in children with and without binocular anomalies by means of a computerised coding test**

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Coding tests are regularly used to estimate the capacity for mental work in children entering school and for younger schoolchildren. The task of the child is to fill a special form by putting conventional symbols (codes) under the rows of test objects in accordance with a sample. The results of such testing reflect both visuomotor and intellectual capabilities since, on one hand, a subject has to perform fast eye and hand movements comparing test objects with the sample and drawing codes but, on the other hand, it is not forbidden to memorise codes and to use an optimal strategy for filling the form. In order to make the coding test more suitable for estimating purely visual capabilities, we evolved a computerised version in which codes were changing at each step, thus making their memorisation useless. Such a coding test was used in an examination of 22 children (age 6–7 years) with binocular anomalies (strabismus, amblyopia) from special kindergartens and 190 normal children (aged 6–9 years) (63 from kindergartens and 127 from school forms 1–3).

The difference between children with binocular anomalies and normal children of the same age was statistically significant ($p < 0.005$). The average indices for normal children of different ages differed significantly increasing from 11.8 (at 6 years) to 24.6 (at 9 years) symbols per minute. The effect of learning was also evident: the indexes of 7-year-old children from the first school form were better than in children of the same age from a kindergarten. The correlation between coding indexes and reading rate was positive but rather weak (0.28) in 52 first-form children tested. [Supported by Malysh Ltd.]

◆ **Performance of 5-year-old children on seven visual perceptual tasks in relation to neonatal ultrasound abnormalities**

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We investigated whether neonatal brain damage can give rise to visual perceptual deficits, in addition to the well-documented impairments in visual acuity. To this end, forty-one children (age

5.02 to 5.89 years) were given four visual object identification tasks and three visuo-constructive tasks. These subjects were neonatal at risk owing to prematurity or birth asphyxia. From neonatal ultrasound scans, the occurrence of intracranial hemorrhage (ICH, $N = 17$), periventricular leukomalacia (PVL, $N = 15$), and/or white matter damage due to either of these conditions (WMD, $N = 9$) was determined for each subject. Scans were normal in fourteen of them. The number of subjects performing at or below Pci0 of same-age normal children was significantly above 10% for each task (range 27%–49%). This was still true when mental instead of chronological age was used for comparison, as shown by the results of nine subjects for which intelligence data were available. This high incidence of impairment is not attributable to loss of visual acuity, since grating acuity was reduced in only four subjects (14–19 cycles deg^{-1}). The frequency of scores $< \text{Pci0}$ correlated significantly with WMD in six tasks, with PVL in 4 tasks, but not with ICH. We conclude that neonatal at risk children are more likely to develop impaired visual perceptual skills, independent of mental disability and visual acuity loss. On ultrasound permanent white matter abnormalities are most strongly associated with visual perceptual deficit, whereas intracranial hemorrhage is unrelated.

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◆ **Slight defects of basic visual functions as a risk factor for mental development in infants**

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The development of the representation of the visual world in infants was investigated and age norms were established for such operations as prediction of direct movement, search for hidden objects, and discrimination and recognition of the form, size, colour, and spatial position of objects. Simultaneously, basic visual functions were assessed: binocular fixation, eye movements, visual fields, and visual acuity. More than 700 infants aged 4–14 months were tested. About 25% of practically healthy infants showed slight defects in some basic visual functions, constituting a 'risk group'. Infants of the risk group performed less well than their normal age-mates in such tasks as search for a toy hidden under a cap; prediction of linear movement; or discrimination of size, form, or colour. The differences between the normal and risk groups remained when the groups were equated for developmental age. Thus even slight defects of basic visual functions in early infancy may correlate with the mental development of a child. Detailed analysis showed that reduced visual acuity (non-attention to small visual objects such as crumbs 0.5–1 mm in diameter in the acuity test) was especially prognostic.

◆ **Developmental demands for successful measurement of visual acuity in pre-school children**

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Adequate application of the Lea symbol and BUST visual acuity tests (Hyvarinen et al, 1980 *Acta Ophthalmologica* 58 507; Lindstedt, 1986 *British Journal of Visual Impairment* 4 49), designed for children over 18 months of developmental age, in young and/or handicapped pre-school children require preliminary assessment of their level of development. To assess the developmental demands more precisely, 162 children aged from 15 to 35 months and 54 older pre-schoolers, most with normal vision, were examined. Nearly half of the children showed some developmental delays in physical and mental capabilities as assessed on the CDI scale (Ireton, 1992, Child Developmental Inventory, Behavior Science System Inc). Nevertheless, in 77% far and/or near visual acuity was successfully measured by combinations of Lea symbol and/or BUST tests. The youngest successful children, 18 and 20 months of age, passed BUST-N and Lea-Domino. For children aged 18–24, 24–29, 30–35 months, and 36 months and above the success rates were, respectively, 39%, 75%, 89%, and 96%. The minimal values of the CDI scale indexes among the successful children may be regarded, in addition to chronological age, as minimal developmental demands, ie conditions necessary, although not always sufficient, for the child to pass visual acuity measurements. These values in months were 16 ('social'), 18 ('self-serving'), 14 ('gross motor'), 16 ('fine motor'), 16 ('speech development') and 19 ('language comprehension'). The value of the last index was the most critical. Since the developmental demands are not very high, there are good prospects of using Lea symbol and BUST tests in young and/or handicapped children.

◆ **Can slip of the retinal image cause amblyopia?**

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One of the main purposes of the oculomotor system is to keep the image projected on the retina stationary in spite of the continuous movement of the head. If the vestibulo-ocular and optokinetic reflexes are defective, the retinal image becomes blurred owing to the uncoordinated movements of the head and the eyes. It is well known that in children retinal blur caused by media opacities or large refraction errors results in amblyopia. In a similar way amblyopia could be caused by slip of the retinal image due to a defective oculomotor system.

Our patient was a small for gestational age A-twin. He developed dystonic diplegia with poor head control. At the age of 7 months he was considered to have cortical visual impairment. In a magnetic resonance image of the brain there were diffuse periventricular changes in the white matter and hypoplasia of the corpus callosum and the cerebellar vermis. Binocular optokinetic reflexes to full-field stimuli were horizontally asymmetric and were missing vertically. The reflexes to rotation of the child were asymmetric in the same way. In order to stabilise the retinal image the head of the child was supported always when he was supposed to look at a target with fine details. Increase in visual acuity measured with a Teller acuity card procedure was apparent after head support. This suggests that retinal slip can cause amblyopia. It is usual practice not to support the head of a child who has cerebral palsy and poor head control. In the case of defective head–eye coordination this practice could be harmful to the normal development of vision.

◆ **Influence of progressive lenses in the retinal image quality**

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Progressive lenses (PL) are widely used to correct presbyopia, a visual dysfunction that affects most of the population aged over 40 years. The methods used to evaluate the optical quality of these lenses are mainly based on ray-tracing and optical bench testing. Psychophysical studies based on measurements of the contrast sensitivity function of human subjects also exist. However, all these methods exhibit important limitations because, in general, they do not take into account the optics of the eye. One of the objective techniques that permits evaluation of the retinal image in-vivo is the double pass method (Santamaria et al, 1987 *Journal of the Optical Society of America A* 4 1109–1114). It has been possible to study the retinal image quality for different correcting optical systems, such as contact lenses, with this technique (Torrens et al, 1996 *Perception* 25 Supplement, 112–113).

We studied the retinal image quality of the optical system formed by the eye and a progressive lens. The retinal image quality, characterised by the modulation transfer function (MTF), was measured for different observers as a variety of lines of sight that covered a lens diameter of 50 mm. We show the MTF variation as a function of the lens region and the capacity of this technique to characterise these optical systems.

◆ **Changes in the functional visual field due to aging and field defects**

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We examined search performance throughout the functional visual field. This has been shown to be an important determinant for performance in daily life tasks. We were interested to see how aging affects performance and whether we could find evidence for compensatory strategies in subjects with visual field defects. The task was to localise a target (C) among 24 distractors (O) and identify the direction of its gap. Subjects were allowed to make eye movements. Using a staircase procedure, performed separately at each of the 25 possible target positions, we determined the stimulus presentation time necessary to reach criterion performance. This method has the advantage over more common reaction time experiments that it is not affected by speed–accuracy trade-offs. Seven young (age 22–28 years) and seven old (age 58–78 years) subjects with normal vision participated. In addition, we tested older subjects with visual field defects (central defects and hemianopia).

Our results show significant ($p < 0.0001$) age-related differences in the presentation time required for criterion performance. In addition, we found a significant ($p < 0.0001$) interaction between age and target eccentricity, with the largest age-related decline in performance occurring

for targets on or near the initial fixation point, and smaller changes occurring for targets further away from this point. Age and target eccentricity turned out to be the main predictors for search performance. We conclude that age significantly affects search performance, but the extent depends on the distance from the initial fixation point. Our results therefore suggest that aging does not equally affect all stages in visual processing. Not surprisingly, field defects influence search performance, but we also found evidence for compensatory strategies.

◆ **A possible role for the antioxidants lutein and zeaxanthin in protecting against age-related increases in lens density**

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Epidemiological data have identified a number of factors that influence risk of developing age-related cataract (ARC). For instance, factors that promote (eg smoking and light exposure) and factors that protect (eg antioxidants) against oxidative stress to the crystalline lens appear to increase and decrease risk of ARC, respectively. Although biochemical studies consistently support a protective role for antioxidants, the epidemiological data are inconsistent. Since ARC is a condition with a protracted latency period, it is possible that the inconsistencies present in the epidemiological literature may be due to the focus on cataractous patients. We focused on the lens health of individuals prior to cataract. Lens health was determined by measuring the optical density (OD) of the lens with a psychophysical technique. OD characterises many of the biochemical changes of the lens and is part of many systems used to classify ARC. Variance in lens OD, stratified by age, was examined for its relationship to variables thought to be important to the etiology of ARC. We report results for the relationship of lens OD to the antioxidants lutein and zeaxanthin (L and Z). For older individuals (>48 years) we noted a significant inverse relationship between dietary intake of L and Z and lens OD ($n = 39$, $r = -0.34$, $p < 0.015$). This was not the case for younger individuals (24–36 years). This relationship is increased when L and Z are measured directly in the retina is a psychophysical technique. For older individuals, retinal L and Z (ie macular pigment) are inversely related to lens OD ($n = 51$, $r = -0.47$, $p < 0.001$). These data are consistent with a role of L and Z in protecting against age-related increases in the OD of the crystalline lens.

◆ **A method for rehabilitating vision after stroke**

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We developed a method for rehabilitating eye movements and binocular fusion, and tested the method in one patient. An infarct of the pons caused the paresis of the lateral rectus muscle of the left eye. Beginning from the third week in hospital, the patient was trained in eye movements and binocular fusion. Fusion was made possible by means of prisms that moved the images of targets in central vision to the threshold of fusion in the primary eye position. During practice sessions lasting 0.5 to 2 h daily the patient kept the images fused by making a horizontal head movement when necessary. Several eye-movement sessions were held daily, consisting of voluntary saccades and fixations as far to the left as possible. The strength of the prismatic correction required for fusion decreased, and four months after the onset of stroke the patient could fuse without prisms in the primary position. His binocular vision became practically normal in one year. The plasticity of the visual system can be utilised in rehabilitation by a practice that uses minimal remedial means necessary for correct function at each level of performance.

◆ **Perception of geometrical figures in persons with damaged temporal lobes**

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Persons with damaged temporal lobes were tested with computerised tests for size and form discrimination developed by A Bulatov and A Bertulis (1994 *Perception* 23 Supplement, 25). 48 persons with damaged right and 54 persons with damaged left temporal lobe were tested. 8 persons showed hemineglect of the right visual field and 10 persons hemineglect of the left visual field. Posner (1987 *Neuropsychologia* 25 135) stated that persons with unilateral spatial neglect had a specific inability to disengage their attention from a given object in order to reallocate it to another object positioned to its left or right. In our studies we determined whether size discrimination abnormalities also occur in the neglected side, opposite to the damaged temporal lobe. We estimated the accuracy with which subjects judged the height of two

squares of different colours. Two squares with sizes varying from 0.2 to 3.0 deg were generated on the right and left side of the monitor. Subjects viewed the patterns binocularly at a distance of 1 m and adjusted the size of the square on the left to make its height equal to that on the right. The error of the setting was recorded. Persons with hemineglect of the visual field were unable to concentrate their attention at two figures located on both sides of the monitor so they were unable to make the comparison. Persons with right and left temporal lobe damage without hemineglect of the visual field judged the geometrical figures better than those with hemineglect but worse than controls. Persons with damaged left temporal lobe judged figures less well than persons with damaged right temporal lobe.

◆ **Computer interactive system for diagnosis, testing, and rehabilitation of visual perception disorders**

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According to the data of A Christianson (1992 *Acta Neurologica Scandinavica* 86 545–554) the testing of half of the visual field is useful when testing patients who suffer from visual perception disorders (VPDs). With this in mind, a new computer interactive system was developed for diagnosis, testing, and rehabilitation of VPDs. Our computer interactive system was composed of several subsystems: test procedure, test records database, and machine learning algorithm. The interactive test procedure was controlled by several parameters. Results (individual tests, averages) were presented in stereo 3-D form. Individual test records were preserved and formed a database. This database was used by the machine learning algorithm (A Raskinis, 1980, FTEPI Technical Report) to create rules for VPD prediction. Medical computer-aided learning experiments with persons with some kind of VPD have been carried out in the Neurosurgical Centre of Kaunas Academic Clinics with the use of a PC (IBM AT 486). So far we have tested 52 persons with damaged right and left temporal lobes. Our objectives were: (1) to diagnose various kinds of VPD; (2) to train and rehabilitate persons with various kinds of VPD; (3) to collect and analyse data on persons who can be treated and trained; and (4) to develop efficient helping measures and new skills from the effects of intensive training.

◆ **Dark adaptation in patients with thyroid optic neuropathy**

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In patients with thyroid optic neuropathy, vision may deteriorate because of compression of the optic nerve by swollen extraocular muscles. We examined dark adaptation in nineteen patients, aged 25–59 years, with thyroid optic neuropathy with an ARP adaptometer. The duration of the disease was less than 1 month in five patients, 1–3 months in eight patients, and more than 3 months in six patients. The age-matched control group consisted of twelve healthy people with normal visual acuity. We found that visual acuity was reduced in fourteen of the patients. In patients with duration of the illness of 1–3 months and over 3 months, dark adaptation was impaired. In patients with less than 1 month duration of the disease, all measurements were within normal limits. The results show that characteristics of dark-adaptation change progressively during thyroid optic neuropathy, thus providing objective and additional information for diagnosis and prognosis. These data are useful in choosing the tactics of treatment.

◆ **Contrast sensitivity and visual-field thresholds in patients with thyroid optic neuropathy**

J Jankauskienė, R Lukauskienė, B Mickienė (Kaunas Medical Academy, Mickevičiaus 9, Kaunas 3000, Lithuania)

Thyroid optic neuropathy is one of the most troubling complications of endocrine ophthalmopathies. It is related to the degree of extraocular muscle swelling in the apex of the orbit. The purpose of this study was to investigate contrast sensitivity and visual-field thresholds in patients with thyroid optic neuropathy. We examined twenty-two patients aged 29–63 years (mean 45.3 years). The control group consisted of fifteen healthy persons of similar age. Contrast sensitivity was measured by means of Volkov's charts (sinusoidal gratings) at eight spatial frequencies from 17.5 to 0.46 cycles deg⁻¹. The visual field was investigated with a static automatic perimeter (Allgan Humphrey Field Analyzer) by means of the central 30-2 threshold test. All patients underwent a complete ophthalmological examination including best corrected Snellen visual acuity, fundus copy, and proptosis measurement with the Hertel exophthalmometer. The mean proptosis of patients was 19.4 mm. Fifteen of the patients had decreased visual acuity. Contrast sensitivity at low spatial frequencies was significantly reduced in the patients. It was established that a reduction of visual-field threshold accompanies the decrease of visual acuity. Our results show that contrast sensitivity and visual-field threshold testing are very sensitive at detecting early optic neuropathy and may be a useful means of following patients after treatment.

◆ **Performance of eye-tracking movements in otoneurological patients**

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Eye movements were recorded in patients with vertigo as they were tracking a horizontally moving object. Effects of the colour of the object (white, yellow, green, blue, violet), the direction of motion (left-right or right-left), and of the caloric test on the left and on the right side (water temperature 30 °C) were investigated. We present a computerised method for objective, quantitative, and precise assessment of the data. The main indices recorded were: duration and relation between the phases, character of the peaks, disorganisation of the movements (if observed), and movement amplitude and area.

The results show that the experimental variables do affect the measured parameters. For example, durations were longer in yellow light (left-right direction) and for red colour (inversion movement), compared with movement in either direction for white, green, and blue. The caloric test shortened time periods and increased amplitudes in most of the conditions. A model of the process based on Fourier analysis is being developed. The aim is to use the proposed method for assessing disease-related changes and the effectiveness of therapy.

◆ **Dark adaptation as a model of the Parkinsonian visual system**

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It has been suggested that the Parkinsonian visual system is like the normal visual system, but is inappropriately dark-adapted (Beaumont et al, 1987 *Clinical Vision Sciences* 2 123-129). Thus it is of interest to ask to what extent dark adaptation of normal subjects produces visual changes like those of Parkinson's disease (PD). One such change is the reduction in apparent contrast of medium and high spatial frequencies in peripheral vision in the illness (Harris et al, 1992 *Brain* 115 1447-1457). Normal subjects judged whether the contrast of a peripherally viewed grating was higher or lower than that of a foveally viewed grating, and a staircase technique was used to estimate the point of subjective equality. Judgements were made at four spatial frequencies (0.5 to 4.0 cycles deg⁻¹) and four contrasts (8.0% to 64%). The display, the mean luminance of which was 26 cd m⁻², was viewed through a 1.5 lu nd filter in the relatively dark-adapted condition.

The ANOVA showed an interaction between dark adaptation and the spatial frequency of the gratings. Dark adaptation reduces the apparent contrast of high-spatial-frequency gratings, an effect which is greater at lower contrasts. This mimics the effect found with PD sufferers, and suggests that dark adaptation may provide a useful model of the PD visual system.

In a second experiment, the effect of dark adaptation on the relationship between apparent spatial frequency in the fovea and periphery was investigated. The experiment was similar to the first, except that judgements were made about the apparent spatial frequency, rather than the contrast, of the peripheral grating. ANOVA showed no differential effect of dark adaptation on the apparent spatial frequency of the peripheral grating. This suggests that the observed reduction in apparent contrast of the peripheral gratings in dark-adapted normals and Parkinson's sufferers may reflect relative changes in contrast gain, rather than relative changes in the spatial organisation of receptive fields.

◆ **Preferred hemifields learn less**

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Subjects were tested on orientation and colour pop-out tasks. Orientation pop-out stimuli were 3 × 3, 5 × 5, or 7 × 7 arrays of vertical light (white) bars (on a black background) with a target element of diagonal (45°) orientation (present on half of the trials). Colour pop-out stimuli consisted of 60° oriented bars with blue distractor and yellow target elements (on a gray background). Inter-element distance was 40 min arc. The arrays were presented eccentrically, in the right or left hemifield, so that the distance of their centres from the fixation cross was 2.5-6.5 deg.

First we tested performance in the right and left hemifields, with interleaved trials. Most subjects (7/9) had a right-hemifield preference for the orientation and/or colour task. The remaining 2 had a left-hemifield preference. For the six subjects tested on both tasks, all but one had more laterality for colour than for orientation. Thus, for the 15 conditions tested (9 orientation + 6 colour), most (8/15) showed better performance in the right hemifield; the minority (2/15) were better on the left; and a third were about equal in both hemifields. Subjects were recalled for a second session with the same tasks, to test improvement due to first session

training. Almost all showed significantly greater improvement for the non-preferred hemifield. This effect was so strong that often preference was switched. Surprisingly, preferred-hemifield performance actually declined for many subjects. Thus, the effect seems related to competition, and perhaps an automatic attention-directing mechanism.

◆ **Does inverting text improve reading performance in homonymous hemianopes?**

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Anecdotal information from rehabilitation practice of reading performance and low-vision practice suggests that where right homonymous parafoveal field loss impairs reading at the visual-sensory level, an improvement in reading speed can be achieved by inverting the text. This is because whilst left-field loss is considered to impair return eye movements to the beginning of a line, right-field loss is considered to reduce the spatial size of the perceptual window and increase its temporal extent by prolonging fixations times, reducing the amplitudes of saccades to the right, and introducing frequent regressive saccades. Inverting the text was thought to reverse these effects as the leading edge of the perceptual window is 'returned' to the sighted field so that in-line saccades can be visually guided.

Here we report that this does not appear to be the case. In our study we measured the eye movements of patients with right homonymous hemianopia and others with peripheral loss due to retinitis pigmentosa as well as normal controls using an infrared video eye-tracker. All groups display a similar proportional prolongation of fixations times, reduction of saccadic amplitude, and proportion of regressive saccades when asked to read inverted text, which suggests a cognitive component of impairment independent of visual field loss in right homonymous hemianopes.

WEDNESDAY

ECVP XX ANNIVERSARY SYMPOSIUM:

PROGRESS AND PARADIGM SHIFTS IN VISION RESEARCH DURING 20 YEARS OF ECVP

◆ Progress and paradigm shifts in spatial vision during 20 years of ECVP

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In the beginning there was light, and form, and visual mechanisms. This presentation traces developments in research on spatial vision over the 20 years of ECVP, with particular attention to the interplay between physiological mechanisms and psychophysics.

◆ Trends in European visual science since 1978

C R Cavonius (Institut für Arbeitsphysiologie an der Universität Dortmund, Ardeystrasse 67, D 44139 Dortmund, Germany; e-mail: cavonius@arb-phys.uni-dortmund.de)

Trends in basic research in visual science in Europe are discussed, as reflected by the topics of choice in this series of meetings.

◆ Single units and sensation: 25 years on

B Lee (Department of Neurobiology, Max Planck Institute for Biophysical Chemistry, D 37077 Göttingen, Germany; fax: +49 551 201 1039; e-mail: blee@gwdg.de)

In 1972 Horace Barlow ("Single units and sensation: a neuron doctrine for perceptual psychology?" *Perception* 1 371–394) proposed a set of dogmas to guide vision scientists in interpreting neurophysiological data. The 20th anniversary of ECVP is an appropriate occasion to ask if single-unit recordings have really helped us understand the visual system. The answer may be affirmative, but interpreting single-unit data has proved to be much more of a challenge than was anticipated in that early and optimistic era of single-unit recording. I review data from retinal and cortical experiments to illustrate this thesis, and ask if Barlow's dogmas are still relevant to current visual neuroscience.

◆ Colour perception 1978–1997

J D Mollon (Department of Experimental Psychology, University of Cambridge, Downing Street, Cambridge CB2 3EB, UK)

In the past twenty years, the spectral sensitivities of the three types of cone have been established with some certainty: direct measurements by microspectrophotometry and electrophysiology are in fair agreement with psychophysical estimates. Particularly significant was the publication of DNA sequences for the four opsins of the human eye, by Jeremy Nathans and colleagues in 1986. This work was soon to transform the understanding of retinitis pigmentosa and other retinal dystrophies, and it has given many insights into the evolution of colour vision; but, curiously, the explanations of dichromacy and anomalous trichromacy have not proved as straightforward as we all expected in 1986. What is clear, however, is that normal colour vision exhibits a genetic polymorphism: much of the intersubject variance in colour matches can be traced to differences in the amino-acid sequence of the opsins for the long-wave and middle-wave cone pigments.

The last two decades have seen a major change in the status of opponent processes. In the 1970s it was still common for professors to tell undergraduates that the Young–Helmholtz theory of colour vision held at the receptor level and the Hering theory at the level of the retinal ganglion cells. It is now clear that the chromatically antagonistic processes revealed electrophysiologically and psychophysically in the early visual system do not correspond to the red–green and yellow–blue processes that Hering postulated on the basis of phenomenological observations. The existence of four unique hues is today one of the unexplained mysteries of colour science.

In one salient respect, research in colour vision has been changed by instrumental advances. Computer-controlled monitors (though offering splendid pitfalls to the unwary) have allowed the study of spatially and temporally complex chromatic displays, notably in the field of colour constancy. Most recently there has been interest in the chromatic statistics of natural scenes: how well is the visual system matched to the statistics of the world and can it adapt to the gamut of chromaticities present in a given scene?

◆ **Assessing interactions through concurrent-judgment experiments**

L A Olzak, T D Wickens (Department of Psychology, University of California, Los Angeles, CA 90095, USA; e-mail: olzak@mail0.lifesci.ucla.edu)

Many important psychophysical questions concern the interaction or combination of different components of a stimulus. Classical psychophysical methods for assessing whether two stimulus aspects are coded independently (eg, masking and summation) provide limited information about the nature of whatever interactions are discovered. In both older work in detection and recent work in complex pattern discrimination, we have used a double-judgment paradigm in which the observer rates two aspects of a stimulus simultaneously. The paradigm provides a rich source of information about the codes underlying each psychophysical decision. It is unique in permitting us to investigate effects resulting from correlations in noise. We review the theoretical, technological, and methodological results that led us to develop this approach. Procedural antecedents lie in theories of dimensional interaction, in signal detection theory, and in information theory. Analytically, we draw on methods from several branches of statistics, including categorical data analysis and structural equation modeling. Also key to our work are advances in computational power: both our experimental procedures and our data analysis would have been difficult or impossible two decades ago.

◆ **Countercurrents in matter and mind**

S Hochstein ¶, M Ahissar # (¶Department of Neurobiology, #Department of Psychology and ¶ # Neural Computation Center, Hebrew University, Jerusalem, Israel; e-mail: shaul@vms.huji.ac.il)

An especially efficient manner of transmission of matter or energy, employed by numerous biological systems, is the countercurrent mechanism. Transfer is effected between two closely aligned streaming currents where the currents flow in opposite directions. Final transfer can be 100% rather than the 50% ceiling of concurrent streams. We now report that perceptual systems may employ a similar mechanism. Information derived from the external world by the senses is transferred to the perceptual system in a hierarchy of processing areas. Simultaneously, this information is intermixed with previously stored internal information. The degree of mixture of previously existing information, with new, unprocessed information is titrated along the hierarchy. The brain may tap various points along the countercurrents to obtain the mixtures required for different tasks. Perceptual learning affects first the inner levels of this cortical hierarchy and only later descends to their input levels to achieve better performance with more difficult task conditions. Learning effects discussed at ECVP over the last two decades are reviewed in the light of this cortical scheme. Many seemingly contradictory findings are reconciled when put in the framework of countercurrent streams which respectively process sensory information and guide perceptual learning.

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◆ **From elements to perceptions**

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Gestalt psychologists in the early part of the century challenged psychophysical notions that perceptual phenomena can be understood from a punctate ('atomistic') analysis of the elements present in the stimulus. Their ideas also inhibited later attempts to explain vision in terms of single-unit recordings from individual neurons. A rapprochement between Gestalt phenomenology and physiology seemed unlikely when the first ECVP was held in Marburg, Germany, in 1978. Since that time, response properties of neurons have been discovered that invite an interpretation of visual phenomena (including 'illusions') in terms of neuronal processing. Indeed, it is now possible to understand some Gestalt phenomena on the basis of known neurophysiological mechanisms.

I begin by outlining the great strides that have been made since the advent of microelectrode recording from single neurons. Initially, cells ('detectors') selectively responding to the contrast, spatial frequency, wavelength, orientation, movement, and disparity of a stimulus placed in their receptive fields were used to interpret simple perceptual phenomena (eg, Mach bands, Hermann grids, tilt aftereffect, MAE). In recent years, cells at higher levels of the visual system have been discovered that might explain a number of more complex phenomena: the perception of illusory (occluded) contours by end-stopped cells in area V2, the filling-in of artificial scotomata by neurons in V3, colour constancy by 'perceptive' neurons in V4, and the perception of coherent motion in dynamic noise patterns by cells in MT. Studies of flow fields and biological motion

in area MST have recently been added to account for our perceptions as we move through our environment. Prompted by these findings, a shift from local to global interactions 'beyond the classical receptive field' has taken place in our search for the neural substrates of perception. Current research has focused on three kinds of mechanisms: (i) converging feed-forward projections as the basis for new response properties emerging at higher levels, (ii) recruitment of lateral connections to explain filling-in, and (iii) backward propagation from higher to lower levels to account for binding and figure-ground segregation. How such mechanisms compute large-scale surface properties such as brightness, colour, and depth from local features—indeed how they construct the surfaces themselves from complex natural scenes—is only one of the many questions that are under scrutiny today.

Future research will have to tackle the all-important question: How does the analysed information come together again? Furthermore, the contributions of eye movements, attention, learning, other sense modalities, and motor actions will have to be taken into consideration before we arrive at a more complete understanding of visual perception.

THURSDAY

ORAL PRESENTATIONS

PLENARY LECTURE

◆ Synaesthesia and external 'projection' of kinesthetic sensations in phantom limb patients and normal individuals

V S Ramachandran (Department of Psychology, University of California, San Diego, La Jolla, CA 92093, USA; fax: +1 619 534 7190; e-mail: vramacha@ucsd.edu)

By combining brain imaging (MEG) studies with psychophysical experiments we have shown that, very soon after amputation of an arm in humans, the sensory input from the face begins to activate the original 'hand area' of the cortex. Many patients with a phantom arm are unable to 'move' their phantom arm. We used a mirror to allow the patient to see the reflection of his normal hand superimposed on the phantom. If he now moved the real arm he not only saw the phantom moving but also experienced vivid kinesthetic sensations in the phantom—a remarkable example of synaesthesia. Finally, we had a normal subject look at his own reflection superimposed on a Halloween mask seen through a half-silvered mirror. If he now made vigorous lip and tongue movements he felt his kinesthetic sensations 'projected' on the mask; and his 'free will' controlling the dummy's face (it is as though the subject regards it as highly unlikely that his own lip sensations and motor commands should be so perfectly synchronised with the movements of the mask, simply by chance). If the mask was now punched in the eye, the subject registered a strong GSR (galvanic response) demonstrating that his 'self' had now temporarily cast off its mortal coil to inhabit the mask.

EYE MOVEMENTS

◆ Compression of visual space before saccades

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We studied how the human visual system recalibrates visual coordinates to compensate for saccadic eye movements. Observers made 20 horizontal saccades to a target on an otherwise featureless red screen, and reported the apparent position of a vertical green bar that was briefly displayed before, during, or after the saccade. Bars presented 50 ms before the beginning of the saccade, or after its completion, were perceived accurately and veridically. However, bars presented immediately prior to the saccade were systematically mislocated, either in the direction of the saccade or in the opposite direction, depending on the spatial position of the bar. This result has been verified by various techniques including Vernier offset estimation, and a forced-choice annulling task. When four bars (straddling the saccade target) were displayed in the interval -25 to 0 ms, they were seen to be merged into 1 bar (forced choice). None of these effects could be mimicked by causing the scene to move at saccadic speeds and amplitudes. The results suggest that each saccade is accompanied by a non-visual signal that displaces the retinal coordinate system, and a momentary compression of visual space. The perceptual compression may be instrumental in ensuring a smooth transition from fixation to fixation.

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◆ Effects of saccades on perceived time

J Ross, M R Diamond (Department of Psychology, University of Western Australia, Nedlands, WA 6009, Australia; fax: +61 9 380 1006; e-mail: jr@psy.uwa.edu.au)

Saccades produce errors in locating objects in space. The question here examined is whether they also produce errors of location in time. Observers judged whether flashed bars appeared before, during, or after saccades, the order of appearance of two bars flashed in sequence, and the apparent interval between two points of light flashed at a SOA of 100 ms.

We found that (1) bars displayed up to 150 ms before saccades were often judged as during saccades, later bars veridically; (2) the accuracy of judgements of order dropped just before saccades; (3) apparent intervals were shorter before saccades, reaching control levels at onset. We conclude that perceived time is foreshortened immediately before saccades. This could be due to selective suppression of magnocellular activity and may function to hide saccades and their effects.

◆ **The accuracy of saccadic and perceptual decisions in visual search**

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Saccadic eye movements during search for a target embedded in noise are suboptimally guided by information about target location (Eckstein et al, 1997, paper presented at ARVO). Our goal was to compare the spatial information used to guide the saccades with that used for the perceptual decision.

Three observers were asked to determine the location of a bright disk (diameter 21 min arc) in white noise (signal-to-noise ratio 4.2) from among ten possible locations evenly spaced at 5.9 deg eccentricity. In the first of four conditions, observers used natural eye movements. In the three remaining conditions, observers fixated a central cross at all times. The fixation conditions consisted of three different presentation times (100, 200, 300 ms), each followed by a mask. Eye-position data were collected with a resolution of ~0.2 deg. In the natural viewing condition, we measured the accuracy with respect to the target and the latency of the first saccade. In the fixation conditions, we discarded trials in which observers broke fixation. Perceptual performance was computed for all conditions.

Averaged across observers, the first saccade was correct (closest to the target location) for 56 ± 7 (SD) % of trials (chance 10%) and occurred after a latency of 313 ± 56 ms. Perceptual performance averaged $53 \pm 4\%$, $63 \pm 4\%$, $65 \pm 2\%$ correct at 100, 200, and 300 ms, respectively. We conclude that, for the signal-to-noise ratio used, at the time of initiation of the first saccade there is little difference between the amount of information about target location available to the perceptual and saccadic systems.

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◆ **Eye movements during geometrical problem solving**

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Diagrams are used extensively in posing and solving geometry problems. It is likely that strategies that good problem-solvers have developed for looking at diagrams reflect their reasoning about each problem. This suggested that the eye-movement patterns of geometry experts, observed while they solve problems posed with diagrams, are likely to contain new information about their reasoning.

Eye-movement data, collected while subjects solved geometry problems posed as diagrams, were examined. Three subjects participated. Two of the subjects ('experts') were skilled at solving geometry problems. The third subject ('non-expert') had last solved such problems over 50 years prior to the experiment, and did not know how to proceed on most of the problems.

The eye-movement pattern reflected cognitive operations used to solve each problem. Fixation durations depended, to some extent, on cognitive or perceptual processing of features at each gaze location. For example, fixations were longer when gaze was on the angle in question, than when gaze was on other angles or line-segments. Likewise, saccades were made to features that were being considered, as indicated by verbal protocols. Expert subjects combined simple features into more complex, imaginary structures, as was required to solve the problem. They scanned the areas of the diagram that fell within the imagined contours of these structures. The non-expert did not construct such structures. He only scanned visible features of the diagram.

Variability in durations of fixations and landing positions of saccades was not due solely to the probabilistic nature of the oculomotor processes. Such processes, however, clearly play an important role in determining the eye-movement pattern in this task, as they do in other visually-guided tasks. [This research was supported by NIMH 5-F32-MH11282-02; AFOSR F49620-94-1-0333.]

◆ **Gaze-accuracy during monocular and binocular viewing**

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Epelboim et al (1996 *Vision Research* 35 3401-3422) reported that cyclopean gaze errors were smaller than either eye's during tapping and looking-only tasks. This raised two questions: (i) does cyclopean gaze accuracy require binocular input, and (ii) when only one eye sees, is its gaze more accurate than the patched eye's? Most oculomotorists probably expect an affirmative answer to both. Neither expectation was fulfilled.

The Maryland Revolving Field Monitor recorded, with exceptional accuracy, eye movements of two unrestrained subjects tapping or only looking, in a specified order, at four randomly positioned LEDs, with monocular or binocular viewing. Subjects either tapped with their finger tips naturally, or unnaturally via a rod (2 mm diameter, 1.5 cm long), glued to a sewing thimble. Instructions were to be fast, but make no order errors.

With binocular viewing, cyclopean gaze accuracy was best during looking-only. During natural tapping, gaze errors increased, becoming no smaller than success required. Both tasks were learned equally fast, but as expected, the younger subject (aged 27 years) performed ~40% faster than the older subject (aged 69 years). Unnatural, monocular viewing produced odd results, eg cyclopean gaze error was smallest when only one eye could see in some conditions. Only the older subject served in the unnatural tapping task because the younger's errors were too close to his gaze control limit. The older subject, who was suitable, reduced his cyclopean gaze error by 56%, from 1.4 to 0.9 deg. These results support our claim that the gaze error allowed is adjusted to the visuomotor demands of different tasks.

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ATTENTION AND VISUAL SEARCH

◆ Measuring object-centred attention based on a cueing paradigm

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Visual attention can be allocated to a location in visual space and/or to a representation of an object in the visual field, independently of their spatial location. In Posner's cueing paradigm, it is assumed that attention is moved to and then engaged at a cued location. If the target appears at an uncued location, attention first has to be disengaged from the cued location before moving to and engaging the target location.

On the basis of this paradigm, we designed an experiment to measure the disengaging of attention from objects, independently of location. For this purpose we used the bistable Necker cube that can be perceived as two different object configurations, depending on the position of the front side of the cube (lower left or upper right). The subject was instructed to react when he perceived the Necker cube as a previously presented model configuration, ie a stable cube. Each condition started with a bistable cube (with equal luminance of the ribs) that gradually evolved into the model configuration, by manipulating the luminance of the ribs of the cube. Prior to this the subject was cued by a cube similar to the model in the valid condition and cued by a dissimilar cube in the invalid condition.

The results showed a significant difference ($F_{1,10} = 7.35$; $p < 0.05$) between the valid and invalid cue condition, indicating a significant cost for the invalid cue condition. This effect is in accord with the well-known set effect found previously with bistable figures. The difference between the valid and the invalid cue conditions will be interpreted as disengaging attention from an object. Thus, object-based components of attention can be examined by paradigms similar to Posner's paradigm for location-based attention.

◆ Active allocation of attention and the motion-induction effect

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Motion induction refers to the illusory motion perceived within an extended stimulus (eg a bar) presented shortly after the abrupt onset of an adjacent localised cue. Motion is perceived in the direction away from the cue. The effect may reflect transient attentional activation triggered reflexively by the cue onset. In this study we examined the time course of the illusion at a cue to which attention was allocated deliberately, rather than in a stimulus-driven manner. While maintaining fixation, observers searched for a target cue defined by a unique conjunction of colour and orientation among irrelevant equiluminant distractors sharing the same features. Observers reported the direction of perceived motion within a horizontal bar which interrupted search at different delays, appearing in the middle between two randomly chosen cues. Because equivalent cues primed the bar from both sides, the direction of motion was balanced unless one of the cues was selected. In a related experiment we measured the effects of attention through cost/benefit analysis of detection times to a low contrast spot probing the vicinity of the cue instead of the bar. The incidence of motion induction was above chance at the target cue where reaction times were also reduced relative to nontarget locations. The two effects developed similarly

over time, peaking at delays optimal for target selection. Also, active inhibition at irrelevant cues preceded facilitation at the target cue, suggesting that these two processes jointly determine the direction of perceived motion. The converging results from different paradigms support the attentional origin of the illusion.

◆ **Spatiotemporal dynamics of attention-induced distortions and illusions**

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Selective attention induces perceptual distortions, ranging from *repulsion* of objects located near the attended area (Suzuki and Cavanagh, 1994 *Investigative Ophthalmology and Visual Science* 35 2081) to *magnification* of inattended objects (Tsal and Shalev, 1996 *Journal of Experimental Psychology: Human Perception and Performance* 22 233–243). Two hypothetical mechanisms have been postulated: a shift of receptive field positions away from the locus of attention (receptive-field shift hypothesis) or the enlargement of perceived space around the attended location (spatial-enlargement hypothesis). The aim of the present study was to distinguish between these two hypotheses, by investigating the spatial and temporal properties of attention-induced distortions.

Perceptual judgments on Vernier alignment, line tilt, line length, and size of outlined figures were used to measure attention-induced changes in perception. Attention was induced exogenously (by blinking a specific set of dots around the test stimuli) or endogenously (by instructing the subject to selectively attend the dots). After inducing attention, the test stimuli were briefly flashed. A staircase method was used to measure the attentional effect. The experiment was performed with 3 Korean and 3 German subjects.

A vertical line was perceived as *repelled* from the locus of attention, and a line segment appeared *longer* when attention was given to its vicinity. In addition, several well-known illusions (eg the Ponzo and the Gibson illusions) were produced by having the subjects merely attend a set of inducing dots. The effects decreased as the distance between the locus of attention or the time between the onset of attention and the stimulus presentation increased. The results imply that the space-enlargement hypothesis provides a better explanation for the attention-induced changes in perception than the receptive-field-shift hypothesis.

◆ **The preparation of goal-directed movements requires selective visual attention: Evidence from the line-motion illusion**

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Previous research has demonstrated that visual attention is focused on the movement target, both before saccadic eye movements and before manual reaching, allowing for spatially selective object recognition (Deubel and Schneider, 1996 *Vision Research* 36 1827–1837; Deubel, Schneider, and Paprotta, 1996 *Perception* Supplement, 13–19). Here we study the illusory line motion effect (Hikosaka et al, 1993 *Vision Research* 33 1219–1240) in a dual-task paradigm to further investigate the coupling of attention and movement target selection.

Subjects were presented a display with two potential movement targets (small circles). When one of the circles flashed, they performed a reaching movement with the unseen hand to the other stimulus; movements were registered with a Polhemus FastTrack system. At a SOA that was varied between 0 and 1000 ms after the movement cue, a line appeared and connected both stimuli. After the reaching movement, subjects indicated the perceived direction of line motion. In a second experiment, saccadic eye movements instead of reaching movements were studied.

The data show that for short SOAs the subjects reported illusory line motion away from the cue location indicating that attention is automatically drawn to the cue. For longer SOAs but well before movement onset the illusory motion effect inverted—evidence for an attention shift to the movement target. The findings were very similar for manual reaching and for saccadic eye movements. The results confirm the hypothesis that the preparation of a goal-directed movement requires the attentional selection of the movement target. We discuss the assumption of a unitary attention mechanism which selects an object for visual processing, and simultaneously provides the information necessary for goal-directed motor action such as saccades, pointing, and grasping.

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◆ Advance in attention allocation in visual search

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We investigated the allocation of visuo-spatial attention during dynamic viewing with a dual task. The primary search task (K, H, O, or V among Xs) required sequential left-to-right eye movements. An additional manual detection response was made to a visual probe that appeared early or late after the onset of one critical eye fixation (25 or 170 ms probe delay). The probe appeared either to the left, or directly above, or to the right of the currently fixated character (−10, −5, 0, +5, or +10 characters probe eccentricity).

As predicted from research with single-eye movement tasks, probe detection became faster near the location of the forthcoming eye fixation, indicating an attention shift to that location. Fixation times increased as a consequence of probing, but less so when the probe appeared in the right compared to the left hemifield. Saccade lengths decreased as a result of probing, but remained largest when the probe appeared at +10 characters. These data support the notion of goal-directed attention shifts prior to eye movements in natural viewing.

◆ Visual search processes in healthy aging

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It is well established that there are two limiting types of visual search, a pre-attentive parallel and an attention-related serial process. Such different types of processing may depend upon different regions of the visual cortex and such a measurable dissociation of function could provide a useful marker for particular types of cortical pathology, such as that associated with Parkinson's disease, aging, and Alzheimer's disease. For example, recent studies in this laboratory have shown that people with Parkinson's disease have abnormal parallel but normal serial search functions. Plude and Doussard-Roosevelt (1989 *Psychology and Aging* 4 98–105) found no difference in parallel processing between older and young adults, but found that older adults performed worse on a conjunction task. The aim of the present experiment was to extend this research and look at the effect of aging on other types of visual search task and to compare these findings to patients with Parkinson's disease and Alzheimer's disease to determine if different patterns of visual function occur.

Twenty-five young adults (mean age 32.6 years) and twenty-five older adults (mean age 63.4 years) performed both a conjunction task and a task involving the detection of a target only slightly larger than the distractors (the 'size' task). Our hypothesis was that for both types of visual search there would be an increase in search slope in the older adult group compared to the younger adults.

Results of a 2-factor (1 between and 1 within) ANOVA performed on the slope values indicate statistically significant main effects of both age ($F = 7.661, p < 0.008$) and search task ($F = 25.426, p < 0.0001$), where in both the conjunction and size task the slope value was significantly greater for the older than for the younger adults. The slope for the size task was significantly greater than that for the conjunction task for both age groups. The results therefore support our hypothesis and further work is in progress to determine the effects of Alzheimer's disease on different types of visual search processing.

MOTION

◆ Awareness and confidence ratings in motion discrimination

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We have extended our earlier investigations that demonstrated above chance direction discrimination of a moving single-dot target, presented within the blindfield of a hemianope (Weiskrantz et al, 1995 *Proceedings of the National Academy of Sciences of the USA* 92 6122–6126). Previous investigations pointed towards two distinct modes of processing, namely correctly discriminating the stimulus direction of motion when 'aware' or 'unaware' of its presentation. There have been arguments and counter arguments for the relationship between confidence and discrimination scores in normal observers [Kolb and Braun, 1995 *Nature (London)* 377 336–338; Morgan et al, 1997 *Nature (London)* 385 401–402].

We have investigated the relationship between correct direction-discrimination scores and both the awareness of a visual event and the confidence with which the discrimination is made as a function of the stimulus speed in a blindsight subject using binary and graded scales. Results show that the introduction of a six-point scale for the expressed level of awareness yielded similar results to those when the subject was given a binary choice to indicate the presence or absence of conscious awareness. Although the subject's confidence ratings in making a discrimination varied monotonically as a function of stimulus speed, the data obtained suggest that confidence and awareness, although related, are not functionally identical. The correct discrimination scores remained significantly above chance for a range of speeds even when the subject reported nonconfident. The correct discrimination scores were poorer but nevertheless well above chance for conditions where the subject was asked to report both confidence and awareness and improved if required to report only one of these parameters.

◆ **Mistaken identity: Temporal-order biases in the perception of speed**

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Biases in the perceived speed of a moving stimulus have been observed for various spatial configurations of a motion stimulus (eg Norman et al, 1996 *Perception* 25 815–830). In general, psychophysical studies are designed to remove any possible source of bias due to the temporal order of presentation. Here, we examined biases in speed perception between the first and second temporal interval in a 2IFC procedure. The stimulus was a circular patch (~ 2 deg) containing 50 translating dots. A standard speed was always presented in the first interval (~ 6 deg s $^{-1}$), with one of 7 test speeds in the second interval. A range of ISIs (0–2.3 s) and stimulus durations (100–900 ms) was tested. We also dissociated spatial location (left/right of fixation point) and direction of dot travel (left/right and vertical/horizontal) of the two stimuli, whilst maintaining the temporal separation.

In all cases we found an increase in perceived speed from 1st to 2nd interval and further, the effect was independent of direction, ISI, duration, and the spatial position of the 1st and 2nd stimuli. We can suggest no simple account of the results based upon neural fatigue in motion detectors, temporal sampling windows, or representational momentum. Tentative models are currently being explored with three interval stimuli.

◆ **The conditions under which opposing motion is seen in transparency or as flicker**

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We present several examples of moving stimuli comprising several harmonic components that can be perceived either as moving independently, or together as a coherent moving pattern. A simple example is two sinusoidal gratings of equal contrast and spatial frequencies moving in opposite directions that are perceived as a single grating modulated sinusoidally over time (counterphase). However, two square waves drifting in opposite directions, while being a superposition of counterphasing pairs, are perceived as two distinct patterns drifting in transparency one over the other. Intermediate situations such as pairs of counterphase gratings can be perceived alternatively as counterphases or as drifting in two directions.

We show that the relative phase of the components plays a fundamental role in whether they group or become transparent. The tendency of a component to become part of a pattern is maximal when the phase relationship is 0 deg, and gradually decreases to a minimum at 90 deg. This agrees quantitatively with previous measurements on different stimuli (paper presented at Del Viva and Morrone, ARVO96), suggesting a common computational mechanism. The data were well modelled by a nonlinear model of motion analysis based on feature tracking, showing sensitivity to the exact degree of nonlinearity.

◆ **Orthogonal optic-flow components are detected independently: Evidence from subthreshold summation**

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Spatial summation to threshold for 2-D motion patterns of rotation, expansion, and deformation has recently been shown for human vision [Morrone et al, 1995 *Nature (London)* 376 507–509; Harris and Meese, 1996 *Perception* 25 Supplement, 129]. Using a 2IFC subthreshold summation

technique, we asked whether superimposed motion patterns of this kind are detected independently. Subjects had to discriminate between random-dot kinematograms constructed from 'signal + noise' in one interval and 'noise alone' in the other interval. 'Signal' comprised one or two components (cmpnt1, cmpnt2) from the set: expansion, contraction, clockwise rotation, anticlockwise rotation, four directions of deformation, and four directions of spiral. In each session, pairs of components were always orthogonal (eg rotation and deformation, but not expansion and spiral). Both temporal intervals (300 ms duration) contained a circular field where dot luminance was softly damped by an annular window, 5 deg in diameter. In each field, 440 randomly positioned dots travelled linearly through 10% of their distances from the origin. In the 'noise' interval, all dots had their directions randomised individually, whereas in the 'signal+noise' interval, a staircase controlled the percentage of 'signal' dots. We measured psychometric functions for detecting cmpnt1, cmpnt2, and the superposition of cmpnt1 and cmpnt2. In most conditions, we found either little or no summation between the two components. In typical cases where summation was found, it was within the boundary of what would be expected from probability summation between two independent detectors. We conclude that in most of the conditions we tested orthogonal optic-flow components are detected independently in human vision.

◆ **Can the visual system measure expansion rates without using optic flow?**

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As an observer moves towards a surface, the visual image of the surface expands over time. Traditional approaches to measuring this expansion rely on computing the divergence of the local flow field. A complementary approach which would work well in contexts with poor flow information would be to measure shifts in the Fourier amplitude spectra of textures over time (analogous to size changes). To test whether the visual system uses the information provided by such a measure, we have created a set of novel stimuli which contain, on average, no local flow. We filtered successive frames of spatiotemporally white noise with band-pass spatial filters whose peak frequency varied in inverse proportion to time. The resulting stimulus is temporally uncorrelated, but contains changes in the spatial Fourier amplitude spectrum consistent with a constant expansion rate. We tested whether subjects could consistently match the expansion rate of such stimuli, which have no local flow information, to the expansion in random-dot cinematograms designed to have no change in their Fourier amplitude spectrum over time. A temporal 2AFC task was employed to find points of subjectively equal expansion between the two types of stimuli. Several rates of expansion were tested and the start and end frequencies in the textured non-flow stimuli were randomised between trials.

We found that the matched expansion rates of the non-flow texture stimuli were monotonic and nearly linear with the true expansion rates of the dot (flow) stimuli. Settings were also consistent across different start and end frequencies. The results suggest that the visual system can use the change in the amplitude spectra of textures over time to make judgments about expansion.

◆ **Continuous use of perceived velocity while hitting running spiders**

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From previous studies examining how we hit moving targets we concluded that the speed and the direction of the hand are determined independently, the former being based on the perceived velocity of the target and the latter on its perceived position. It is known that the direction in which the hand moves is continuously adjusted on the basis of the perceived target position, with a delay of about 110 ms. In the present study we examined whether the speed of the hand is also under such continuous control, or whether it is determined in advance.

Subjects were instructed to hit targets (spiders) as quickly as possible with a rod. They were presented with moving targets that appeared at unpredictable moments on a screen in front of them. Some time within 400 ms of their appearing on the screen, the velocity of the target abruptly changed. We found that this influenced the speed with which the rod hit the target as long as the change occurred at least 200 ms before the hit. Considering that the movement time of the hand was more than 200 ms, the perceived velocity must have influenced the speed of the hand during its motion. We conclude that the speed of the hand is continuously adjusted to maintain its relationship with the speed of the target.

◆ **Layout perception during simulated locomotion**

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Our purpose was to show how the modification of visual information available to moving observers can change the way they perceive their path and the structure of the environments they pass through. Stimulus trials simulated locomotion across a tree-filled plane while the gaze was directed at a particular tree. In the first experiment we varied the angle between the line of gaze and the simulated direction of movement (GMA) between 0° and 20°. In the second experiment we used either inward displacement (ID) of some objects (moving towards the fovea) or other flow patterns. After each trial, participants drew their path or the position of the particular tree on a schematic map of the environment. In the first experiment, with respect to the fixation point, as GMA increased so did the shift in the drawn paths, and we measured a significant correlation between the two. In the second, ID changed the accuracy of depth representation for the most distant objects in the visual field.

In conclusion, the strong relation between GMA and the reproduced paths, even though they are discrepant from the true paths, suggests that the maintenance of course in the real world may not be based on a maplike mental representation of one's trajectory. In addition, opposite motions in the same region of the visual field (as encountered with ID patterns), may significantly modify the information used for integrating spatial relationships in the environment. The attractive power of these regions in gaze control may also renew our theoretical interest in selective attention.

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SYMPOSIUM

ACROSS THE MODALITY BORDERS: INTEGRATION OF VISION WITH OTHER SENSES

◆ **Integration of sensory information in the brain**

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That sensory cues in one modality affect perception in another has been known for some time, and there are many examples of 'intersensory' influences within the broad phenomenon of cross-modal integration. The ability of the CNS to integrate cues from different sensory channels is particularly evident in the facilitated detection and reaction to combinations of concordant cues from different modalities, and in the dramatic perceptual anomalies that can occur when these cues are discordant. A substrate for multisensory integration is provided by the many CNS neurons (eg, in the superior colliculus) which receive convergent input from multiple sensory modalities. Similarities in the principles by which these neurons integrate multisensory information in different species point to a remarkable conservation in the integrative features of the CNS during vertebrate evolution. In general, profound enhancement or depression in neural activity can be induced in the same neuron, depending on the spatial and temporal relationships among the stimuli presented to it. The specific response product obtained in any given multisensory neuron is predictable on the basis of the features of its various receptive fields. Perhaps most striking, however, is the parallel which has been demonstrated between the properties of multisensory integration at the level of the single neuron in the superior colliculus and at the level of overt attentive and orientation behaviour.

◆ **The development of multisensory integration in the brain**

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Multisensory integration in the superior colliculus (SC) of the cat requires a protracted postnatal developmental time course. Kittens 3–135 days postnatal (dpn) were examined and the first neuron capable of responding to two different sensory inputs (auditory and somatosensory) was not seen until 12 dpn. Visually responsive multisensory neurons were not encountered until 20 dpn. These early multisensory neurons responded weakly to sensory stimuli, had long response latencies, large receptive fields, and poorly developed response selectivities. Most striking, however, was their inability to integrate cross-modality cues in order to produce the significant response enhancement or depression characteristic of these neurons in adults.

The incidence of multisensory neurons increased gradually over the next 10–12 weeks. During this period, sensory responses became more robust, latencies shortened, receptive fields decreased

in size, and unimodal selectivities matured. The first neurons capable of cross-modality integration were seen at 28 dpn. For the following two months, the incidence of such integrative neurons rose gradually until adult-like values were achieved. Surprisingly, however, as soon as a multi-sensory neuron exhibited this capacity, most of its integrative features were indistinguishable from those in adults. Given what is known about the requirements for multisensory integration in adult animals, this observation suggests that the appearance of multisensory integration reflects the onset of functional corticotectal inputs.

◆ **Integration of impaired visual as well as impaired phonological information can cause reading errors**

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Developmental dyslexia is a common problem amongst school children (5%–10% are afflicted), yet controversy surrounds the explanation for its cause. Fluent reading requires rapid association of visual with phonological information—therefore problems with either visual or phonological processing could cause reading difficulties. It is known that dyslexics' speech perception is often impaired, giving rise to 'fuzzy' or 'underspecified' phonological representations. This leads, in turn, to difficulties with letter-to-sound mapping during reading.

Dyslexic individuals also find it unusually difficult to detect flickering or moving visual stimuli, consistent with impaired processing in the magnocellular visual stream. This raises the question of whether dyslexics' reading problems may be caused not only by abnormal phonological processing but also by magnocellular impairment.

We suggest that, when children read, impaired magnocellular function may degrade information about where letters are positioned with respect to each other. We predicted that this might cause reading errors which contain sounds not represented in the printed word. We call these orthographically inconsistent nonsense errors 'letter' errors. To test this idea we assessed magnocellular function in 58 children by using a coherent-motion detection task. We then gave these children a single-word reading task and found that the likelihood of them making 'letter' errors was best explained by independent contributions from motion detection (ie magnocellular function) and phonological awareness (assessed by a spoonerism task). This result held even when chronological age, reading ability, and IQ were controlled for. These findings suggest that, when visual and phonological information is integrated during reading, impairments in both domains may indeed affect how children read.

◆ **Effects of gaze direction in vision and audition**

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We asked to what extent the respective gaze direction influences (i) the spatial congruence of perceived direction of auditory and visual cues, and (ii) the discrimination of the direction of target motion.

With fixed head position, subjects directed their gaze in various positions and localised auditory targets (band-pass noise, 2 kHz) presented at one of nine positions (straight ahead, or four symmetric positions to the left or right separated by 2.75 deg, respectively). Forced-choice judgements, whether the sound was perceived to the left or right of a visual reference light, show that the azimuth of the sound was perceived as slightly shifted to the left of a visual reference when the gaze was directed to the left, and vice versa. The maximum of this relative auditory–visual shift was 4.7 deg over a range of 45 deg (left or right) of gaze directions.

In (ii), a spot of light started at the centre of a monitor and moved at 2 or 12 deg s⁻¹ leftward or rightward. Subjects reported the direction by pressing a key; their gaze was directed at 0, 8, or 16 deg to the left or right. Mean choice-reaction times increased with increasing gaze eccentricity, but differently depending on stimulus direction and speed: with left fixation they were shorter for leftward than rightward motion; with right fixation they were shorter for rightward motion. This effect was stronger for the slow than for the fast stimulus speed. Thus, facilitation occurs when stimuli move with moderate velocity toward the direction of gaze.

While the auditory-visual shift in (i) may reflect an incomplete transformation of spatial (craniocentric and oculocentric) coordinates as suggested by recordings in the primate midbrain, the results in (ii) conform with reports of specialised units in the posterior parietal cortex (areas LIP, 7a, MST) that, in registering oculomotor position, modulate visual sensitivity.

◆ Audiovisual speech perception

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Persons with hearing loss use visual information from articulation to improve their speech perception. Even persons with normal hearing utilise visual information, especially when the stimulus-to-noise ratio is poor. A dramatic demonstration of the role of vision in speech perception is the audiovisual fusion called the 'McGurk effect'. When the auditory syllable /pa/ is presented in synchrony with the face articulating the syllable /ka/, the subject usually perceives /ta/ or /ka/. The illusory perception is clearly auditory in nature.

We recently studied the audiovisual fusion (acoustical /p/, visual /k/) for Finnish (1) syllables, and (2) words. Only 3% of the subjects perceived the syllables according to the acoustical input, ie in 97% of the subjects the perception was influenced by the visual information. For words the percentage of acoustical identifications was 10%. The results demonstrate a very strong influence of visual information of articulation in face-to-face speech perception. Word meaning and sentence context have a negligible influence on the fusion.

We have also recorded neuromagnetic responses of the human cortex when the subjects both heard and saw speech. Some subjects showed a distinct response to a 'McGurk' stimulus. The response was rather late, emerging about 200 ms from the onset of the auditory stimulus. We suggest that the perisylvian cortex, close to the source area for the auditory 100 ms response (M100), may be activated by the discordant stimuli. The behavioural and neuromagnetic results suggest a precognitive audiovisual speech integration occurring at a relatively early processing level.

POSTERS

MOTION

◆ Dynamic visual performance between the ages of 4 and 80 years: results for 1850 normal subjects

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The effect of age on dynamic visual performance was investigated in a sample of 1850 healthy male and female subjects between the ages of 4 and 80 years with the use of a form-from-motion analogue to the Landolt ring (Wist et al, 1996 *Pflügers Archiv* 431 O23). Within a random-dot display, Landolt rings of the same average luminance as their surrounds become visible only when the dots within the ring are moved briefly while those of the surround remain stationary. Thus detection of gap location is based upon motion contrast (form-from-motion) rather than luminance contrast. With the size and exposure duration of the centrally presented ring held constant, motion contrast is manipulated by varying the percentage of moving dots within the ring (100%, 50%, 30%, and 20%). Subjects reported gap location (top, bottom, left, or right) either verbally, by button press, or moving a joystick. An expected percent correct responses decreased from an average of 90% at 100% motion contrast to 65% at 20% motion contrast. A developmental trend was clear for the age variable with performance improving at all motion contrast levels from the age of 4 to 20 years followed by a plateau and a clear decline after the age of 50 years. Intersubject variability increased appreciably beyond this age, consistent with the hypothesis of a differential decline of dynamic vision with age. Applications of this test to date include the testing of glaucoma patients and truck drivers.

◆ Rating visual velocities: presentation order versus frequency of occurrence

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Given equal frequencies of occurrence of stimuli, identical velocities receive higher or lower ratings depending on whether slow or fast velocities happen to occur on the early trials of a run (Ehrenstein and Sokolov, 1996 *Perception* 25 Supplement, 34–35). When stimuli vary in their frequency of occurrence, this presentation-order effect might enhance or substitute the well-known frequency effect (Parducci's range–frequency theory) on category ratings. The aim of the present study was to contrast these two effects for ratings of visual velocities. Two groups of observers had to rate five stimulus velocities (3, 4.5, 6, 7.5, and 9 deg s⁻¹) of a single luminous dot using three categories (slow, medium, fast). Respective frequencies of occurrence

for these velocities were either 4–4–8–14–20 (group 1, negative skewing for frequency) or 20–14–8–4–4 (group 2, positive skewing). The quasi-random presentation order of each set, on the contrary, corresponded to either positively skewed (group 1) or negatively skewed (group 2) frequency distributions. No significant differences in the ratings of two groups (other than a slight preference for the presentation-order effect beyond 6 deg s^{-1}) were found, as if the presentation order and frequency effects had cancelled each other. This suggests that the presentation order of velocities is at least as powerful as their frequency of occurrence. Lack of agreement between our results and predictions of computer-simulated Haubensak's consistency model as well as of Parducci's range–frequency theory requires a model which accounts for an interaction of the two effects.

◆ **Up–down asymmetries in speed perception**

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We compared speed matches for pairs of stimuli that moved in opposite directions (upward and downward). Stimuli were elliptical patches (2 deg horizontally by 1 deg vertically) of horizontal sinusoidal gratings of spatial frequency 2 cycles deg^{-1} . Two sequential 380 ms foveal presentations were compared. One of each pair of gratings (the standard) moved at 4 Hz (2 deg s^{-1}), the other (the test) moved at a rate determined by a simple up–down staircase. The point of subjectively equal speed was calculated from the average of the last eight reversals. The task was to fixate a central point and to determine which one of the pair appeared to move faster. Eight of ten observers perceived the upward drifting grating as moving faster than a grating moving downward but otherwise identical. On average ($N = 10$), when the standard moved downward, it was matched by a test moving upward at $94.7 \pm 1.7(\text{SE})\%$ of the standard speed, and when the standard moved upward it was matched by a test moving downward at $105.1 \pm 2.3(\text{SE})\%$ of the standard speed.

On extending this paradigm over a range of spatial (1.5 to 13.5 cycles deg^{-1}) and temporal (1.5 to 13.5 Hz) frequencies, preliminary results ($N = 4$) suggest that, under the conditions of our experiment, upward motion is seen as faster than downward motion for speeds greater than $\sim 1 \text{ deg s}^{-1}$, but the effect appears to reverse at speeds below $\sim 1 \text{ deg s}^{-1}$ with downward motion perceived as faster. Given that an up–down asymmetry has been observed by other investigators for the optokinetic response, both perceptual and oculomotor contributions to this phenomenon deserve exploration.

◆ **The effect of attentional cueing upon speed discrimination**

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Motion processes have often been regarded as being preattentive in nature. Additionally, in a few attention studies attempts have been made to incorporate the methodology common to classical psychophysics. Speed discrimination with multiple grating patches has been investigated with uncertainty/search paradigms (Verghese and Stone, 1995 *Vision Research* 35 2811–2823). Another method commonly used in attentional research is the cueing paradigm, which we have used here.

In this study participants had to discriminate, using a 2AFC method, whether one of four grating patterns moved faster or slower than the other patches (of a standard speed 6 deg s^{-1}). The speed of this test stimulus was altered from trial to trial with the use of an adaptive staircase procedure. Whilst the gratings were in motion a brief (32 ms) cue was presented. This could be either valid (58%), invalid (14%), or neutral (28%) in respect to the patch of grating which was moving at a different speed.

The results demonstrate that cueing had a strong effect upon the discrimination judgement. The invalid trials had up to a factor of four increase in discrimination thresholds when compared to the valid trials. Further experiments with post-stimulus cueing suggested that a decision theory model may account for a large proportion of these cueing effects. This is in agreement with similar cueing studies (Kinchla et al, 1995 *Perception & Psychophysics* 57 441–450) in which participants discriminated between different array elements.

◆ **Speed discrimination in luminance and colour stimuli as a function of contrast**

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We measured speed discrimination for isoluminant red-green and luminance-defined moving stimuli. The horizontal profile of the stimuli was a Gabor function with a carrier frequency of 2 cycles deg⁻¹. The standard stimulus was a luminance stimulus with a fixed speed of 2 deg s⁻¹ and a fixed contrast of 0.1. The comparison stimuli were either luminance stimuli (cone contrasts: 0.05, 0.1, 0.2, 0.4) or chromatic stimuli (cone contrasts: 0.025, 0.05, 0.1). The speed of the comparison stimuli was varied by an adaptive procedure. After each trial the observer indicated which of the 2 intervals contained the slower moving stimulus. The stimuli always moved horizontally and the direction was chosen randomly at each trial.

The main findings were: (i) For luminance stimuli, the perceived speed was independent of contrast (ranging from 0.1 to 0.4). For colour stimuli, the perceived speed increased with contrast for two out of four observers. (ii) The sensitivity for speed discrimination was independent of contrast for luminance and for colour stimuli. (iii) There was no consistent difference in speed discrimination sensitivity between colour and luminance stimuli when the stimuli were equated in cone contrast.

◆ **Discrimination and detection of changes in the velocity of visual motion: Effect of aperture size**

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Recently Mateeff and Hohnsbein (1996 *Vision Research* 36 2873–2882) showed that the critical frequency for detection of modulated velocity of motion was invariant with respect to the viewing distance. The critical frequency was a function of the ratio between the mean velocity and the size of the aperture through which the motion was observed. In the present study we examined whether the velocity/aperture ratio affects velocity discrimination and detection of single velocity changes. Six subjects observed a random-dot pattern that could move within an invisible square aperture. In the discrimination task, two motions of 250 ms duration with slightly different velocities were presented with a 1 s interval between them. The subject had to report which of the motions was faster. In the change-detection task the same two motions were presented without an interval between them and the subject had to report whether the change was from a low to a high velocity or vice versa. Mean velocities of 8 and 64 deg s⁻¹ and aperture sizes of 10 and 40 deg were employed in both tasks. Weber fractions were determined by the method of constant stimuli. The discrimination accuracy was not affected by aperture size at either mean velocity. The detection task was also unaffected by aperture size at 8 deg s⁻¹. However, at 64 deg s⁻¹ decreasing aperture size impaired the Weber fractions by a factor of about three. We suggest that the decrease of the lifetime of the dots of the pattern at high velocities and small apertures may be the critical factor for the impairment of the change detection. This factor is of less importance for the velocity discrimination task.

◆ **Perceived velocity in dynamic random-dot patterns is influenced by noise type**

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Local motion signals can be pooled to detect the direction of coherent motion in random-dot kinematograms (RDKs) having a high proportion of random noise. Noise type does not appear to affect direction discrimination in such displays (Scase et al, 1996 *Vision Research* 36 2579–2586). We have observed that RDKs with low coherence yet an obvious global direction appear to move slower than similar RDKs with high coherence. Using judgements of relative speed between RDKs containing different proportions of noise in a 2AFC paradigm we have quantified this effect and sought to determine if the type of noise influences perceived velocity.

Levels of coherence in all dot patterns were well above the thresholds for directional judgements. Dots were assigned as 'Noise vs Signal' randomly on each frame of the RDK. Noise dots were either of type 'random position' or of type 'random walk'. Position noise dots were randomly repositioned within the area of the display on each frame and had an isotropic distribution of directions and variable speeds. Random-walk dots moved at the same speed on successive frames (their displacement matched to that of the signal dots) but in a randomly chosen direction. The two noise types yielded statistically different results. In RDKs containing

random-walk noise, decreasing the coherence of the display (30% signal, 70% noise) reduced perceived velocity (on average to 0.75 of the actual velocity), while increasing the coherence of the display increased perceived velocity until at high coherence levels (80% signal, 20% noise) the perceived velocity approximated the veridical velocity (on average 0.96). The proportion of position noise in a display had no effect on perceived velocity. These basic results are discussed in relation to current models of motion detectors and velocity perception.

◆ **Motion contrast: a new metric for direction discrimination**

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The Adelson–Bergen energy model (1985 *Journal of the Optical Society of America A* 2 284–299) is a standard framework for understanding 1st-order motion processing. Its output, the opponent energy for a given input, is calculated by subtracting one directional energy measure (R) from its opposite (L), and its sign indicates the direction of motion of the input. Our observers viewed a dynamic sequence of gratings (1 cycle deg^{-1}) equivalent to the sum of two gratings moving in opposite directions with different contrasts, and had to report the dominant direction of motion. The ratio of contrasts was varied across trials. We found that opponent energy was a very poor predictor of direction discrimination performance. Heeger (1992 *Visual Neuroscience* 9 181–197) has suggested that divisive inhibition amongst striate cells requires a contrast gain control in the energy model. A new metric can be formulated in the spirit of Heeger's model by normalising the opponent energy ($L - R$) with flicker energy, the sum of the directional motion energies ($L + R$). This new measure, motion contrast $(L - R)/(L + R)$, was found to be a good predictor of direction discrimination performance over a wide range of contrast levels, but opponent energy was not. Discrimination thresholds expressed as motion contrast were around 0.5 for the sampled drifting gratings used in our experiments, corresponding to an energy ratio ($L : R$ or $R : L$) of 3 : 1 at discrimination threshold. Such high values suggest that the outputs of motion energy filters are very noisy (variable over space and time) or that the use of them is inefficient.

◆ **Perceived speed of moving cyclopean corrugations increases with increasing disparity amplitude**

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In order to investigate how cyclopean motion is coded by the visual system, the points of subjective equality (PSEs) were measured for (i) speed, (ii) spatial frequency (SF), and (iii) temporal frequency (TF) as a function of peak-to-trough disparity amplitude for cyclopean corrugations. Two panels (3.0 $\text{deg} \times 7.0 \text{ deg}$) of dynamic random-dot stereograms were located 0.5 deg on either side of a central fixation spot. Each panel contained a horizontally oriented sinusoidal cyclopean corrugation whose SF, TF, and disparity amplitude were under experimental control. On each trial, the cyclopean corrugations were displaced vertically in opposite directions. Subjects judged which panel contained the higher SF, TF, or speed depending on condition. The reference stimulus was a sinusoidal corrugation with SF = 0.4 cycles deg^{-1} , TF = 0.8 Hz, speed of 2.0 deg s^{-1} , and peak-to-trough disparity amplitude of 8 min arc around fixation.

We found that, as the peak-to-trough disparity amplitude of the test stimulus increased from 2 min arc to 32 min arc, the PSE for speed decreased from 2.21 deg s^{-1} to 1.67 deg s^{-1} , compared to a reference speed of 2.00 deg s^{-1} . However, across the same levels of disparity amplitude, the PSE for SF remained constant and the PSE for TF varied but with no consistent pattern. Thus, perceived speed increases with increased disparity amplitude. As all levels of disparity amplitude were above threshold, cyclopean speed cannot be detected by a purely 'feature-tracking' mechanism. These metamers and the poor TF matching performance suggest that cyclopean speed is coded by a sparse number of temporal mechanisms.

◆ **Spatial characteristics of motion integration**

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We asked how the characteristics of a surround could affect the perception of a central component undergoing translational motion. Two adjacent patches of moving dots (100 dots per patch; diameter 2.5 deg) were presented on a VDU screen. A central 'target' patch consisted of a combination of signal dots, undergoing left–right translational motion, and noise dots, which moved in random directions at the same speed as the signal dots. To the right of this a 'probe' patch contained dots undergoing translational motion. A simple 2IFC task was used to detect the presence of left–right translational motion in the target patch. An adaptive staircase varied the ratio of translating (signal) to noise dots to measure the 79.4% correct point.

Preliminary findings indicate that both the directional characteristics of the probe and the degree of separation between the two patches influence sensitivity to the target motion. At large separations, probe characteristics do not influence target sensitivity. As the two patches become closer together, probe motion parallel to the target patch increases sensitivity, whereas orthogonal probe motion decreases target sensitivity. Surprisingly, as the separation between the patches becomes even smaller, sensitivity to the target motion is reduced by a parallel probe and increased by an orthogonal probe. This suggests that spatial motion integration involves facilitation and inhibition between different motion directions, and that these two effects have different spatial characteristics.

◆ **Motion integration over time and space**

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The effect of temporal and spatial overlap on globally coherent motion was studied. Two lines oriented 60° and 300°, respectively, moved horizontally, creating the perception of either an integrated coherent motion on the horizontal axis, or two distinct component motions orthogonal to each line. The overlap of presentation time was varied: 100% (simultaneous), 50% (partial overlap), and 0% (successive). With respect to the spatial condition, the two lines were presented (1) superimposed in a single aperture, (2) in two adjacent apertures, or (3) in two distant apertures.

We found that, when the lines were presented simultaneously, the percentage of perceived coherent motion was consistently high, regardless of spatial condition. However, when temporal overlap was lower, the percentage of perceived coherent motion decreased according to the number of apertures and their distance. In the 0% condition there were fewer than 50% coherent motions reported, even in the single-aperture condition. An effect of the intersection of the two lines was observed in the 50% condition, but not in the 100% condition. These and other findings suggest that timing is the most critical factor, and spatial effects, as expressed by the distance between the lines and by the intersections, play a less important role.

◆ **Velocity threshold for relative and uniform motion**

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We measured velocity thresholds for relative and uniform motion as functions of spatial frequency and contrast. Stimuli were two horizontal bands on top of each other, both filled with vertical sinusoidal gratings. The gratings drifted either to the right or to the left, in opposite directions in the relative-motion condition but in the same direction in the uniform-motion condition. Observers had to report the direction of motion, and the velocity was varied until a velocity threshold was obtained. The results showed that the shapes of the threshold function plotted against spatial frequency are quite different for uniform and relative motion. The threshold for relative motion had a minimum at around 5 cycles deg⁻¹, whereas the threshold for uniform motion had no such minimum, at least at higher contrasts (10% or higher). The difference was unclear for lower-contrast stimuli, however. The threshold profile as a function of contrast was also different between relative and uniform motion. Although the threshold decreased with increasing contrast in both cases, this dependence saturated at around 10% contrast for uniform motion, while it continued up to the highest contrast (85%) for relative motion. This difference held for all the spatial frequencies examined (from 0.75 to 12.1 cycles deg⁻¹). The results suggest that the detection mechanisms for relative motion and uniform motion are different.

◆ **Detection time for changes in direction of visual motion**

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Subjects observed a random-dot pattern that moved within an invisible aperture. In experiment 1 the pattern moved horizontally for 0.9 s, then changed its direction of motion by an angle between 12° and 180° for a time t and returned to horizontal motion. The threshold duration t for detection of the direction change was measured for speeds of motion of 2, 4, 8, and 16 deg s⁻¹. The thresholds decreased with increasing angle of change, reaching an asymptotic level of 10–15 ms at about 60° for speeds between 4 and 16 deg s⁻¹. It is suggested that the asymptotic course of this relationship reflects the bandwidth of the directional tuning of the motion-detection system. In experiment 2 we found that the temporal thresholds for detection of

a velocity reversal (180° change in direction) are equal to those for detection of an increase in speed by a factor of three, and that the time to detect an abrupt cessation of motion is nearly equal to the time for detection of a change in speed by a factor of two. Measures such as 'delta' contrast and Michelson contrast are shown to be inappropriate for describing the detection of these changes in velocity. We suggest that the absolute value of the vector difference $V_2 - V_1$ between the velocities before and after the change may be a meaningful measure for the description of the detection performance.

◆ **Effect of motion on the recognition of area by rhesus monkeys in a pseudo-matching task**

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We examined the effect of target motion on the visual recognition of target area in rhesus monkeys. We used a pseudo-matching visual task, where ten adult monkeys were trained to recognise and point out the bigger one of two achromatic squares of different areas but having the same luminance and presented on the same background. The video screen was placed 0.5 m in front of their faces. The two areas were randomly sampled out of five areas (49, 72.25, 100, 132.25, and 169 mm²). The speed of the targets was varied in this paradigm (0, 6, 11, 16, 21, or 26 deg s⁻¹). Performance in terms of area recognition thresholds was calculated for each monkey on the basis of 100 trials in standardised environmental conditions. Statistical analysis showed that performance with a target speed of 16 deg s⁻¹ was significantly better than in the other conditions ($p < 0.01$). We conclude that this pseudo-matching task, based on a cognitive paradigm, reveals a significant effect of motion on the visual recognition of area in rhesus monkeys. The activities of specific cortical areas (V4 and V5) should be studied by other techniques in order to characterise those involved in remembering an object's qualities and those responding to motion. The links between V4, V5, and inferior temporal cortex could be tested with the aid of this pseudo-matching task.

◆ **Differential velocity detection in motion parallax fields**

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Processing of motion parallax relies on the ability of the visual system to segregate locally different motion signals and integrate them over space and time in order to reconstruct a 3-D structure. In a series of experiments, we evaluated the thresholds for differential motion detection and their dependences upon the spatial structure of the optic-flow field.

Visual stimuli were large moving random-dot displays (80 deg × 60 deg). Each dot was randomly attributed one of two velocities whose difference ranged between 0% and 80% of their average velocity, which ranged between 2 and 64 deg s⁻¹. Stimulus duration was from 130 to 1040 ms. Subjects were instructed to stare at a central fixation mark and had to decide whether the display specified one or two surfaces. At a duration of 130 ms, subjects needed more than 40% difference between the two velocities to reach a 75%-correct detection criterion. Thresholds reached a minimum value of about 20% at a duration of 500 ms. Thresholds always increased with the average velocity and were not affected when a static form segregation cue was added to the displays. They were always larger than thresholds for velocity discrimination in successive displays (about 10% at 260 ms). We finally investigated the spatial properties of differential velocity detection. The visual field was divided into horizontal stripes of equal widths. Adjacent bars alternately contained random dots moving with one of two velocities. Thresholds for differential velocity detection increased monotonically when the bandwidth decreased, up to an asymptotic value, equal to those observed with a transparent display.

◆ **A pedestal blocks the perception of non-Fourier motion**

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We wanted to know whether the mechanisms that discriminate the motion of first-order patterns (defined by spatial variations of luminance) differ from those that detect the motion of non-Fourier or second-order patterns (defined by spatial variations of contrast). To address this question we tested whether motion discrimination performance of first-order and second-order patterns was affected by a pedestal (Lu and Sperling, 1995 *Vision Research* 35 2697–2722). A pedestal is a static replica of a moving pattern. We used pedestals with contrast or modulation depth twice the value at which it becomes possible to discriminate the direction of a moving pattern. A two-interval forced-choice task was used to determine how direction discrimination varies with contrast of sine gratings

(1 cycle deg^{-1}) and modulation depth of amplitude-modulated gratings presented either alone or with a pedestal. The amplitude-modulated gratings had a 5 cycles deg^{-1} carrier modulated at 1 cycle deg^{-1} . Three different temporal frequencies (1, 3, and 12 Hz) were studied.

Performance with sine gratings was unaffected by the pedestal at all temporal frequencies tested. For amplitude-modulated gratings the pedestal raised the modulation depth at which it became possible to discriminate the direction of motion. This elevation in threshold decreased when the mean contrast of the pattern was high. This result shows that immunity to pedestals of texture-contrast patterns (Lu and Sperling, 1996 *Journal of the Optical Society of America* **13** 2305–2318) does not generalise to other non-Fourier motion stimuli.

◆ **Measurement of the shortening effect on the perceived path of stroboscopic movement**

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When two vertical short lines are alternately flashed at certain SOAs, a shortening of the apparent path of the stroboscopic movement is perceived. In the experiments reported here, factors influencing the shortening effect were studied with lines created on a CRT display.

Experiment 1 was designed to study the effect of SOA. Each stimulus line was always presented for 100 ms, but intervals were varied in the range from 25 to 800 ms. With short and long SOAs almost no shortening illusion was observed, whereas the SOA for optimal stroboscopic motion (200 ms) also produced the largest illusion (ca 16%). This agrees with the classic study by Scholz (1924 *Psychologische Forschung* **5** 219–272) who found the largest illusion (25%) at the optimal frequency for stroboscopic motion.

Experiment 2 dealt with the effect of inversions (I), mirror reflections (M), and rotations (R) of the line during the stroboscopic movement (see Kolars and Pomerantz, 1971 *Journal of Experimental Psychology* **87** 99–108). The particular movements were signalled by means of a short horizontal line added to one end of each of the two vertical lines of experiment 1. The configurations were (1) $\left[\begin{smallmatrix} | \\ | \end{smallmatrix} \right]$, signifying parallel motion in one plane; (2) $\left[\begin{smallmatrix} | \\ | \end{smallmatrix} \right]$, locomotion with rotation around the vertical axis (M); (3) $\left[\begin{smallmatrix} | \\ | \end{smallmatrix} \right]$, locomotion with rotation around the horizontal axis (I); and (4) $\left[\begin{smallmatrix} | \\ | \end{smallmatrix} \right]$, locomotion with rotation in the plane of the display (R). In all these conditions, the shortening illusion was significantly larger than in experiment 1. The differences between the four conditions were not statistically significant, but the illusion under condition (1) seemed smaller than in the other three conditions. With SOAs for optimal stroboscopic motion, 'rotation' paths tended to appear three-dimensional.

◆ **Perception of the rotation direction in structure from motion displays**

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The ability of human observers to extract the three-dimensional shape of visual objects from optic flow depends on the estimation of the characteristics of the flow. A convenient way to describe optic flow is to decompose it into translational and rotational components. Theoretical considerations [Koenderink, 1990, in *Perception and Control of Self Motion* Eds R Warren, A Wertheim (Hillsdale, NJ: Lawrence Erlbaum Associates)] suggest that the local orientation and shape extracted from the optic flow depend on the direction of the axis of rotation. We performed a set of experiments to evaluate the ability of human observers to determine the elevation and the azimuth of the rotation axis in structure-from-motion displays. The stimuli were pseudo-random dot patterns. The motion of the dots corresponded to the two-dimensional projections of opaque spherical, elliptical, or hyperbolic surface patches. A matching procedure was used. The results show that the estimation of the elevation is more precise and reliable than the azimuth of the rotation axis and does not depend on differences in stimulus shape or on the azimuth values. The best estimates were obtained for vertical and horizontal axes of rotation. The results are discussed in relation to the role of rotation axis evaluation for the extraction of the local shape of the three-dimensional objects, as well as to the possible mechanisms for the determination of this global characteristic of the optic flow.

◆ **Accurate recovery of structure from motion under perspective projection**

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For small objects rotating over a small angle, the 3-D structure and motion are inseparable. Increasing the angle of rotation helps to define image accelerations while increasing the angular size of the object produces greater perspective effects. Both of these cues could be used by the visual system to disambiguate the structure and motion.

In a 2×2 design we tested the influence of angular size (8 deg 'S' or 32 deg 'L') and projection type (perspective 'P' or orthographic 'O') on the perceived dihedral angle of vertically hinged planes ('open books'). Stimuli depicted hinged planes with dihedral angles ranging from 35° to 169° rotating over angles ranging from 2° to 58° . The task of the subjects was to match the perceived dihedral angle to that of a probe defined by motion, texture, and binocular disparities. Spearman rank order correlations of subjects' settings with the simulated dihedral angles were high in condition LP ($r = 0.93$) and decreased in the order $LP \geq SP \geq SO \geq LO$. In the same order, correlations with the total displacement of the projected points increased, up to $r = -0.94$ in condition LO, indicating that structure and motion become more and more confounded.

While for small rotations and small dihedral angles, the settings are heavily influenced by the amount of rotation, for larger rotations and larger dihedral angles settings are more constant over rotation. These results show that both image acceleration and perspective effects play an important role in increasing the veridicality of perceived structure from motion.

◆ **Breakdown of apparent motion under stereoscopic viewing**

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To study the effect of binocular disparity on apparent motion, we measured the cumulative time of its breakdown during a 30 s fixation viewing period. Two light spots, both on the left side of the fixation point, were alternately presented one by one on a CRT display (unilateral condition). These spots were binocularly disparate and viewed through a stereoscope. While one spot near the fixation point was presented on a zero disparity plane, the other spot (more peripheral) was either on a zero, uncrossed, or crossed disparity plane, so that three-dimensional motion could be seen depending on disparity values. We found that the duration of the breakdown of apparent motion was longer when uncrossed and zero-disparity spots were paired to produce apparent motion, and it was shorter when crossed and zero-disparity spots were paired. However, such disparity-specific tendencies were not obtained when the two spots were presented on both sides of the fixation point (bilateral condition). The disparity-specific tendencies in the unilateral condition can be explained by assuming that three-dimensional apparent motion that is consistent with the motion perspective may be stable because we experience it more frequently. Thus, we assume that perception of motion, both apparent and real, may develop through everyday experiences of moving to and fro in the environment rather than seeing objects move.

◆ **The stereokinetic phenomenon from two or three points**

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The stereokinetic phenomenon occurs when certain 2-D patterns are rotated in the frontoparallel plane. Zanforlin explained this phenomenon by the hypothesis of the minimisation of velocity differences. Our visual system minimises relative velocity differences between the various points of the pattern, which determines the apparent height of the stereokinetic cone.

Zanforlin and Vallortigara applied the hypothesis to a rotating straight line or the two end-points of a straight line. They showed that the apparent length of the line does not depend on the absolute physical velocities of the end-points but rather on the relative velocities, and the absolute physical velocities merely affect the apparent position of the line with respect to the plane of the disk.

In the present experiments with two points, the apparent length indeed depended on the relative velocities, but the absolute velocities did not affect the apparent position. The apparent position of the line with respect to the plane of the disk depended on whether or not the centre of rotation was between the two end-points.

Adding one more point gave a triangle that appeared slanted into 3-D space. The shape composed of three points was held constant, even when rotated and slanted. The height of the apparent triangle also depended on the relative velocities.

◆ **Effect of luminance contrast on the motion aftereffect**

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The effects of luminance contrast and spatial frequency in the transient channel were investigated by making use of the motion aftereffect (MAE) caused by adaptation to a drifting sinusoidal grating. Two experiments were performed. The PSE of the velocity was measured as an index of the MAE. The adapting grating was made to drift at a velocity of 2.28 deg s^{-1} and its spatial

frequency was 0.8, 1.6, or 3.2 cycles deg^{-1} . In the first experiment, the MAE caused by a luminance contrast grating or an equiluminous chromatic grating was measured. In the second experiment, luminance contrast gratings were used to measure the effect of the contrast differences between adapting and test gratings. The largest MAE was observed when a low-luminance-contrast grating or an equiluminous chromatic grating was presented as test stimulus after adaptation to a high-luminance-contrast grating in the low-spatial-frequency condition. Generally, the MAE increased with increasing adapting contrast and with decreasing test contrast or spatial frequency. Little MAE was observed at high test contrasts. The results may be explained by assuming that activity in the sustained channel (or parvocellular pathway) inhibits activity in the transient channel (or magnocellular pathway) owing to the domination of sustained channel activity when the test is a static high-luminance-contrast grating providing much information about position and form.

◆ **What is the transition point between static and dynamic motion aftereffects?**

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The motion aftereffect (MAE) measured with a dynamic test pattern (eg a counterphase-flickering grating) is distinguishable by a number of properties from the classical MAE obtained with a static test pattern. For a dynamic MAE, however, it is not sufficient simply to introduce dynamic properties into the test pattern. In two experiments we attempted to determine the transition point in the temporal-frequency domain at which a dynamic MAE becomes distinguishable from the static MAE. First, we examined the interocular transfer (IOT) of the MAE with conventional first-order (luminance) gratings. The amount of IOT increased with temporal frequency, and was almost complete at 1 Hz and above. In addition, the IOT of a dynamic MAE shows a drastic reduction in the peripheral visual field, possibly reflecting difficulties in feature tracking or the loss of involuntary attention. Second, we examined the MAE with second-order motion as the adaptation stimulus (contrast modulation of two-dimensional static noise). Under these conditions, similar results were obtained for first-order and second-order test gratings: MAE was not observed at low temporal frequencies and a substantial MAE was observed only at 1 Hz and above. The results agree with recent findings which showed a gradual loss of spatial-frequency selectivity with increasing temporal frequency of the test pattern (Mareschal et al, 1997 *Vision Research* 37 1755–1759). The present results support the idea that two mechanisms underlie the different kinds of MAE: a low-level mechanism responsible for the MAE observed at low temporal frequencies, and a high-level mechanism operating predominantly at high temporal frequencies with a transition point at about 1 Hz.

◆ **Performance-based measures of transparency in locally-balanced motions**

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In order to perceive transparent motions the visual system must compute and represent two (or more) motion signals at some level of spatial representation. We have developed performance-based measures of transparency, based on the precision of a joint directional judgment of two superimposed global motions in a random-dot kinematogram (RDK). Qian, Andersen, and Adelson (1994 *Journal of Neuroscience* 14 7357–7366) have reported that transparent motion is not perceived in RDK stimuli if each leftward moving dot is paired with a rightward moving dot that it meets at the midpoint of a short trajectory (locally balanced). Using performance-based measures of transparency we investigated the conditions for the occurrence of transparency in locally balanced stimuli. Using stimuli with the same parameters as Qian et al we found that the critical distance that the dots must travel to abolish transparency was 0.2 deg or less. Offsetting one set of dots, orthogonally to its motion direction, by 0.3 deg or more allowed for transparency-based judgments with the same degree of accuracy as for random distribution of the two motion directions. These values differ slightly from those reported by Qian et al (0.4 deg and 0.2 deg respectively), perhaps because Qian et al depended solely on subjective reports of transparency. The data suggest that different processes may be involved in detecting transparency when the trajectories are extended and when they are offset. When the trajectory length was varied, transparency-based judgments were possible when each dot pair had an average separation of approximately 0.1 deg over the course of their lifetimes. For the offset stimuli, transparency-based judgments required the dots to have an average separation of approximately 0.2 deg. However, our data are consistent with transparent motion signals not being represented at the most local levels of motion analysis, as proposed by Qian et al.

◆ **The extrinsic/intrinsic classification of motion signals is a high-level process**

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It has been proposed that the 2-D motion signals elicited by the bar endings of a barber-pole stimulus disambiguate 1-D motion signals with a variable strength which depends on depth (Shimojo et al, 1989 *Vision Research* 29 619–626): these signals would be ‘abolished’ when they are extrinsic (ie the moving grating is behind the plane of the background containing the aperture), whereas they would be given full strength when they are intrinsic (ie the plane of the grating is in front of the background). These authors have suggested that the intrinsic/extrinsic classification is an early process. However, the very long duration (2300 ms) used in their study suggests other interpretations. Therefore, we tried to test whether the barber-pole illusion could be abolished with a shorter duration when the grating had an uncrossed disparity relative to the aperture plane, as initially described in the above-mentioned study (our 30 observers had to adjust an arrow to indicate the perceived direction of the grating). In accordance with our prediction, we could not replicate their finding with a duration of 400 ms. Surprisingly, increasing the duration up to 2300 ms was not sufficient to obtain a large bias towards 1-D signals. To understand this unexpected result, we tried to isolate the relevant difference between the initial study of Shimojo et al and our. We found that the main determinant of the suppression of the barber-pole illusion was the experimental procedure: when our observers had to assess the perceived direction of the barber-pole by choosing between horizontal and vertical, as in the initial study, the results did show a much larger bias towards 1-D signals. We suggest therefore that the extrinsic/intrinsic classification is a high-level process which can be influenced by the observer’s expectations.

◆ **Estimation of time-to-contact from retinal flow**

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We investigated four models for estimating time-to-contact (TTC) from retinal flow. Lee’s model can deal with sparse flow but fails if the flow contains a rotational component. Koenderink’s model, based on div, can deal with rotation but fails if the flow is sparse or if the world does not vary coherently in depth. Two new models were developed by representing retinal flow as the sum of an expansion and a rotation component. The first operates on pairs of points and can deal with sparse flow but fails if the world does not vary coherently in depth. Uniquely, this model provides TTC estimates without prior knowledge of either the focus of expansion (FOE) or focus of rotation (FOR). The second model estimates both the FOE and the FOR and then operates on a point-by-point basis. This model can deal with incoherent depth variations.

We compared human performance with these different model properties by requiring subjects to estimate FOE and TTC from random-dot kinematograms. We used kinematograms depicting smooth planes and random 3-D clouds of points, and systematically varied the density of the flow. Performance was not substantially reduced by sparse flow or by incoherent depth, which argues against Koenderink’s and the first of our own models. Performance remained good when rotation was added to the flow, which argues against Lee’s model. Overall, the data favour a model that first decomposes flow into expansion and rotation components and then estimates TTC on a point-by-point basis.

◆ **Neural modelling of disparity influences in optic-flow processing**

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Last year, we reported a new disparity effect on optic-flow perception. It occurs when a flow field of radially moving random dots is transparently superimposed by a unidirectional motion pattern. Subjects asked to locate the centre of the expansion pattern perceive it shifted away from its true position (Duffy and Wurtz, 1993 *Vision Research* 33 1481–1490). The magnitude of this shift depends on binocular disparity between the two superimposed patterns: presenting the translation in front of the expansion causes a massive reduction of the shift, presenting it behind the expansion yields only a slight reduction.

To determine possible mechanisms for this interaction, we tried to model our results by modifying a previously developed neural model for optic-flow processing (Lappe and Rauschecker, 1995 *Vision Research* 35 1619–1631). We compared three possible mechanisms of disparity influence. The first was based on the assumption that the absolute distance of the stimuli from the observer was known. The second was based on a disparity-based spatial integration, as found in ‘tuned’ neurons in primate visual area MT. Neither could account for our data.

Finally we included a disparity-dependent weighting function in the model, assuming that distant flow vectors contribute more strongly than near ones to the processing of optic flow. This reproduced the experimental findings. Surprisingly, the optimal weighting function was similar to the disparity-dependence of the so-called 'far-neurons' in area MT. We conclude that the visual system uses disparity in optic-flow processing by putting special emphasis on distant flow vectors, and that far-neurons in MT might serve as a neuronal substrate for this. [Supported by DFG SFB 509.]

◆ **Visual perception of optic flow in the left and in the right visual hemifield**

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Recently we have found right visual hemifield (HF) superiority in detection of local texture optic flow discontinuity (H O Levashova and O V Levashov, 1996 *Perception* 25 Supplement, 128). In the present work we investigated a possible difference between hemifields in the perception of global optic flow.

The stimulus consisted of two large texture fields which moved across the screen to the left and to the right from a central vertical line. It gave the illusion of motion through an infinite corridor with high walls. The left or the right wall could be curvilinear (convex) while the other one was flat. In order to make the task more difficult the central vertical meridian of the screen was occluded by a black mask with a width of 5 deg. The task of the subject was to detect the curvilinear wall and press the 'left' or the 'right' key in accordance with target position. When the target was absent (in some presentations both the walls were flat) or when the subject could not detect it he/she had to press the third key. The distance from the screen was 57 cm. One experimental session consisted of 100–150 trials. All subjects showed a superiority of the right hemifield (the difference was significant, $p < 0.05$).

The observed right-hemifield superiority in the detection of large texture flow could suggest that the left hemisphere has a certain dominance in visual perception of optic flow. This is in agreement with the hypothesis that the left hemisphere is more 'phasic' and the right hemisphere is more 'tonic' [O V Levashov, 1989 *Computational Models of Sensory Systems* (Moscow: VINITI) (in Russian)].

◆ **Perception of self-motion induced by moving-dot patterns: The interaction of the stimulating area and the speed of the pattern**

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A linear moving-dot pattern was presented to observers to induce self-motion. A stimulating circular area of more than 28.1 deg diameter induced self-motion perfectly, and even areas ranging from 5.7 deg to 11.4 deg diameter were able to elicit self-motion (Kano, 1995 *Perception* 24 Supplement, 108). In the present study the interactive effects of the size of the stimulating area and the speed of the moving pattern on the perception of self-motion were examined.

Random-dot patterns were moved downward in a circular area on a screen in a dark room. The diameters of the circular area were 5.7, 11.4, 22.6, and 43.6 deg. The speeds of the dot pattern were 9.49, 18.85, 28.07, 36.73, and 45.08 deg s⁻¹. Observers were twenty-six students of Keio University.

When the size of the area became larger and the dot pattern moved faster, self-motion was generally induced with shorter latencies. However, a significant interaction was found between size and speed; for the smallest area (5.7 deg diameter circle) latency was shorter at the lower speeds (9.49 to 28.07 deg s⁻¹) than at the higher speeds (36.73 and 45.08 deg s⁻¹). For the 11.4 deg diameter circle speed had no effect on latency. For the 22.6 deg diameter circle, however, latency decreased with increasing speed. For the 43.6 deg diameter circle latency was very short and constant under the four higher speeds, but remained considerably longer at the lowest speed. The results show that the effect of speed depends on the size of the stimulating area. When the size was large enough, speed had little effect on the latency of self-motion.

◆ **Visual motion perception and field dependence**

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The aim of this research was to throw light on the relationship between the visual field dependence, as measured by a rod-and-frame test (RFT), and the amount of recorded postural sway subsequent to a visual motion of the environment. Two groups of fifteen adult participants were split according to their results in an RFT test. They were asked to maintain an upright stance within a large-scale scenery animated by a texture flow generator. The flow consisted of either an approaching (AP) or a receding (RE) texture with respect to the observer. An ELITE system recorded antero-posterior body sway after onset and offset of stimulus motion.

Both field-dependent (FD) and field-independent (FI) participants showed little reaction to AP whereas only FD participants presented a forward shift in the direction of RE at the onset. Postural responses opposite to AP and RE were marked for both groups at the offset. In conclusion we may assume an interaction between the direction specificity of the sways and a greater field dependence. [Supported by FNRS Grant 1114-043581.95.]

◆ **Active control of heading and depth**

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The addition of depth information has been reported to improve performance on a locomotor heading judgement task in a cloud of dots. Van den Berg and Brenner [1994 *Nature (London)* 371 700–702] used stereoscopic disparity as a depth cue. Coding dots with disparity provides both cues for depth order and for identity between successive frames (each dot may be disambiguated from its 2-D neighbours by its 3-D position). Here, we attempted to determine the relative importance of depth and identity, by dissociating disparity-depth and disparity-identity.

We employed an active steering task that dissociates gaze and heading direction. Participants underwent simulated (18 Hz) locomotion through a cloud (100 dots, lifetime 440 ms) at 2 m s^{-1} for 8 s from an initial trajectory 15 deg ($\pm 20\%$) to the left or to the right of a target tower. Heading was adjusted with a joystick and simulated gaze was continuously computer adjusted so as to keep the tower centred on the projected display (20 deg horizontal). Mean unsigned heading error (gaze-heading angle) over the time course provided a performance measure.

Four types of stimuli were used: (i) veridical disparity depth; (ii) non-veridical disparity (disparity and associated motion-in-depth was randomly assigned to each point in the display); (iii) the left half image of the previous condition to both eyes; (iv) synoptic images (no disparity). No marked advantage was observed when the display contained veridical disparity, and non-veridical disparity produced only a minor impairment in performance in a subset of conditions. We suggest that depth information per se may not be utilised in the perception and control of heading.

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◆ **Vection with degraded real-world stimuli**

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Psychophysical studies have revealed that the retinal periphery plays a dominant role in inducing vection, i.e. the visually induced sensation of self-motion. This suggests that the quality of the visual stimulus is not an important factor for vection. However, since abstract stimuli were used in these studies, it is not clear whether the quality of real-world visual stimuli could still play a critical role in inducing vection. We investigated how vection induced by real-world visual stimuli was affected when the stimuli were spatially or temporally degraded.

Stereoscopic video clips were taken through the windshield of a car driven on a sharply curved and hilly road. These clips were degraded spatially by using a mosaic effect, or temporally by using a strobe effect on a video editing system. The perceived direction and strength of vection were measured while subjects were viewing these visual stimuli presented on a 63 deg wide and 38 deg high video projection monitor. Degradation of the visual stimuli was found to have little effect on the assessment of direction in horizontal vection. Assessment of the direction of vertical vection, however, was significantly disturbed by both spatial and temporal degradation of the stimuli. Temporal degradation reduced the strength of vection significantly for both horizontal and vertical motion. In contrast, although spatial degradation of visual stimuli reduced the strength of vection in both dimensions slightly, the effect was not statistically significant. We conclude that the spatial quality of real-world visual stimuli does not play a significant role in inducing vection.

◆ **Apparent motion of a wallpaper illusion with lateral head movement**

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We measured the magnitude and direction of apparent motion of the wallpaper illusion produced by a lateral head movement. The wallpaper illusion was produced by converging on a grating stimulus located between a far and a near grating stimuli placed, respectively, higher and lower than the fixated middle stimulus. The proximal size of the stimuli was held constant. Observers

were asked to move their head laterally on a sliding chinrest and to report the magnitude and direction of the apparent motion of each stimulus. The independent variable was the extent (2.5, 5.0, and 7.5 cm) of the head movement. The results for five observers showed that: (a) the larger mean magnitude of apparent motion was associated with larger extent of head movement, and (b) the direction of apparent motion for the far stimulus was the same as that of the head movement, and that for the near stimulus was opposite to that of the head movement. These results are consistent with Gogel's hypothesis of an apparent concomitant motion of the object with head movement when the egocentric distance of the object is misperceived.

◆ **A simplified, low-level account of the bistable perception yielded by objects drifting toward and past one another**

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It is conjectured that the relative frequency of *streaming* vs *bouncing* percepts yielded by two objects drifting toward and past one another reflects the relative 'strength' of the underlying 'continuity' and 'discontinuity' motion vectors in the stimulus. The frequency of the two perceptual states should then be predictable from the relative effective contrast of these components which, in turn, is governed by the relative speed sensitivity and spatiotemporal integration range of the underlying sensors. Three distinct experiments were run to test this hypothesis. Percentage bouncing (%B) was assessed with two equal variance Gaussian blobs of equal contrasts as a function of their trajectory length at a given speed (experiment 1), and as a function of their relative physical contrast at a given speed and trajectory length (experiment 2; this latter manipulation was meant to control the relative input to the two competing motion sensors). Apparent contrast of a single drifting blob was independently measured as a function of its speed and trajectory length (experiment 3). The %B obtained in experiment 1 was inferred from experiments 2 and 3 by means of a transformation relating relative apparent contrast (at a given trajectory length) and %B (for that same trajectory) as a function of the relative physical contrast of the continuity and discontinuity motion components. This transformation translates the effect of trajectory length (and speed) in terms of an objective contrast effect. Measured and predicted %B in experiment 1 (ie as a function of trajectory length at a given speed) are in rather good agreement. The phenomenology of simple (and perhaps more complex) Ternus-type stimuli can thus be derived from the sensitivity/apparent contrast and the spatiotemporal integration characteristics of the underlying motion sensors.

◆ **The effect of implied mass on representational momentum: Negative evidence from a two-body collision paradigm**

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The phenomenon of representational momentum (RM) refers to distortions of visual memory for the final position of an object whenever the object is preceded by a series of displays that imply smooth transformations of the object in the picture plane. Past research has demonstrated that the magnitude of memory distortion observed in RM is closely related to kinematic factors such as implied velocity and acceleration depicted in the inducing displays, suggesting that, as a mental analogue to physical momentum, RM may arise from an internalisation of regularities governing the physical world. It is not clear, however, whether or not RM is equally affected by regularities in the kinetic or dynamic domain (eg mass).

We examined this issue in three experiments, using a two-body collision paradigm. The impression of the implied mass was created by simulating the collision of a moving ball of less mass with a stationary ball of greater mass. Although subjects were able to experience and report momentary sensation of objects with different mass, such impressions were not carried over to affect the magnitude of memory distortions in the subsequent RM task where those objects were used as inducing displays. These results imply that the sensation of mass cannot be reliably sustained over a long period by visual information, and as a consequence RM revealed by distortions of visual memory is not affected by implied mass.

◆ **Spatial and temporal integration of biological motion**

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We studied spatiotemporal integration of biological motion using a summation technique. Subjects had to identify coherent from incoherent motion of a synthetic walker against a background of

noise, where incoherence is produced by moving the upper and lower body in opposite directions. Performance (defined as the maximum added noise for reliable discrimination) increased steeply with exposure duration, up to very long intervals, in the order of seconds, far longer than for simple motion targets (complete by about 100 ms). Varying the speed of the walker suggested that the limiting factor for performance is the total information about the stimulus (accrued over seconds), rather than stimulus duration per se. Sampling the joints during the motion sequence (with a 'limited lifetime' paradigm) revealed very strong spatial summation. Sensitivity increased with the cube of the spatial information content. The spatial and temporal summation seemed to be independent of each other.

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◆ **The effect of the centre of moment on gender recognition from biological motion**

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Cutting (1978 *Perception* 7 393–405) suggested that the 'centre of moment' (C_m) plays an important role in the perception of biological motion, especially in gender recognition. The aim of the present study was to examine whether observers could detect a difference in gender from the biological motion pattern and to what degree the C_m index was effective in the recognition of gender. Five males and five females (aged 20 to 25 years) walked in front of a camera from left to right to generate point-light walkers. These point-light walkers consisted of 13 moving dots which were generated by the motion of the actual walking humans. The sequences were replayed in the middle of a TV monitor at 30 frames s^{-1} . Thirty subjects (fifteen males and fifteen females) observed ten different point-light walkers which were presented five times in random order. Subjects recognised the gender more correctly in the case of male walkers (70%) than female walkers (52%). The responses were examined for those point-light walkers showing C_m values similar to the C_m for males of 0.56–0.57 and the C_m for females of 0.50–0.51. It was found that some people could be recognised whereas others could not, even if they had similar C_m values. The C_m index seems to be useful for recognising gender in some point-light walkers but not in others. To conclude, masculine or feminine walking styles are not defined only by differences in the C_m index.

◆ **Perception of a point-light walker produced by eight lights attached to the back of the walker**

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The Johansson demonstration, achieved with point-lights placed on the main joints of a walker, gives a vivid impression of an invisible human being. An experiment was devised to test the degree to which gender and age of an individual could be correctly identified by observing a point-light-walker (PLW).

Eight point-lights were attached to the backs of each of eight actors, four men and four women, aged 18 to 62 years, at the shoulders, hips, knees, and heels. In a dimly lit room, the actors stood on a treadmill and walked for 1 min on an endless belt moving at speeds from 1.0 to 3.0 $km\ h^{-1}$. The movements made by the point-lights were recorded with a video camera and projected on a screen (96 cm high and 120 cm wide). The PLW demonstrations were viewed by 144 undergraduates, divided into five groups, at observation distances of 4.8 to 13.3 m. They were asked to identify and write the gender and age of the perceived gait. On average, there was a 74% correct identification of the genders, especially of the PLWs of the older actors, which were 80% or more correctly identified. Recognition of age, however, was less robust and the PLWs were mostly judged as 20 to 40 years old. Of particular interest was that the PLW demonstrations by two actors of about the same age were quite differently judged; one as old and the other as young. Comparison of these two PLWs revealed that the point-lights corresponding to the shoulders and heels moved very differently. The extents of both the horizontal distance of the right shoulder and the vertical distance of the left heel were measured at intervals of 100 ms. When the obtained values were plotted on the abscissa (shoulder) and ordinate (heel), the relation between the movements could be represented as a pattern corresponding to the italic letters *S*, *O*, and *D*; pattern *S* was typical of the PLWs judged as 'young', pattern *O* as 'old', and pattern *D* as in between. These findings lead to the suggestion that the correlative changes between the movements of point-lights could become a useful aid in the studies of gender and age recognition in the PLWs.

◆ **Detection of a point-light walker within a mask: effect of display orientation**

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How, if at all, does display orientation affect the extraction of a known structure in biological motion? A computer-generated 11-point-light walker was simultaneously masked by 66 dots that corresponded to scrambled triads of points on his limbs. At each of 5 randomly presented orientations between upright and inverted (0°, 45°, 90°, 135°, 180°), observers saw a sequence of 210 displays, half of which comprised a walker within a mask, while the rest presented only a 77-dot mask. In a confidence-rating procedure, they had to judge whether a walker was present. A sample of the target was demonstrated before each experimental sequence. ROC analyses showed that detectability decreased with changing orientation: performance began to deteriorate already at 45°. For orientations of 90°, 135°, and 180°, the ROC curves were situated close to one another. Nevertheless, given the complexity of the mask and the brief viewing period (1 s), with inversion (180°) detectability was still surprisingly high (cf Bertenthal and Pinto, 1994 *Psychological Science* 5 221–225). Comparison with data on spontaneous recognition of biological motion (Pavlova, 1996 *Perception* 25 Supplement, 6) suggests that display orientation affects bottom–up visual event processing more strongly than top–down. We consider the relative power and interrelation of processing constraints (such as axis of symmetry, dynamical constraints) in the perception of invariant structure from biological motion.

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VISUAL SEARCH, ATTENTION, AND EYE MOVEMENTS

◆ **Effects of target discriminability on colour-based and location-based selection**

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How can we find one visual stimulus in a world filled with thousands of simultaneous stimuli? In particular, how does the search for a looked-for stimulus proceed when we know its colour or location?

We examined the effect of target–distractor confusability on colour-based and location-based selection. The displays consisted of two elements. The target was either an orange or a green line-segment surrounded by a square. The distracting element was either easily distinguished from the target or more confusable with it. Subjects were cued to the colour or location of the target and made a rapid discrimination response to the direction of the target. In different conditions, the most likely target location (above or below the centre of the display) and colour were cued. With a clear distinction between the target and the distractor, performance differed with valid and invalid cues only in the location-cuing condition. When the distinction was poorer, both colour and location cues had a significant effect. The results show that, if necessary, attentional selection can be triggered by different stimulus attributes, even though selection may always proceed via space.

◆ **Colour mechanisms underlying visual search with heterochromatic distractors**

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We studied the colour mechanisms involved in a visual search task. The test stimulus consisted of a coloured target randomly positioned among heterogeneous distractors of two colours. Colours of the target and distractors were specified in the equiluminous plane; a pair of distractors was set to lie on a circle around the target and characterised by the radius, central angle, and chromatic direction of a right bisector of the chord between the pair. The stimulus was presented briefly, and observers were asked to report whether a target was present. Target detectability quantified by d' depended on the central angle and the chromatic direction of the bisector. The central angle affected the detectability of the coloured target but not that of the white one. The coloured-target detectability decreased and reached chance level with increasing central angle from 0° to 180°. For a fixed obtuse central angle, maxima of the coloured-target detectability occurred at two bisector directions, one orthogonal to the target direction and the other along the target direction. This suggests that only two orthogonal colour mechanisms were at play and they changed with the colour of the target. These results and previous findings that the target was detected preattentively when it was linearly separable from the distractors in colour space (D'Zmura, 1991 *Vision Research* 31 951–966; Bauer et al, 1996 *Vision Research* 36 1439–1465) may be explained by the same processes, colour selective filters that linearly combine cone signals followed by peak detectors.

◆ **Conjunction search for stereo and colour is serial**

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We examined whether visual search for a conjunction target defined by stereoscopic disparity and colour is parallel, as indicated by Nakayama and Silverman [1986 *Nature (London)* **320** 264–265]. The stimuli consisted of arrays of variable size, containing either 15, 25, or 35 elements. The elements were squares and bordered with a frame to ensure stereoscopic fusion. They were clearly distinguishable either in terms of stereoscopic depth or colour. The target was an element with a combination of stereoscopic depth and colour that was unique in each display. Before search, subjects were either instructed to find a target with defined properties, or to find the odd target. When the subjects knew the target properties, there was a significant effect of set size, although overall search times were short. When the subjects were asked to search for the odd target, search times were long and increased as a function of set size. These results suggest that conjunction search for stereo and colour is serial.

◆ **Perceptual integration of motion and form in a visual search task**

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Three visual search experiments were designed to investigate the processes involved in the efficient detection of motion–form conjunction targets. In experiment 1 the number of movement directions in the display were varied, and we tried to establish whether or not the target direction was predictable. Search was less efficient when items moved in multiple directions compared to just one direction; whether items moved in two, three, or four directions made relatively little difference. Pre-cuing of the target direction facilitated the search to a small, but non-negligible, extent; the facilitation was not due to better predictability of the display region that contained the target at the start of a trial.

Experiment 2 was designed to estimate the relative contributions of stationary and moving nontargets to the search rate. Search rates were primarily determined by the number of moving nontargets; stationary nontargets sharing the target form also exerted a significant effect, but this was only about half as strong as that of moving nontargets; stationary nontargets not sharing the target form had little influence.

In experiment 3 we examined the effects of movement speed and item size on search performance. Increasing the speed of the moving items ($> 1.5 \text{ deg s}^{-1}$) facilitated target detection when the task required segregation of the moving from the stationary items; when no segregation was necessary, increasing the movement speed impaired performance. When the display items were 'large', motion speed had little effect on target detection; but when the items were 'small', search efficiency declined with item movement faster than 1.5 deg s^{-1} . A 'parallel continuous processing' account of motion form conjunction search is proposed.

◆ **The dynamics of perceptual learning in different visual search tasks: psychophysics and psychophysiology**

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Serial visual search can become parallel with practice (Sireteanu and Rettenbach, 1995 *Vision Research* **35** 2037–2043). Our purpose was to examine whether psychophysiological indices reflect the changes in reaction time during training.

We used targets and distractors that differed either in orientation ('tilt'), or in local brightness: closed circles with or without an additional line element ('added line'), or circles with gaps of different width ('gap'). The subjects' task was to indicate the presence or absence of a target on a computer screen by immediately pressing a button and pointing to the location of the target if the trial was positive, or raise the hand if negative. No feedback was given. Response time and error rate were recorded. In addition, electrocardiograms, galvanic skin response, respiration rate and amplitude, horizontal eye movements, and electromyograms were monitored. Two naive and two experienced subjects participated in at least 16 experimental sessions.

Before training, slopes differed for the three tasks, ranging from parallel search for the feature 'tilt' to a very steep serial search for the feature 'gap'. These differences were reflected in the psychophysiological parameters. Reaction time and error rate decreased continuously with learning, leading to parallel search after prolonged practice for all three tasks (see Nase et al,

1995 *Perception* 24 Supplement, 84). Preliminary results indicate that the psychophysiological measures do not follow the perceptual changes during learning. We conclude that, despite the perceptual parallelisation with practice, the attentional load remains high for initially serial tasks.

◆ **Search asymmetries in the detection of shape orientation: The role of implicit axes of elongation and symmetry**

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Two-dimensional (2-D) shape identification is sometimes described in terms of access to structural descriptions based on the extraction of principal axes of elongation and symmetry. In four experiments we examined the effects of implicit axes of elongation and symmetry on visual search for shape orientation, on the basis of previous observations of search asymmetries in the detection of the orientation of line segments. We found search asymmetries in the detection of vertical versus oblique line segments and in 2-D shapes, studied earlier by Quinlan and Humphreys (1993 *Perception* 22 1343–1364): search times for a vertical target among oblique distractors (rotated 18° from the vertical) are higher than those for an oblique target among vertical distractors.

We found that the search asymmetry in the detection of shape orientation is larger when the shape contains an unambiguous axis of elongation or symmetry. Search asymmetries disappear when the principal axis of the shape is oriented horizontally, or when the shape contains no unambiguous axis of elongation or symmetry. Overall search times tend to decrease when the axis of elongation is aligned with an axis of symmetry. These results suggest that the detection of implicit axes plays a role in the perception of object shape and orientation.

◆ **Attentional shifts and the mislocalisations at the beginning of a movement**

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When subjects are asked to determine where a fast moving stimulus enters a window, they typically do not localise the stimulus at the edge, but at some later position within that window (Fröhlich effect). We report four experiments aimed at exploring this illusion. An attentional account is tested, on the assumption that the entrance of the stimulus in the window initiates a focus shift towards it. While this shift is under way, the stimulus moves into the window. Because the first phenomenal representation of the stimulus will not be available before the end of the focus shift, the stimulus is perceived at some later position.

In experiment 1 we established the Fröhlich effect and showed that its size depends on stimulus parameters such as movement speed and movement direction. In experiment 2 we tested whether the effect changes when the stimuli started from different eccentricities. In experiment 3 we showed that the processing of the moving stimulus benefits from a preceding peripheral cue, and in experiment 4 we showed with a detection task that feature information about the moving stimulus gets lost when it falls into the critical interval of the attention shift. In conclusion the presented attentional account shows that selection mechanisms cannot only be space-based but that they can establish a spatial representation that is also used for perceptual judgement, that is selection mechanisms can be space-establishing as well.

◆ **The effects of attentional spread and attentional effort on orientation discrimination**

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We investigated the spatial properties of visual attention, and its relation to attentional effort. We show that stimulus detectability changes as a function of attentional beam width and of the degree of task difficulty. We used a matching-to-sample paradigm, presenting two Gabor patches simultaneously as sample stimuli and as test stimulus, the stimuli being at three different distances. Task difficulty was graded by changing the orientation difference of the two Gabor patches on nonmatching trials. 'Difficult' nonmatching probe trials were embedded within an easy block of trials (easy condition), and vice versa for 'easy' probe trials. Differences in the detectability, d' , between probe trials in the two conditions were taken as a measure for the change in attention. Our results show that the detectability of a pair of stimuli decreases with an increase in the distance between stimuli. In addition, the results indicate an increase in attentional effort for different attentional beam widths, and also suggest a decrease in the SD of the internal stimulus representation during the task conditions that require more attention.

◆ **Attention to colour? Detecting and discriminating luminance changes**

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It is well established that cueing the location of a target stimulus can improve performance on certain visual tasks over 'uncued' locations. Here we ask whether cueing the colour of a target can produce similar gains in performance.

Subjects viewed a screen on which a large number (16, 32, or 64) of circles were randomly arranged. At random, half were coloured green and half red. After a short period the luminance of one of the circles was altered and the subject's reaction time to this change was measured. Within a block of trials subjects were informed that the target would be one of the red elements, green elements, or could be of either colour. We found that reaction time to detect this change was (1) unaffected by the number of elements on the screen and (2) unaffected by cueing the target colour. The reaction time to discriminate the polarity of this change was (1) unaffected by the number of elements on the screen and (2) faster when the target colour was cued.

We therefore demonstrate that cueing the target colour can serve to improve performance under some conditions. We account for these results by suggesting that subjects give greater 'weight' to signals from the target colour into a map that guides visual attention—in line with guided search type models (eg Wolfe, 1994 *Psychonomic Bulletin and Review* 1 202–238). This cueing effect is therefore only demonstrable in tasks that require 'focal attention' (eg Sagi and Julesz, 1985 *Perception* 14 619–628).

◆ **A subliminal effect in a colour-discrimination task and its modulation by spatial attention**

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Three experiments were performed to examine the effects of masked colour stimuli on the response to masking stimuli. In experiment 1, two coloured squares were presented successively at the same position so that the first one could not be perceived owing to backward masking. The task was to respond to the colour of the second square as quickly as possible. The results showed that the subject's response was affected by the unperceived first square: both error rate and reaction time increased when the two squares had different colours. It was also found that reaction times for wrong responses were shorter than those for correct responses; this suggests that wrong responses occurred when the neural activation representing the first square succeeded in triggering a motor response before being suppressed. In experiment 2 we examined whether spatial attention modulated this effect or not. Eight squares (one coloured and seven white) were displayed and the spatial relation between the coloured square in the first frame (prime) and that in the second frame (target) was varied. The performance of subjects when the target location was pre-cued and when no cue was given was compared. The results indicate that in the no-cue condition the subliminal effect was observed uniformly irrespective of the spatial relation. In contrast, in the pre-cue condition the effect was diminished when prime and target occupied different positions, that is when the prime appeared outside the attended region. The result of experiment 3, with another stimulus configuration, showed a similar attentional modulation. The underlying mechanism is discussed.

◆ **Selective visual attention during multiple-process control**

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During multiple-task control, eye movements are central for the performance of aimed actions and the development of working strategies. In order to investigate visual and informational workload the behavioural pattern has been analysed. Information presented on a screen has to be visually analysed in order for a decision to be reached on the action to be performed. Normally peripheral vision and the knowledge of the displayed optical structure are used to select the next position of fixation. The resulting scan path is determined by the context and the dynamics of the processes to be controlled. Therefore, the question arises to what extent characteristics of the eye movements are affected by the amount of workload.

In order to test this an experimental setup was designed which makes it possible to record eye and head movements simultaneously. From these data the gaze position on the screen could be computed. During the experimental sessions trained subjects were asked to control a complex process simulation by means of cursor movements. This simulation displayed on a

high-resolution colour screen consisted of four process units similar to Crossman's water bath paradigm. Temperature and flow rate represent the control variables for each process unit and have to be adjusted to and kept within a certain tolerance range. The visual scan path and all actions on the graphic tablet were recorded continuously during the experimental sessions.

An attempt is made here to describe the allocation of attention during multiple-task performance. The results provide evidence that the contextual structure of the task determines the uptake of specific visual information. The amount of visual workload affecting the subject during the control of all four simulated processes is determined by two independent variables: the flow rate (kinetics) and the number of activated processes. On the one hand fixation duration is affected by the kinetics and on the other hand the stability of the activated processes is very sensitive to both independent variables. These effects are due to the limited capacity of the subject to deal with more than one process state within a certain time interval. He or she is forced to divide his or her attention between different processes. There seems to exist only a poor mental representation of the dynamics of several processes running in parallel.

◆ **Attention facilitates sequential recruitment in the perception of motion direction**

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Sensitivity to the global direction of motion in a random-dot kinematogram (RDK) increases as the number of RDK frames is increased from 2 to about 10. This increase in sensitivity has been termed sequential recruitment and is thought to reflect cooperativity among motion detectors in V5. If attention is not a control state projected from executive to other brain areas, but rather cooperative activity in any brain area as multiple analysers converge on a single stimulus interpretation, then sequential recruitment should be impaired if RDKs are not attended.

Motion direction sensitivity in 2-, 3-, 6-, or 10-frame RDKs was assessed under two conditions. In the first, RDKs appeared at central fixation on a random 80% of the trials and 6.5 deg to the right on the remaining 20%. Here, observers would attend the central but not the peripheral RDKs. In the second, RDKs appeared 6.5 deg to the right of fixation on 80% of the trials and centrally on the others. Observers would attend the peripheral but not the central RDKs. In both conditions, RDKs were 8%, 14%, 25%, 45%, or 80% coherent. Similar results emerged for both central and peripheral RDKs: Threshold was higher for 3-frame, but not 2-, 6-, or 10-frame RDKs when RDKs were unattended rather than attended, suggesting that recruitment is slowed in the absence of attention. These results support a network cooperativity view of attention and suggest that attention may influence relatively basic motion perception mechanisms.

◆ **Interruption of late visual processing causes an attentional blink**

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When the task is to detect two letter targets in a stream of non-letter (digit) distractors in rapid serial visual presentation, an attentional blink (AB; ie a deficit in the detection of a second target when it follows the first by approximately 100–500 ms) is often found to occur. In a series of four experiments with different numbers of display positions, with or without masking, we show that: (1) the AB, which occurs when all items are presented at the same display location, is reduced when targets and distractors are presented randomly dispersed over 4 or 9 adjacent locations; (2) the AB is reduced with the spatially distributed presentation even when backward masks are used in all possible stimulus locations and when the location of the next item in the sequence is predictable; (3) the AB is not due to either a location-specific forward or backward masking effect occurring at early levels in visual processing.

We conclude that the AB is primarily a function of the interruption of late visual processing produced when the item following the first target occurs at the same location. It seems that, in order for the AB to occur, the item following the first target must be presented at the same location as that target so that it can serve both as a distractor and as a mask interrupting or interfering with late visual processing.

◆ **Saccade automation**

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The comparative analysis of basic saccade characteristics (interval, amplitude, and coefficient of asymmetry) has shown considerable similarities in adults and first-year babies. Distribution

curves of intersaccadic intervals under different test conditions all have only one maximum in the range of about 0.4 s, and in all cases the most frequently met intersaccadic intervals (0.1–1.0) comprised comparable proportions of all (71.5%–90.5%).

The concept of saccade automation was formulated on the basis of these data (Filin and Filina, 1989 *Zhurnal Vysshei Nervnoi Deyatelnosti* 29 603–607). In our opinion saccade automation is the basic law of saccadic activity, and all diversity of eye-movement activity takes place against the background of saccade automation. Microsaccades and macrosaccades, nystagmus, and rapid eye movements during sleep may be seen as special cases of saccade automation. Saccade automation is conditioned by the activity of brain structures with pacemaker function. Thus saccades are driven at one basic frequency, which is modulated by afferent influences from the retina of vestibular apparatus, proprioceptors of eye and neck muscles, and efferent signals (forehead and occipital sections of cerebral cortex, cerebellum). At the same time, only one parameter is modulated at one particular moment, for example saccade amplitude in which case interval and orientation are given in a ready form.

Saccade automation has a great functional importance. It increases the scanned area tenfold, it provides compensation of defects in the sensors and the impellent eye apparatus and for the deletion of consecutive images, maintaining the continuity of visual perception. Moving the image on the retina increases the information of the visual channel.

◆ Eye movements in judgements of facial expressions

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We recorded eye movements by the method of corneal reflection while ten subjects viewed schematic faces drawn by lines. Each subject viewed different emotional faces: happy, angry, sad, disgusted, interested, frightened, and surprised. We measured the subject's judgements in terms of percentage 'correct' and reaction time. Schematic faces were composed of the face outline contours and of the brow, eyes, nose, and mouth which could all be modified to produce particular expressions. By masking parts of the face, we examined which features would have the greatest effects on judgements of emotion.

Subjects always gave a saccade to the eyes and fixated even when the eyes were not important for the judgement. They also gave a saccade to the centre of the face and fixated it even when only the mouth was presented. The presentation of only the brow decreased the correct rate on the expression of 'surprise' but played an important role in the 'sad' judgement. The 'angry' judgement depended significantly on the brow and mouth. The eyes contributed greatly to the 'disgusted' judgement. These results suggest that the judgement of facial expressions of emotion can be strongly affected by each part of the schematic face. The concentration of saccades on the centre of the face suggests that the 'configuration balance' of the face is also likely to be important.

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◆ Top-down versus bottom-up control of saccades in texture perception

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An experiment was conducted to examine the influence of luminance, contrast, and spatial frequency content on saccadic eye movements. 112 pictures of natural textures from Brodatz were low-pass filtered (0.04–0.76 cycles deg⁻¹) and high-pass filtered (1.91–19.56 cycles deg⁻¹) and varied in luminance (low and high) and contrast (low and high), resulting in eight images per texture. Circular clippings of the central parts of the images (approximately 15% of the whole image) were used as stimuli.

In the condition of bottom-up processing, the eight stimuli derived from one texture were presented for 1500 ms in a circular arrangement around the fixation cross. They were followed by a briefly presented target stimulus in the centre, which in half the trials was identical to one of the eight test stimuli. Participants had to decide whether the target stimulus was identical to any of the preceding stimuli. During a trial, their eye movements were recorded by means of a Dual-Purkinje-Image eye tracker. In the top-down condition, the target stimulus was presented in each trial prior to the display of the test stimulus. It was assumed that the priming with a target produced a top-down processing of the test stimuli. The latency and landing site of the first saccade were computed and compared between the top-down and bottom-up conditions.

It is hypothesised that stimulus characteristics (luminance, contrast, and spatial frequency) play a more prominent role in bottom-up processing, while top-down processing is adjusted to the particular characteristics of the prime.

◆ **The perception of involuntary prosaccades in an antisaccade task**

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In an antisaccade task subjects are required to generate a voluntary saccade to the side opposite to a small visual stimulus. With fixation-point offset preceding stimulus onset (gap) subjects produce some involuntary saccades to the stimulus and correct them by a second saccade. We wanted to know whether the subjects recognised their errors and whether a recognised sequence (error followed by correction) is different from an unrecognised sequence. To test the access to the correction mechanism, subjects were asked in subsequent experiments to produce the error-correction sequence voluntarily (voluntary sequence).

We used the gap = 200 ms condition. A valid cue was presented 100 ms before stimulus onset. This manipulation increased the error rate (Fischer and Weber, 1996 *Experimental Brain Research* 109 507–512). Subjects indicated errors by key-press. The rate of recognised and unrecognised errors, saccadic size, reaction times (SRT), and correction times (CRT) were determined.

Altogether 93 data sets (400 trials each) from 38 subjects were analysed. The mean error rate was 20%, of which 62% went unrecognised. In sessions with high error rates the fraction of unrecognised errors was high. The SRT of the errors ranged from 80 to 170 ms with a strong mode of express saccades at 100 ms. Both types of errors had the same mean SRT of 117–119 ms. The unrecognised errors were 0.4 deg smaller. They were corrected after a mean CRT of 95 ms. The recognised errors were corrected after 127 ms; in the voluntary sequence the correction occurred after 217 ms. The CRT distributions differ from each other with the unrecognised errors having an extra peak around 45 ms, suggesting different modes of correction, to which perception has different access. These results raise the question why the large and long-lasting changes of the retinal image escape the conscious perception so often.

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◆ **A visual-field anisotropy of the Filehne illusion**

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During pursuit eye movements stationary objects are perceived to move in the direction opposite to the ocular pursuit (the Filehne illusion). The strength of this illusion, which indicates a loss of position constancy, was quantified by a cancellation method. Subjects pursued a small target that moved horizontally at 6 deg s^{-1} over 18 deg. When the target reached the midpoint of its trajectory, a test spot was exposed for 200 ms, either 0.5 or 1 deg above or below the target. Subjects reported the direction in which the test spot appeared to move. Test-spot speed was varied according to subject response (by means of an adaptive program Best PEST) to determine the point of subjective stationarity. This test speed was divided by the target speed to derive a percent measure of the illusion (eg 0% if no cancellation was needed, 100% if cancellation speed equalled that of pursuit). Whereas the magnitude of the Filehne illusion did not depend on the separation of the target and the test spot, it depended strongly ($p < 0.01$) on whether the test stimulus was in the upper (26% illusion) or lower (36.5% illusion) visual field. The present anisotropy is compared to corresponding anisotropies in motion sensitivity (Ehrenstein et al, 1991 *Pflügers Archiv* 418 R39) and pursuit velocity (Schlykova et al, 1996 *NeuroReport* 7 409–412) and conforms with a general view of a differentiation of visual and oculomotor functions between upper and lower visual fields, serving far-space and near-space orientation, respectively (Previc, 1990 *Behavioral and Brain Sciences* 13 519–575).

◆ **Saccadic and electrodermal responses to television violence**

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The concern for TV violence has not been followed by any way to discriminate one type of violent show from another. To ascertain which stimulus elements of TV violence elicit emotional responses we attempted to correlate the electrodermal response with the general saccadic responses.

The simultaneous electrodermal and saccadic responses of children watching violent TV shows were analysed. The saccadic movements were derived from the corneal reflection, computer enhanced, and superimposed on the violent video. Allowing for the individualised response latency, the analog recording of the electrodermal response (as well as an audiometric response) was also superimposed. We found that most electrodermal responses (41%) actually occurred to nonviolent

but frightening stimuli (eg villain's face; grave). Few responses (8%) occurred to actual violent stimuli (eg stabbing). Auditory stimuli (eg gun shot) elicited intense electrodermal responses, the correlation being positively associated with the audiometric level. Statistical evaluation by ANOVA confirmed the significance of the above findings at $p < 0.01$.

We conclude that (1) actual violence may provoke less electrodermal responses than implied violence; and (2) sound potentiates the electrodermal response to elements of violence. We hope that this computer superimposition technique will make it easier to discriminate one violent show from another.

VISUOMOTOR PERFORMANCE

◆ Environmental pitch and three types of pointing

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Many studies have shown that large errors are made when setting a target (T) to visually perceived eye level (VPEL) in a pitched environmental surround. The error in judgement of VPEL is typically about 50% of the environmental pitch angle. An observer can, however, point to the level of the target (T) with much smaller errors (eg Stoper et al, 1992 *Bulletin of the Psychonomic Society* 30 439, found a shift of pointing of only 4% of the environmental pitch). These small pointing errors are found when the observer reaches out with an unseen hand and touches the surface on which T is presented. We call this 'type I pointing'. If longer distances (183 cm) are used the observer must walk (with closed eyes, as in 'pin the tail on the donkey') in order to touch the surface on which T is presented. We call this 'type II pointing'; it results in much larger errors, approaching in angular magnitude the errors in judgement of VPEL.

In the present experiments the observer indicated the level of T by touching a point on an unseen pole which was just to the right of the observer's eyes, and thus separated from T by the viewing distance [as in the 'manual task' used to judge apparent height by Stoper and Bautista (1992 *Investigative Ophthalmology and Visual Science, Supplement* 33 962)]. We call this 'type III pointing'. This method, for both long and short distances, produced large errors similar in magnitude to those of type II pointing. These results are explained by the assumptions that environmental pitch causes an error in the judgement of the apparent horizontal in the sagittal plane (sagittal apparent horizontal; SAH) and that SAH is used in pointing of types II and III, but not of type I.

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◆ Can learning one grasp facilitate novel grasps?

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We investigated whether knowledge acquired during repetitive grasping can be used to grasp a similar object differing in position or size. We conducted two experiments using a mirror to project a computer-generated image to the location of an object to be grasped. Subjects saw the image until initiation of the grasp but were unable to see either their hand or the real object. The training phase consisted of repetitive grasps to a single cube in a fixed position displaying a corresponding image. In the test phase we used the same cube in different positions but displayed only a small position-marker (experiment 1). In experiment 2 subjects grasped for differently sized cubes in the trained position. To indicate size changes we displayed appropriately sized cubes at a different location. In the subsequent control phase of each experiment subjects saw fully rendered cubes in appropriate positions and sizes instead of the position-marker or size cue.

Performance in the test and control phase was similar for all measured grasp parameters, including maximum preshape aperture, maximum speed, and grasp duration. In experiment 2, in which the size of the cubes changed, variability in grasp duration (± 110 ms vs ± 40 ms) and maximum preshape aperture (± 10 mm vs ± 4 mm) was greater in the test phase than in the control phase, indicating increased uncertainty in grasping.

Had subjects learned a single motor routine they would not have been able to grasp so well for objects differing in position or size. Together with our previous results (Ernst et al, 1997, paper presented at ARVO) these findings indicate that subjects can make use of stored representations of an object's position and size to produce an appropriate grasp under open-loop conditions.

◆ **Mentally simulated reaches for visual objects: Effects of stimulus orientation and biomechanical constraints**

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Recent evidence suggests that mentally simulating an action involves many of the same neuropsychological mechanisms as overt performance. A series of experiments were conducted to evaluate whether representations involved in mentally simulated reaches are constrained by the same biomechanical factors that limit actual movements. Subjects were asked to use either the right or the left hand to acquire a dowel presented visually in one of 24 different orientations within the picture plane. In reaching studies, subjects responded by grasping the target using either an overhand or underhand grip; in the mentally simulated studies, subjects responded by vocally indicating whether they would prefer an overhand or underhand grip if they were to actually grasp the object.

Results indicate substantial correspondence between actual and mentally simulated reaching. Grip preferences in both situations are highly correlated, and reflect biomechanical constraints on rotation of the forearm. In both actual and mentally simulated tasks, subjects show clear preferences for grips that minimise perceived awkwardness. In contrast to related work, the time required to perform mentally simulated reaches for visual objects was found not to increase linearly with distance from the resting posture of the response hand.

Findings are discussed with respect to the hypothesis that actual and mentally simulated actions involve the same internal representations.

◆ **Accuracy of pointing to invisible landmarks in a familiar environment**

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Humans develop a mental representation of their environment that enables them to solve their day-to-day navigation tasks. The nature and quality of this representation can be probed experimentally by studying spatial tasks like distance and bearing estimation. We investigated pointing accuracy in an outdoor environment as part of a larger project in which we compare spatial behaviour in real environments with that in virtual environments (virtual reality).

We carried out experiments in the centre of Tübingen (ca 600 m × 400 m). Standing near one of eleven well-known landmarks, subjects had to turn a pointer in the estimated direction of each of the other ten invisible (occluded) landmarks (all ten subjects had lived in Tübingen for at least two years). The estimated directions were read by the experimenter from a hidden compass and later compared with the actual directions. This procedure was repeated from all eleven locations along the subjects' route through the town.

The mean absolute angular error of pointing was 10.8°, while the individual subject's means ranged from 9.1° to 15.0°. We found highly significant differences in pointing accuracy for the different locations; mean absolute error ranged from 6.3° to 15.8° ($n = 10$). Systematic asymmetries in pointing from one landmark to another and back were not found.

The pointing accuracy found in this study is clearly better than that found in most other studies, which might relate to the familiarity and the size of the environment. The apparent absence of an asymmetry in the pointing directions between two locations is consistent with the notion of a metric mental map.

◆ **Even experienced drivers have the wrong concept about how to change lanes**

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Imagine changing lanes on a motorway, and in particular the series of angles through which the steering wheel passes in completing the manoeuvre. The vast majority of us describe turning the wheel once and then returning the wheel to the middle position. This is wrong, because we have failed to describe the appropriate symmetrical motion of the steering wheel in the opposite direction required to straighten the car. To investigate this misconception and so as to determine the type of motor programs used during steering, we tested the ability of subjects to change lanes with and without visual feedback. Five licensed drivers drove in a simulated environment projected on a 180° screen using a force-feedback steering wheel. A straight four-lane motorway appeared alternately with normal (daylight) or zero visibility (dark tunnel). In both conditions subjects were asked to change lanes—either to the left or to the right. In the condition without visual feedback no other feedback about performance was given.

Without visual feedback the results showed a predictable increase in variance in the final heading but also suggested a systematic deviation of heading towards the direction of the lane change ($p < 0.001$), due to the subjects' failure to complete the lane changing manoeuvre. Hence, we conclude that despite the highly practised nature of the task of lane changing, it is not stored as a complete motor program, but is instead achieved by the interplay of a simple steering program and visual feedback about current heading and location on the road.

◆ **What spatial frames of reference are used to guide off-axis aiming?**

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What spatial frames of reference are used to guide body centred actions such as pointing and aiming? Do observers learn to use body-scaled frames of reference with specific points of origin (eg hip vs shoulder)? Do they extrapolate general information about body scaling? Do they learn about the position of the body (and its individual parts) in absolute space? We investigated these questions using two kinds of aiming: off-axis aiming vs along-axis aiming. Subjects aimed a 'gun' (a laser pointer mounted at the end of a stick with a button at the other end) at various targets under three conditions. They practised aiming in one position for 60 'shots' and then changed to a new position and completed another 60 shots. Transfer across position of 'gun' in absolute space, across position of body in absolute space, and across position of gun relative to body were assessed. Results suggested that off-axis aiming was controlled by a closed-loop error correction system requiring sight of results for learning to occur. Further, changes in the position of the body in absolute space (from kneeling to standing or vice versa) led to the worst aiming performance. Changes in gun position relative to the body or in absolute space had less effect on aiming accuracy, which suggests that it is not dependent on specific learned sensory-motor linkages. On the basis of these results we propose a preliminary model for off-axis training.

◆ **Is rotation of visual mental images a motor act?**

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The relationship between the mechanisms of vision and of visual mental imagery, such as mental rotation, has been well established. The relations between mental rotation and motor action, on the other hand, have hardly been studied, despite the fact that, ecologically, most non-mental rotation is the result of motor actions such as manual manipulation of medium-sized objects. I propose the following motor/imagery hypothesis: transformations of visual mental images are functionally closely related to the planning stages of the motor system. There is a certain amount of indirect support for this hypothesis in the literature. In the present work the motor/imagery hypothesis was tested directly, by means of a dual task paradigm. Subjects performed two tasks simultaneously: the Shepard-Cooper visual imagery task, which involves mental rotation; and a motor rotation (which could not be seen), turning a joystick handle in the plane of the visual image at a previously learned angular speed and direction. The motor/imagery hypothesis predicts a correlation between corresponding features of the two rotations.

The results strongly confirm the motor/imagery hypothesis. The concurrent motor task shifts the classic V-shaped mental rotation RT curve: mental rotation is faster and less error-prone when it is in the same direction as the motor rotation than when it is in the opposite direction. Moreover, there is a strong correlation between the speeds of the two rotations: all else being equal, subjects' mental rotations were slower when their manual rotations were slower, and vice versa.

◆ **Visual motion induces effector movement**

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A left-hand response to a left-hand stimulus is faster than a right-hand response to the same stimulus, even when spatial location is irrelevant to the task at hand. The existence of this spatial stimulus-response correspondence effect suggests that spatial properties of actions to be performed can be pre-specified by spatial properties of perceived events, so that actions are induced by perceptual content. If this view is correct, one should be able to show that not only spatial positions of actions can be pre-specified by properties of perceived events, but other features of actions as well. Specifically, I attempt to show that the direction of a to-be-executed movement can be specified by the direction of a moving stimulus.

To study this question a variant of the Simon paradigm was developed: subjects were required to monitor a spot-like stimulus moving from left to right or from right to left on a display. At some point in time the spot would change its colour (from white to blue or red) and the subject had to respond differentially to the respective colour. Two aspects of this situation were varied. First, the type of the action-relevant signal was varied: it could either be a dynamic moving signal or a static non-moving one. Second, the type of response was varied: subjects were required to respond to the colour either with a dynamic response (moving a stylus to the left or right) or with a more static response (pressing a button on the left or on the right).

◆ **People with good nonverbal thinking show high scores in 'virtual aircraft landing'**

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We have used a 3-D studio to generate a situation of virtual aircraft landing with the object of investigating if everyone can solve this task successfully. A virtual surface was covered with green texture which had large grains. Landing had to be done at an angle of about 30°. The space above the surface was divided into seven adjacent layers. Landing began from the first layer and went through all the layers, the seven layer being adjacent to the surface. The task of the subject was to stop the virtual landing in a given layer by pressing a key and using only visual cues of approaching the surface. Seventh subjects participated in the experiment; each made about 180–300 trials. Two subjects showed the highest score (A-group); three could not solve this task at all (they worked at the level of guessing) (B-group); the remainder produced intermediate scores. At the same time all subjects were tested by means of standard verbal and nonverbal tests to evaluate the type of thinking. Subjects from the B-group had a clear verbal or mathematical type of thinking. On the contrary, subjects from the A-group had the highest scores in the Kettel and Raven tests (tests for nonverbal thinking). Moreover the two subjects from the A-group had the highest level of driver skill in comparison with the others. Thus individuals with poor nonverbal thinking appear to perform worse at sensory-motor activities such as driving and aircraft landing.

INTEGRATION OF VISION WITH OTHER SENSES

◆ **Active visual examination of static and dynamic autostereograms: effects of performance in a visuomotor task**

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The purpose of our experiments was to investigate whether visual perception could be influenced by extended presence 'inside' a 3-D virtual reality of computer-generated autostereograms (AST). In addition to usual ASTs (with stationary hidden figures, words, and 3-D surfaces) we used novel, dynamic autostereograms (DASTs), generated in a 3-D studio as a short film, where consecutive frames were ASTs with small modifications of the disparity values. The percept resembled textured 'mushrooms' rising towards the observer from the main frontal plane. When the disparity rose to some limiting value, the growth stopped and was inverted: a convexity was gradually transformed into a concavity and vice versa. The maximum range of local disparity change was ± 0.6 deg. Our ASTs and DASTs were arranged in a sequence of increasing complexity. During a 'training' session (3–15 min), the subject had to actively examine the sequence and recognise all hidden forms.

Performance in threading a needle with one (the right) hand was recorded before and after 'training'. The needle was set at a 50 cm distance from the subject, turned so that the eye of the needle was not visible. The total time of five successful trials was measured for each of five right-handed subjects with normal or corrected vision. In two sets of experiments, this visuomotor task was carried out under binocular and monocular viewing, respectively.

In both conditions, performance improved significantly (Fisher's criterion) after the 'training' session. The total time decreased from 50–55 s to 35–40 s in the binocular condition and from 70–75 s to 47–55 s in the monocular condition. The results are discussed in terms of 'tuning' of vergence eye movements during autostereogram examination.

◆ **Effects of observer orientation on perception of ego- and exocentric spatial locations**

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Perceived eye position and/or the perceived location of visual targets are altered when the orientation of the surrounding visual environment (Cohen et al, 1995 *Perception & Psychophysics* 571 433) or that of the observer (Cohen and Guzy, 1995 *Aviation, Space, and Environmental Medicine* 66 505) is changed.

Fourteen subjects used biteboards as they lay on a rotary bed that was oriented head-down -15° , -7.5° , supine, head-up $+7.5^\circ$, and $+15^\circ$. In the dark, subjects directed their gaze and set a target to the apparent zenith (exocentric location); they also gazed at a subjective 'straight ahead' position with respect to their head (egocentric location). Angular deviations of target settings and changes in vertical eye position were recorded with an ISCAN infrared tracking system.

Results indicated that, for exocentric locations, the eyes deviate systematically from the true zenith. The gain for compensating changes in head orientation was 0.69 and 0.73 for gaze direction and target settings, respectively. In contrast, 'straight ahead' eye positions were not significantly affected by changes in the subject's orientation. We conclude that subjects make systematic errors when directing their gaze to an exocentric location in near-supine positions. This suggests a systematic bias in the integration of extra-ocular signals with information regarding head orientation. The bias may result from underestimating changes in the orientation of the head in space. In contrast, for egocentric locations, where head orientation information can potentially be discarded, gaze directions were unaffected by head orientation near supine.

◆ **Effects of head orientation on the variations in the discrimination of shading orientation**

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We have previously shown that errors in judging the direction from which a smooth surface is illuminated (ie shading orientation) are not random (Moshonkina et al, 1993 *Perception* 22 Supplement, 100), but vary with this direction in a regular manner. In the experiments described here we investigate whether the same regularities occur when the head is tilted—specifically, whether the gravitational or the head frame of reference is predominantly used in estimation of shading orientation.

Stimuli were computer images of spheres (23 deg diameter) presented briefly (for 100 ms, excluding effects of eye movements). The spheres were apparently illuminated from one of 24 directions spaced at equal (15°) intervals around the sphere in the plane of the display. One of these was randomly chosen for each trial. The task was to define the direction of the apparent illumination on a clock scale with half-hour accuracy. The subject's head was either upright or tilted to the left by 30° . Viewing was left monocular.

The errors in the estimation of illumination direction showed the same systematic dependence on 'true' direction regardless of head orientation. These regularities can be described as follows. (1) Estimates were most accurate when the shading gradient was along the horizontal axis (ie with the illuminated pole of the sphere on the right or the left), with greater errors when the gradient was along the oblique axis or vertical. (2) With oblique shading, the estimates showed a systematic tendency to bring the illumination direction closer to the horizontal axis than in 'reality'. (3) The largest errors occurred when the illuminated pole was oriented downwards. This suggests that the gravitational frame is important in the discrimination of shading orientation.

A significant effect of head orientation was observed when the illuminated pole was oriented downwards. The most probable estimation error was -30° with head upright but -60° with head tilted. This difference is opposite to that expected from application of the head frame of reference.

◆ **Superior detection of audio-visual signals over visual signals: Are overt movements necessary?**

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Perrott et al (1990 *Perception & Psychophysics* 48 214–226) suggested that the use of auditory information to guide saccadic eye movements may mediate the facilitation of visual search by auditory spatial information. We modified a later paradigm (Perrott et al, 1991 *Human Factors* 33 389–400) to re-examine the nature of auditory facilitation for both covert and overt orienting to targets located $\pm 15^\circ$ from a central fixation point.

Participants made a 2AFC response to the orientation of a visual target in each of four conditions: the target was presented (1) alone, or target onset was accompanied by (2) a spatially coincident sound, (3) a centrally located 'status' sound, or (4) a change in the fixation point. The auditory stimulus was a 10 Hz click train: the visual target appeared on the left or right of the fixation point at $\pm 15^\circ$ azimuth and 0° elevation. In experiment 1 foveal vision was necessary to identify the target. However, the stimulus used in subsequent experiments could be accurately identified without overt receptor movement. Subjects were instructed to use eye movements (experiment 2) or to maintain fixation on a central cross throughout the session (experiment 3).

Spatial and status sounds had a significant facilitatory effect on target identification both when overt and when covert orienting were employed. This strongly suggests that audio-visual facilitation is not dependent upon overt orienting.

◆ **Characteristics of visual and haptic functions relate similarly to alpha rhythm parameters**

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Visual short-term memory (STM) for digits and reaction times (RT) has been found to correlate significantly with parameters of the occipital background EEG: the dominating alpha frequency and the alpha spindle duration (Markina and Maltzeva, 1993 *Proceedings of 7th EMPS in Trier* pp 311–314). STM span is more closely related to the latter, RT to the former of these parameters. We studied how certain characteristics of accuracy in haptic performance correlated with the same alpha parameters. We measured the control of line-length scatter, and the quantity of metrically accurate copies, in the standard task of blindly copying zigzag lines. The two measures were statistically independent of each other. We found that these characteristics of haptic performance show a similar pattern of correlation with alpha parameters as do STM and RT. Line-length scatter, as an index of control processes in the motor system, is related to alpha spindle duration. The quantity of metrically accurate copies, as an index of how precisely external metrical parameters are mapped to a subjective representation, is related to the dominating alpha frequency. The results are supported by factor analysis. They imply that (1) there are similar types of structures in visual cognition and haptic processes, and (2) the alpha rhythm parameters considered underly both kinds of processes.

◆ **Deafness and attentional visual search: a developmental study**

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Neurophysiological (epigenetic specialisation of cortical areas) as well as behavioural (sign language, visual control of spatial surroundings) constraints suggest that deaf people should develop heightened abilities of processing parafoveal/peripheral visual information. Electrophysiological (visual event-related potentials) and psychophysical research using visual detection tasks on congenitally deaf adults corroborates this viewpoint (Neville, 1994 *The Cognitive Neurosciences* 219–231). The aim of this study was to examine whether this ability remains when the visual detection task requires a spatiotemporal organisation of attention.

Forty congenitally bilaterally deaf (from a specialised institution) and sixty-four hearing subjects, subdivided into five age groups (from 7 years of age to young adults) performed four visual search tasks. The results showed that the younger deaf children performed dramatically worse than the aged-matched hearing children. This difference in performance between deaf and hearing children, however, disappeared at an age level of 11 years. Deaf adults did not perform significantly better than hearing adults. The data obtained in children have been replicated in a longitudinal study (re-test two years after). We are currently trying to determine which attentional mechanisms are more deficient in young deaf children (spatiotemporal organisation of search, engagement/disengagement of attention, etc) and what underlies the apparent amelioration of their deficit during development.

◆ **Fusion of visual and proprioceptive information about hand position prior to movement**

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The problem whether movement accuracy is better in the full open-loop condition (FOL, hand never visible) than in the static closed-loop condition (SCL, hand only visible prior to movement onset) remains widely debated. To investigate this controversial question, we studied conditions for which visual information available to the subject prior to movement onset was strictly controlled. The results of our investigation showed that the accuracy improvement observed when human subjects were allowed to see their hand, in the peripheral visual field, prior to movement: (1) concerned only the variable errors; (2) did not depend on the simultaneous vision of the hand and target (hand and target viewed simultaneously vs sequentially); (3) remained significant when pointing to proprioceptive targets; and (4) was not suppressed when the visual information was temporally (visual presentation for less than 300 ms) or spatially (vision of only the index fingertip) restricted. In addition, dissociating vision and proprioception with wedge prisms showed that a weighed hand position was used to program hand trajectory.

When considered together, these results suggest that: (i) knowledge of the initial upper limb configuration or position is necessary to plan accurately goal-directed movements; (ii) static proprioceptive receptors are partially ineffective in providing an accurate estimate of the limb posture, and/or hand location relative to the body, and (iii) visual and proprioceptive information is not used in an exclusive way, but *combined* to furnish an accurate representation of the state of the effector prior to movement.

◆ **The MacKay phenomenon: Is it all hand-waving?**

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When a table-tennis bat with a light-bulb in its centre is waved about by another person in a stroboscopically lit room, the light appears to float free from the bat, although it is physically fixed. A related phenomenon was reported originally by MacKay [1958 *Nature (London)* **180** 507–508]. This illusion disappears in an active condition, where observers move the bat with their own hands, which suggests a proprioceptive basis for the illusion. In our implementation with a Power Macintosh computer, the illusion occurred in both conditions. Thus ‘hand-waving’ is not inherent to the illusion but may exert its effect indirectly by promoting predictive eye-tracking movements.

To test the hypothesis that the perceived position of the bulb is extrapolated between a visual icon, tied to retinal coordinates, and its actual physical location thus causes the displacement illusion we performed two experiments. From experiment 1 we found that for simple one-dimensional movement, the displacement illusion occurs only when there is a change in direction such that the bulb appears to ‘overshoot’ the bat. In experiment 2, using random two-dimensional movement, we manipulated the length of the dark (non-visible) period. The overshoot increased from around 30 min arc at 65 ms to around 60 min arc at 300 ms. For longer dark periods (up to 2000 ms), the illusion occurred providing the change in direction was within the 300 ms window after stimulus offset. These results show that during discontinuous illumination, perceived location is determined by extrapolation.

FRIDAY

ORAL PRESENTATIONS

PLENARY LECTURE

◆ The conscious vision of the blind

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The most fundamental function of the visual brain is to acquire knowledge about the constant, essential properties of the visual world, in conditions in which the information reaching the brain is never constant from moment to moment. This requires the brain to undertake complex operations on the incoming visual signals, discounting all that is not essential for it to acquire knowledge about the world, selecting that which is important, and subjecting the latter to operations that make the brain independent of the continually changing and non-essential information reaching it. One strategy that the brain uses in undertaking this task is that of functional specialisation, through which different essential features, such as motion and colour, are extracted in specialised and geographically distinct visual areas lying outside the primary visual cortex area V1. Our recent psychophysical experiments show that, just as the processing systems for different attributes of vision are separate, so are the final perceptual systems, since different attributes of the visual scene such as colour, form, and motion are perceived at different times, with colour being ahead of motion by about 80 ms, thus leading to a perceptual asynchrony in terms of real time. The end-result of the operations in these individual areas is the acquisition of knowledge. But knowledge can only be acquired in the conscious state. A conscious awareness is therefore the corollary of activity in the specialised areas. Recent experiments using imaging and time resolution methods as well as patients blinded by lesions either in V1 or in more extensive parts of the visual cortex show that the activity in one or a small number of visual areas, without involvement of V1, can give rise to both conscious experience and a crude knowledge about the visual world. This leads us to the conclusion that consciousness itself may be modular.

[The work of our laboratory is supported by the Wellcome Trust, London.]

COLOUR

◆ Photoreceptor nonlinearities can account for the MacAdam ellipses

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Colour perception is known to be nonlinear, as highlighted by D L MacAdam (1942 *Journal of the Optical Society of America* 32 247). He showed that the just noticeable difference (JND) between two colours is not constant and depends nonuniformly on the values of these two colours: under constant illumination, the constant-JND loci, drawn in the xy colour space around various centres, appear as ellipses of different orientations and eccentricities. Though this phenomenon encompasses the whole perception chain, from receptors to higher levels, we show that it can be accounted for mainly by the nonlinearity of receptor transduction.

We start from the colorimetric space XYZ defined by the CIE (1931) and its linear transformation into the cone-excitation space LMS , using data from V C Smith and J Pokorny (1996 *Color Research and Applications* 21 5). Then we consider a perceptual colour space obtained by the nonlinear correspondence between the L , M , and S cone inputs and the l , m , and s cone outputs, through a compression law of Michaelis-Menten type, eg: $l = L/(L + L_0)$. In this space, the JNDs are circles, drawn on the surface corresponding to the nonlinear transformation of the constant-luminance plane in LMS , around the corresponding centres. By looking at the projections of those circles onto the constant-luminance plane in LMS , and their representations in the colorimetric space xy , we naturally obtain the ellipses of MacAdam. The formulas, fitted to the data, provide the parameters of the LMS -to- lms transformations.

◆ Studying colour appearance by the uniform scaling of colour circles

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Scaling experiments presented at ECVP 1996 (Ovenston and Whittle, 1996 *Perception* 25 Supplement, 16) demonstrated the importance of the background chromaticity in setting subjective equal-interval colour scales along the L(-M)-cone and S-cone axes of Macleod-Boynton isoluminant chromaticity space.

In the current experiments we also investigate colour scaling but around circles centred on different background chromaticity points. This is done in a logarithmic version of the MacLeod–Boynton diagram, which is much closer to an equal-subjective-interval diagram than the linear version. However, colour circles set with even geometrical spacing in the log diagram do not appear to have even subjective spacing. Preliminary results show that setting hue to even subjective spacing is a convenient and powerful method for studying the role of constant-cone-excitations and opponent-colour axes in determining hue.

◆ **Measurements of ‘von Kries’ contrast colours**

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At two previous ECVPs we showed demonstrations and preliminary measurements of contrast colours in a haploscopic display. Colours were presented in different uniform surrounds to the two eyes, superimposed in the binocular field so that they appeared to be in the same surround. Here we report more extensive matching experiments. The principal results are as follows: (1) To a first approximation, in a log MacLeod–Boynton space, perceived colour is determined by the surround-to-colour vector (SCV). The remaining results are second-order deviations from this von Kries scheme. (2) Increment colours are tinged with the hue of the surround, even though that surround hue cannot be seen. This effect of the sign of luminance contrast seems to be just a multiplicative shift: otherwise, increment and decrement data can be superimposed. (3) SCVs for a constant perceived colour shrink and expand slightly with movement along the S-cone axis, suggesting that the transform of S-cone excitation is less compressive than a logarithmic function. (4) SCVs show consistent small rotations, suggesting that $L - M$ and $S - (L + M)$ axes are not completely independent.

◆ **Chromatic response curves of surface colours**

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Basic data in colour vision such as chromatic response curves were obtained with aperture colours. It is not possible to apply the cancellation technique to define redness or yellowness components etc in a surface colour. A method was developed to obtain such information (Indow, 1987 *Die Farbe* 34 253–260), which was based on the expanded form of multidimensional scaling. The results by an improved method are presented. First, it is shown how multiattribute perceptual differences between two Munsell colours, P_j , P_k , are predicted by distances d_{jk} in the current Munsell solid. Colour differences d_{jk} are defined by matching with lightness differences in Munsell gray scale and root-mean-squares of $(d_{jk} - d_{jk})$ is $0.2 \sim 0.3$ in the unit of Munsell Chroma C. Second, principal hue vectors f_α , $\alpha = R, Y, G, B$, or P in addition, are defined in the current Munsell solid. As shown before, f_B is shifted from $5R$ in the direction of $5P$, irrespective of whether P is included or not. Overall root-mean-squares of (scaled values of principal hue α in a colour j —coordinates of P_j on f_α) is about 0.6 in the unit of C. On the basis of these findings, it becomes possible to define principal hue components for any Munsell colours and hence chromatic response curves are obtained as a function of H, V, and C.

◆ **Discrimination of reflectance changes under simultaneous illumination changes**

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Relational colour constancy refers to the perception of constant relations among surface colours under illumination changes. We tested whether the ability of human observers to discriminate illumination from reflectance changes in a scene involves high-level attentional mechanisms. Observers were shown pairs of computer-generated Mondrian patterns with the number of patches varying between 2 and 49. On each trial a Mondrian pattern was presented for 1 s and replaced by a second pattern. In half of the trials in each experimental condition, the chromaticity of one patch was changed. Observers were required to discriminate whether a reflectance change occurred. Three conditions were run. In condition A, the illumination of the second Mondrian underwent a chromaticity change. In condition B, the chromaticity of the second Mondrian illumination remained constant, whereas its overall level was either increased or decreased. In condition C (control), the illumination was exactly the same in both Mondrians. Functions relating reaction time to number of patches in the display were compared. Data suggest that different mechanisms are involved in discriminating reflectance changes associated with different types of illuminant changes.

◆ **Evidence for a dual colour code for 'object colour' and 'illumination colour' in centre-surround configurations with inhomogeneous surrounds**

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We provide evidence that the surround-dependent change in appearance of an infield in a centre-surround configuration is not to be understood as an elementary recoding of channels by a simple surround-dependent gain control but in fact mirrors the triggering of a much more complex mechanism for establishing a dual code for 'object colour' and 'illumination colour'.

We constructed centre-surround configurations—referred to as Seurat configurations—whose surrounds are given by 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. Unique yellow settings were made for the infield. Our results suggest that the visual system seems to interpret a reduced variance of receptor codes for the surround as an indication of an illuminant that has to be discounted at the location of the infield. Furthermore, for the case of an isoluminant surround with strong spatial red-green modulation only, the unique yellow settings strongly tend towards the ones of an achromatic surround, ie the surround seems to be almost ineffective with respect to a differential gain control.

While our data on Seurat configurations with same space-averaged surrounds refute simple notions of functional equivalence, they suggest an interpretation in terms of a triggering of elementary perceptual categories related to 'object colour' and 'illumination colour'.

◆ **Effect of ambient illuminant on surface colour constancy**

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Generally, we are completely enclosed in a real environment, which may act as an entire view-field or adapting field. But in most studies on colour constancy experiments have been made with spatially restricted stimuli. We built a room with gray (N5) walls inside to measure the effect of ambient illuminant on colour constancy. The room illuminant could change its colour from white (D_{65}) to either blue, orange, green, or purple. The observer sat in this main room and adapted to the illuminant for 5 min before the start of the experiment. The observer was shown a smaller room, which had the same variable-colour illuminant, through an aperture (11 deg × 8 deg) in the left side wall. We set the illuminant for each room independently, but in asymmetric illuminant-colour conditions either was set to white. The observer viewed the central part of a colour CRT monitor, placed behind a small aperture (5 deg × 5 deg) in the front wall, and matched its colour appearance to four OSA colour chips in the smaller room.

Under symmetric illuminant conditions, eg blue vs blue, the observers' settings showed a complete match with the physical chromaticities of the colour chips. In asymmetric illuminant conditions, eg white vs blue, matched colours showed systematic deviations from both physical chromaticities and colour constancy. This implies that taking the ambient illuminant as adapting field did not yield perfect colour constancy. We introduce a simple model based on incomplete adaptation to the ambient illuminant and a spatial-interaction mechanism, which accounts for our results.

◆ **Colour constancy in birds: an alternative mechanism?**

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When recognising a surface colour, the visual system discounts the illumination, apparently by using some reference surfaces (like a spectrophotometer). To recover the illuminant colour it uses signals from different, sometimes remote, parts of the scene viewed either in sequence or in parallel. As a result, humans and animals fail to recognise the colour of a patch that is locally illuminated with a narrow light beam different in colour from the ambient illumination, but show good colour constancy when the beam envelops the surrounding scene.

The results obtained in birds distinguish them from humans and all animals hitherto investigated. The behaviour of hole-dwelling birds was studied in the wild by the method of alternative choice of entrance into experimental nesting-boxes having three entrances marked with coloured stimuli made from papers painted in different shades of blue, grey, or orange (see Maximov and Derim-Oglu, 1996 *Perception* 25 Supplement, 98, and the corresponding WWW site: <http://www.digipark.com/science/meta>). The spectral content of the direct sunlight illumination was changed by filters, either locally at the stimuli or over the whole front panel of the experimental box. In such artificial lighting conditions the birds proved to be incapable of using a neighbouring

white surface as a sign of the illumination to discount its effect on the colour of objects. These unexpected results can be explained by the ability of animals with colour vision of rather high dimensionality to take recourse to local mechanisms of colour constancy that extract the colour information which is invariant to changes of the illumination, using certain a priori constraints on environmental light spectra. Natural daylight spectra have been shown to satisfy these constraints.

TEMPORAL PROCESSING

◆ The detection of interocular phase differences

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When dynamic visual noise such as the 'snow' on a detuned television receiver is viewed with a temporal delay between the two eyes, the noise appears to rotate in depth around a vertical axis [Ross, 1974 *Nature (London)* **248** 363–364; Morgan and Tyler, 1995 *Proceedings of the Royal Society of London, Series B* **262** 371–376]. Random noise evidently contains a wide spread of spatiotemporal Fourier components, including those for horizontal motion, which may cause a Pulfrich effect when there is an interocular delay. To investigate the temporal-frequency components necessary for the effect, a display was designed containing only a single temporal frequency. Spatially broad-band grey-level noise was flickered, such that each pixel of the noise was sinusoidally modulated over time. An interocular delay was introduced as a phase lag of the flicker in one eye. This produced a rotating depth effect. The threshold for detecting the phase shift was about 5° of phase angle, irrespective of temporal frequency, except for frequencies greater than ~20 Hz, when the depth effect was no longer seen. Tests of several models of the phase-lag detection are described, including the possibility that there are dichoptic motion detectors also tuned to stereodisparity.

◆ Temporal phase affects spatial binding in depth perception

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The temporal linking of spatial information is essential for coherent space perception. We investigated the effect of the temporal phase of flickering 'inducers' in depth perception. Stereo half-images were generated on the left and right halves of a large-screen video monitor and viewed through a mirror stereoscope. The half-images portrayed a solid-black vertically oriented bar seen against a white background. Two brackets immediately flanking this bar could be placed in crossed or uncrossed disparity relative to the bar. A pair of thin white 'bridging lines' could appear on the black bar, always at zero disparity. Brackets and bridging lines could be flickered either in-phase or out-of-phase. Observers judged whether the brackets appeared in front of or behind the black bar, with disparity varied over trials according to a method of constant stimuli.

We found that when bridging lines were absent, the depth location of the brackets was predictably dependent on disparity sign, with a small bias for "behind" judgements owing to occlusion. When bridging lines and brackets flashed in temporal phase, depth judgements were markedly biased toward "in front"; when the bridging lines and brackets flashed out of phase, this bias was much reduced. This biasing effect also depended on the spatial offset of lines and brackets. We conclude that depth perception is strongly influenced by the temporal phase of the spatial information. [Supported by grants from JSPS and NIH]

◆ Central visual persistence as measured by the redundant target effect

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We measured the duration of central visual persistence by testing normal subjects for the redundant target effect (RTE), ie the speeding up of reaction time to redundant visual stimuli in comparison to similar single stimuli. Brief LED-generated flashes were presented to 14 normal subjects either singly or in a pair at peripheral visual field locations (5 or 30 deg along the horizontal meridian). Stimulus pairs could appear either in the same hemifield at different locations or in opposite hemifields with a stimulus onset asynchrony (SOA) ranging between 0 and 100 ms. The subject's task was to press a key as soon as possible following the appearance of either a single stimulus or of the first stimulus in a pair. We found a robust and consistent overall RTE with double stimuli yielding faster RTs than single stimuli for both intrafield and interfield presentations. The effect decreased significantly from 0 ms to 40 ms SOA and at longer SOAs the speed of response to stimulus pairs was indistinguishable from that to a single stimulus. We believe that the longest SOA compatible with a reliable RTE (40 ms) reflects the duration of central persistence. Evoked-potential evidence gathered in our laboratory suggests that the locus of such persistence may be the extrastriate visual cortex.

◆ **Detection of chromatic and achromatic patterns at threshold: RT evidence of sustained and transient mechanisms**

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In primates, relatively slow sustained-like physiological mechanisms mediate chromatic processing and rapid transient-like mechanisms mediate low-spatial-frequency achromatic processing. Our objective was to investigate the role of transient and sustained mechanisms in the detection of chromatic and achromatic gratings with the use of a reaction time (RT) paradigm. Following Tolhurst (1975 *Vision Research* **15** 1143–1149), we constructed RT histograms using near-threshold grating stimuli. Tolhurst showed that, for low-spatial-frequency achromatic patterns, the RT histograms cluster around the onset and the offset of the pattern, indicating transient detection. His onset and offset distributions were consistent with probability theory. With high spatial frequencies, RTs are evenly distributed over the duration of the stimulus presentation, showing the operation of a sustained mechanism.

When we used low-spatial-frequency ($0.22 \text{ cycle deg}^{-1}$) isoluminant red–green gratings, the RT histograms were unimodal, revealing detection mechanisms with predominantly sustained characteristics, as expected. RT histograms obtained with low-spatial-frequency achromatic stimuli in our study were bimodal. However, when we compared small and large fields, the shape of the RT histogram varied in a manner which could not be accounted for by a simple probabilistic model. This can be rationalised if onsets and offsets are not equally detectable.

◆ **Multiple visual latency**

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It has long been known that the time taken to detect a dim visual stimulus is longer than that to detect a bright one, with a relative delay of up to several tens of milliseconds. Systematic studies of various phenomena demonstrating this delay have revealed that the perceptual latency decreases monotonically as the stimulus intensity increases. Because latencies measured by psychological methods and cortical evoked responses are very similar to electroretinogram latencies, it has become a common belief that there is little in the intensity-dependent latency function that cannot be explained by retinal processes. We report evidence that there is not one absolute visual delay common to the whole visual system, but that the delay varies considerably in different perceptual subsystems. The relative visual latency was found to be considerably shorter in a movement-discrimination task than in other perceptual tasks which presume visual awareness of the onset of visual events, or of their temporal order.

◆ **Stimulus location is processed faster than stimulus colour**

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There is a convergence of anatomical, electrophysiological, neuropsychological, and psychophysical data to support the dissociation of visual pathways into two main streams projecting from occipital to frontal cortex via the posterior parietal lobe (dorsal route) and via the inferotemporal lobe (ventral route). It is usually assumed that the dorsal route provides information that is useful for driving an action toward the stimulus (ie metric properties, such as localisation), whereas the ventral route extracts information useful for identifying it (ie intrinsic properties, such as colour). It is known that pointing movements can be reoriented to a novel target location within a short delay (about 110 ms), even when the target jump cannot be detected because of saccadic suppression. Electrophysiological studies have suggested that inputs to the dorsal pathway have a latency shorter than inputs to the ventral pathway.

We compared latencies of visuomotor processing for colour and location during a pointing task. Target location and/or colour were altered upon movement onset. Instructions were to correct movement direction or to interrupt the movement according to the target change. We found that in both cases colour processing was slower (by about 100 ms) than location processing of the same target. Performance observed for identical movement speed was always higher for location responses whereas movement duration spontaneously chosen by subjects was longer when they had to process colour. Strikingly, corrections were also observed with the interruption instruction. We conclude that (1) colour is processed more slowly than location, and (2) automatic corrections can be observed prior to response inhibition for fast movements.

TEXTURE AND IMAGE SEGMENTATION

◆ What statistics determine segmentation of orientation-defined textures?

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Beck suggested that texture segmentation is based upon differences in the first-order statistics of stimulus features such as orientation, size, and contrast. However, this theory does not indicate how these differences might be quantified, or what properties of the statistics might be used. Some alternative models postulate that texture segmentation is determined by the responses of spatial-frequency channels, where the channels contain both a linear filtering mechanism and various nonlinearities. Such models do a good job of predicting human performance, but do not give us much insight into what textures will segment, since the comparison carried out by the model is often obscured by the details of the filtering, nonlinearity, and image-based decision processes.

It is suggested here that, for orientation-defined textures (eg in which each 'texel' has a single orientation), segmentation is well-described by something like the 'significance' of the differences between (1) the mean orientations, and (2) the angular variances of the two textures. The 'significance' of the difference in means takes into account the variability in the texture, so that two homogeneous textures with means differing by 30° may easily segment, while two heterogeneous textures with the same difference in mean may not. Furthermore, it is shown that these statistics may be computed in a biologically plausible way, which greatly resembles the typical filter-based approaches to texture segmentation. Thus the connection between statistical theories of texture segmentation and spatial-frequency channel models becomes more transparent.

◆ Texture segmentation and the familiarity effect

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Texture segmentation performance is usually defined as being data-driven and bottom-up: visual features of the stimulus—like orientation differences between target and background texture elements—are then evaluated automatically. The question investigated in the experiments reported here is: Are there some hints that not only 'pure visual features' determine segmentation performance, but other factors like the familiarity of the stimulus material already exert an influence at these early stages of information processing? The familiarity effect is revealed by better performance when detecting an unfamiliar element embedded in familiar elements (eg an inverted letter 'N' among correct 'N's) compared with the familiar element embedded in unfamiliar elements (see, eg, Frith, 1974 *Perception & Psychophysics* 16 113–116).

In a series of experiments, spatial and temporal factors of the stimulus conditions (eg density, jitter, display size, presentation time) have been varied, so as to determine the constraints under which the familiarity effect influences texture-segmentation performance. Results showed that the familiarity of texture elements had a rather strong influence on early visual processes. This influence disappeared only under very restricted display conditions (very short presentation time, very high density). This provides further information on which framing conditions are typical for data-driven early vision processes.

◆ From contour to texture: Static texture flow is a strong cue to surface shape

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Contours projected from geodesic boundaries of developable surfaces (as are formed by folding and twisting flat surfaces) are particularly salient cues to 3-D surface shape. Textures which are strongly anisotropic (highly oriented) provide a similar source of information. The natural definition of homogeneity for such textures leads to the constraint that the oriented 'flow' of texture on a surface follows geodesics of the surface (on average). In the current work, it is shown that the shapes of contours projected from geodesics of developable surfaces, and analogously of oriented texture flow, reliably determine the shapes of the surfaces. On the basis of this analysis, it is suggested that human perception of surface shape from texture has two modes of operation: an isotropic mode, in which the visual system infers surface shape from local texture compression information, and a texture flow mode, in which the curvature of local texture flow determines local surface curvature, based on a geodesic constraint. In order to test the theory, planar texture patterns have been isometrically mapped with varying degrees of global orientation (ranging from isotropic to purely oriented) onto developable surfaces. The theory predicts that subjects' ability to make judgements about surface shape will be good for the isotropic textures

and for highly oriented textures, but not for anisotropic textures that are only weakly oriented. As predicted, images of the surfaces with isotropic texture patterns induce strong percepts of shape, as do those of highly oriented textures. Images of anisotropic, weakly oriented patterns, however, elicit only weak percepts of shape.

◆ **An illusory contour induces texture segmentation**

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It is known that neurons in V1 can signal a contour between two out-of-phase gratings [Groszfeld et al, 1993 *Nature (London)* **365** 550–552]. We demonstrate that this type of illusory contour can segregate areas of surfaces without any luminance, contrast, or textural difference between the areas.

We have studied the conditions under which the illusory contour induces texture segmentation. The target was a circular contrast-inverted area (diameter 0.22–8.3 deg) in the centre of an isotropic narrow-band noise texture (centre spatial frequency 0.4–7 cycles deg⁻¹). Generally, segmentation was effortless in low-spatial-frequency textures but gradually disappeared with increasing spatial frequency although the contour remained visible. In a staircase experiment, the highest spatial frequency allowing segmentation was measured for each target size. The task was to tell whether the stimulus contained an object or just a contour. A negative power function relates the target diameter and the highest spatial frequency allowing segmentation. The visibility of the contour was independent of the target size. The illusory contour 'captures' the texture inside. However, the process is spatially limited. In a separate experiment, the subject used a cursor to point out how far from the contour the capture spreads. A negative relationship between the spatial spread and the spatial frequency of the texture was found. These findings are consistent with the idea that low-level mechanisms signalling illusory contours are involved in perceptual scene segmentation.

◆ **Peripheral advantage in texture segmentation: The role of spatial and temporal factors**

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Previous studies (eg Kehrner, 1989 *Spatial Vision* **4** 45–62; Gurnsey et al, 1996 *Journal of Experimental Psychology: Human Perception and Performance* **22** 738–757) have shown that performance peaks several degrees from fixation in texture segmentation tasks, and performance falls as the target texture moves closer to the fovea or further into the periphery. There are two theories for this phenomenon: (1) neural processing speed in the fovea is slower than in the periphery (Kehrner 1989), and (2) the spatial frequency band of the texture is too low (ie too coarse) for the foveal receptive fields (Gurnsey et al 1996). However, the use of backward masking in previous studies made it impossible to decide between the two factors. The purpose of the present study was to isolate them.

In experiment 1 a new stimulus configuration with backward masking was used, and previous reports were replicated. In experiment 2, the same texture was presented for 110 ms without a mask, but with added random-dot noise. Without limitations on processing time, the mid-peripheral advantage disappeared, which indicated that the previous findings were due to slower neural processing in the fovea. In experiment 3, a new type of texture was devised consisting of pairs of vertical lines with a horizontal offset. The offset was reversed for the target. Performance for unmasked 110 ms presentation was worst near the fovea and improved monotonically up to 12 deg. This peripheral advantage was spatial, not temporal, because it arose from larger receptive field sizes in periphery. When these results are taken together, the present study demonstrates that there are two independent causes for the mid-peripheral advantage in texture segregation.

◆ **Fading of textured targets on textured background**

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In 1804 Troxler reported that with strict fixation, a small, low-contrast target presented to the peripheral visual field will tend to fade and ultimately become invisible. Further studies have shown that, in addition to stationary targets, moving and flickering targets will also fade. We studied the role of a texture difference between the target and its background on fading. We found that textured targets fade as quickly as, or even faster than, uniform targets. Typically, the target becomes less salient and after a while disappears in the background.

Specifically, we asked whether orientation contrast would influence the time of perceptual disappearance. A grating disk of 2 deg diameter and 0.8 cycle deg⁻¹ spatial frequency was presented binocularly on an equally striped background, 15 deg from the fixation point. The orientation of the target relative to that of the background was varied in steps of 15°, yielding eleven stimuli which were presented in a random order. Each orientation was shown a total of nine times. Luminance, spatial frequency, and contrast were the same for both the target and the background. Time to fading was measured for each target orientation.

The results show that orientation contrast strongly affects fading. Time to fading was longest when the grating target and the background were oriented at right angles and decreased symmetrically with decreasing orientation contrast. This result supports the hypothesis that fading is an active neuronal process of long-range lateral interactions.

SYMPOSIUM

BRAIN IMAGING

◆ Higher-order motion perception in human visual cortex: evidence from fMRI

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fMRI was used to investigate human visual cortex responses to higher-order motion stimuli. Acquisition was on a Siemens 1.5 T scanner (T2*, gradient-recalled EPI, TR 3000 ms, TE 84 ms, flip angle 90°, 2 mm × 2 mm voxels, 256 mm FOV, 10 4-mm slices, 54 acquisitions per run). The measured volume included occipital and posterior parietal cortex. T1 scouts and, in some subjects, high resolution T1 volume images were also acquired. Visual stimuli were gamma-corrected movies (480 × 480 pixels), presented by a PowerMac via an LCD projector, shown through the rear of the scanner onto an adjustable mirror fixed above the subject's eyes. Three types of stimuli were used: (1) first-order motion, (2) second-order motion (both radial sine waves on random-dot backgrounds), (3) structure-from-motion consisting of two rotating circular patches (5 deg diameter) within which dots moved in a constant (centripetal) direction, superimposed on randomly moving dots. Three interleaved comparisons were made: stimulus vs blank, first-order vs second-order, and random motion vs structure-from-motion (27 s each phase, 3 repeats).

Analysis was based on a correlation coefficient method, after head-motion correction. Initial correlation was with the stimulus profile vector, then with an average BOLD response vector. Voxels with a correlation >0.5 ($p < 0.0003$) were accepted as significant. In all subjects (seventeen normals), all stimuli evoked bilateral activity in V1/V2 (BA17/18), and in extrastriate area V5/MT (BA37/19). Bilateral activation was also found in areas V3/V3a (BA19) and BA7. A more pronounced activation of area MST/V5a (BA37/39) was found in response to the structure-from-motion stimulus, compared with random motion.

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◆ An fMRI investigation of a patient with cerebral achromatopsia: evidence for a role of chromatic extrastriate mechanisms in motion encoding

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We have previously reported psychophysical results of tests on a patient (WM) who suffered from cerebral achromatopsia but nevertheless showed strong signs of unconscious access to chromatic information. This took the form of (a) better performance when chromatic modulation was added to existing luminance modulation in the stimulus, and (b) evidence suggesting that the chromatic information was supplied by a fast, non-opponent set of channels (Troscianko et al, 1996 *Current Biology* 6 200–210). The psychophysical findings led us to predict that WM should show strong potentiating effects of chromatic modulation, and that these should be evident in

enhanced activity of extrastriate areas thought to respond to fast flicker and motion, particularly V5 (Brodmann area 37/39 in lateral occipito-temporal cortex), when a (luminance + colour) stimulus is presented as compared to a luminance-only stimulus.

WM was tested with susceptibility-based functional magnetic resonance, by applying gradient-recalled echo-planar imaging (EPI) sequences, with and without visual motion stimulation. Anatomical and functional images were recorded with a 1.5 T Siemens Magnetom Vision scanner (TR 3000 ms, TE 70 ms, flip angle 90°, FOV 250 mm, matrix 112 × 128, 12 4-mm slices through visual cortex). The visual stimuli were drifting sinusoidal gratings with either luminance-only, or colour + luminance modulation, and with the addition of either static or 25 Hz dynamic luminance noise. After correction for head-motion artifacts, we found (a) a significantly enhanced extrastriate (V5/V5a) response when chromatic information was added, and (b) that fast dynamic noise affected the same areas.

We conclude that colour information can activate (or modulate the activity of) motion-specific mechanisms usually thought to be colour-blind. This finding has implications both for the understanding of unconscious information processing in vision, and for considerations of neural efficiency when encoding redundant image information.

◆ **Functional organisation of human visual cortex revealed by fMRI**

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Until recently, comparatively little was known about the functional organisation of human visual cortex. Functional magnetic resonance imaging (fMRI), in conjunction with cortical flattening techniques and psychophysically relevant visual stimulation, has greatly clarified human visual-information processing.

To date, we have completed cortical surface reconstructions (flattening), coupled with a wide range of visual stimulus testing, on 28 normal human subjects. Visual activation was acquired on a 1.5 T GE MR scanner with ANMR echo-planar imaging, with the use of a custom, bilateral, quadrature surface coil covering posterior cortex.

Approximately ten visual cortical areas can now be functionally localised each with unique functional and topographical properties. The most well-defined areas are: V1, V2, V3, VP, V3A, V4v, MT, SPO, and perhaps MSTd. Most of the properties in these human areas are similar to those reported in presumably homologous areas of macaque, but distinctive species differences also appear to exist, notably in V3/VP, V4v, and V3A. Human areas showing prominent motion-selectivity include V3A, MT/MSTd, SPO, and a small area near the superior sylvian fissure. Retinotopic areas include V1, V2, V3, VP, V4v, and V3A. The human cortical magnification factor appears higher towards the fovea than in macaque, but, like macaque, preferred spatial frequency tuning varies inversely with eccentricity in all retinotopic areas in which sinusoidal gratings are effective stimuli.

◆ **Human brain regions involved in visual discriminations**

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We have used simple visual discriminations as a tool to investigate the human visual system with PET and fMRI. In discrimination tasks, stimuli in which an attribute is defined by a cue are presented in a position in the visual field and the subjects compare the stimuli with each other or with a standard. We have manipulated each of these four aspects. Manipulation of stimulus position engages visuo-spatial attention mechanisms in parietal and frontal cortex (Vandenberghe et al, 1996 *Brain* **119** 1263–1276; 1997 *Journal of Neuroscience* in press). Manipulation of the cue has revealed the kinetic occipital (KO) region involved in the processing of kinetic contours (Orban et al, 1995 *Proceedings of the National Academy of Sciences of the USA* **92** 993–997; Dupont et al, 1997 *Cerebral Cortex* in press). Using luminance-defined patterns presented centrally and contrasting successive orientation discrimination with identification we have demonstrated the involvement of right fusiform cortex in temporal comparison of orientation (Orban et al, 1997 *European Journal of Neuroscience* **9** 246–259). The same region is involved in spatial comparison of orientation as well as in temporal comparison of speed and direction of random-dot motion. This set of experiments shows that processing in the human visual system depends not only on the attribute used but also on the nature of the task to be performed. The direction and speed discrimination experiments also reveal the involvement of the lingual motion area in these tasks, but surprisingly very little involvement of human MT/V5.

◆ **A neuromagnetic view of the human visual brain**

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A visual stimulus typically activates several cortical areas, both sequentially and overlapping in time. Characterisation of this temporal activation sequence has significantly improved with the recent development of whole-scalp neuromagnetometers. The magnetoencephalographic (MEG) signals mainly arise from time-locked cortical activity. Although the spatial localisation of several simultaneously active areas is ambiguous because of the non-uniqueness of the inverse problem, the comparison of estimated source regions across observers and utilisation of previous functional knowledge can usually resolve this ambiguity. Visual object naming, for example, generates cortical activation progressing bilaterally from occipital to temporal and frontal lobes. Simultaneously, the parieto-occipital alpha rhythm dampens as a function of task demands. Similarly, this rhythm is at a lower level after objects than non-objects in an object-detection task, which suggests that the parieto-occipital area is active when attending to visual form. In addition, this area generates evoked responses after voluntary blinks, saccades, and luminance increments, which in turn suggests that it participates in the updating of visual percepts.

The sources of extrastriate MEG signals are generally in good agreement with the location of activation found with other imaging methods: visual motion activates the V5 in the ascending limb of the inferior temporal sulcus, faces the ventral temporo-occipital cortex, and objects the lateral occipital (LO) regions. Interestingly, the strength of the right LO activity closely follows the proportion of correctly detected objects. The future neuromagnetic studies will focus not only on functional localisation of the active areas, but also on how the brain processes various stimuli.

◆ **Organisation and interrelationships of functional maps in cat and monkey striate cortex**

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Optical imaging of intrinsic signals allows mapping of the cortical functional architecture in vivo at high spatial resolution. The ability to image activity patterns evoked by many different stimuli in the same piece of cortex can provide information on the spatial relationships between different functional maps. Our findings on the organisation of multiple functional maps in cat and monkey striate cortex are reviewed. The main focus is on the recent finding in cat of two subsystems differing in their response to spatiotemporal aspects of the stimulus.

We used grating stimuli of different spatial frequencies in an attempt to verify the existence of spatial frequency columns in cat area 17. Rather than observing a map of continuously changing spatial frequency across the cortical surface we found two distinct sets of domains, one preferring low and one preferring high spatial frequencies. By using different drift velocities we also found that the low-spatial-frequency domains preferred higher speeds than the high-spatial-frequency domains. Comparison of these spatiotemporal frequency domains with the cytochrome oxidase staining pattern revealed that the cytochrome oxidase blobs in cat striate cortex coincide with domains devoted to the processing of the low-spatial-frequency and high-temporal-frequency contents of the visual scene. Together with recent anatomical results these data suggest that spatiotemporal frequency domains are the manifestation of parallel streams in cat visual cortex with distinct patterns of thalamic inputs and extrastriate projections.

In the same experiments we also imaged the orientation preference and ocular dominance maps. We investigated the relationships between these three columnar systems, and compared them to an earlier study of orientation, ocular dominance, and blobs in macaque striate cortex. We found systematic relationships between the three systems. While some of these relationships were much weaker than those found in monkey, the organisational principles are similar.

POSTERS

SPATIAL AND SPATIOTEMPORAL VISION

◆ **Size distortions: space-time interaction**

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We used a modified method of constant stimuli to measure spatial interval discrimination thresholds. Horizontal intervals were indicated by a pair of dark vertical lines on a bright background. In each experimental session, thresholds were measured for seven reference stimuli, presented in random

order. Reference stimulus separations varied from 9.52 to 16.66 min⁻¹ in increments of 1.95 min⁻¹. The interstimulus interval (ISI) was varied (50, 200, 500, and 1000 ms) between experimental sessions. Stimulus duration was constant at 500 ms.

For all ISI durations, the point of subjective equality (PSE) for small spatial separation references was less than physical equality, the PSE for larger separations was greater, and the PSE was close to physical equality for reference stimuli in the centre of the range. This result is consistent with the modular model [V D Glezer, 1995 *Vision and Mind* (Mahwah, NJ: Lawrence Erlbaum)]. However, the magnitude of the PSE shifts was affected by the ISI duration: at 50 and 1000 ms, the small spatial intervals were more underestimated and the large ones were more overestimated than at 200 or 500 ms. The discriminability thresholds based on the slopes of the psychometric functions varied inversely with the ISI duration, but at the ISI of 1000 ms increased again. These findings demonstrate that in the sequential mode of presentation the temporal separation can be as important as the spatial separation distribution in determining the PSE. This suggests that these size distortions result more from memory processing than from spatial processing.

◆ **Late maturation (age >5 years) of long-range spatial interactions in humans**

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We have studied the development of long-range spatial interactions in children (age 5–14 years) with normal vision. In our field study involving 410 normal children we used a battery of contour-integration cards that were developed earlier to test amblyopic patients (Kovács, Polat, and Norcia, paper presented at ARVO 1996). Each card consisted of a closed chain of collinearly aligned Gabor patches (contour) and a background of randomly oriented and positioned Gabor patches (noise). Subjects were asked to identify the location of the contour, and also to trace the contour within each card. The value of P was varied across cards ($1.1 > P > 0.65$), where P is the ratio of noise spacing to contour spacing. It is assumed that long-range, orientation-specific facilitatory interactions connect collinear contour segments together for $P < 1$. The strength of long-range interactions is defined by the minimal value of P yielding contour segregation. Children in the 13–14 years age group were able to see most of the contours ($P_{\min} < 0.7$), while 5–6-year-old children missed the contours in about half of the cards ($P_{\min} < 0.9$). This result indicates a very late maturation of long-range spatial interactions. It is possible that the late formation of horizontal connections in superficial layers of the human primary visual cortex (Burkhalter et al, 1993 *Journal of Neuroscience* 13 1916–1931) is the neural basis of our developmental finding.

◆ **Spatial causality in bilateral symmetry detection**

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We studied the influence of spatial scale on the detection of vertical and horizontal bilateral symmetry. The causality principle in scale–space theory states that increasing the spatial scale in a representation can only result in a decrease of structure. Consequently, a pattern can be random on the fine scale and symmetric on the coarse scale, never the reverse.

Stimuli were bilaterally symmetric or random patterns, black-and-white on a grey background, with a circular aperture. The minimal scale was systematically varied and stimuli ranged from conventional noise patterns, through Dalmatian texture, to cow-like patterns. Observers had to judge whether a briefly presented pattern was 'symmetric' or 'random'.

Symmetric patterns resulted in a high accuracy (95%) with no influence of scale, and reaction times with a small linear decrease for increasing scale. Random patterns yielded an accuracy increasing from 70% at the smallest scale to 95% at the middle scales. Reaction times showed a similar pattern: largest at the smallest scales and decreasing to values equal to the symmetric condition at the middle scales. Results were similar for vertical and horizontal bilateral symmetry, though the effect for small scales in the random condition was more pronounced in the horizontal case. We conclude that bilateral symmetry is processed at multiple scales with coarse structures available slightly earlier than fine ones. The dramatic decrease of performance for fine-scale patterns is due to the causality effect; random patterns are judged as symmetric when the smallest scale information is not (yet) available.

◆ **Dynamic spatiotemporal restructuring of visual receptive fields through selective attention: a model**

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Cells in the lateral geniculate nucleus (LGN) strongly change their behaviour covarying with different EEG states. During sleep and drowsiness (synchronised α , δ -wave EEG) short transient responses prevail whereas during a desynchronised 'alert' EEG (β -waves) long-lasting tonic responses are observed. We propose that this is part of a mechanism used to restructure the spatial and temporal characteristics of the receptive fields in LGN and cortex reflecting changing states of selective attention. To this end we present a model of the primary visual pathway using integrate-and-fire neurons to simulate the afferent signal flow (retina, LGN, V1). The model also implements excitatory topographically arranged lateral intracortical and corticofugal connections which act as a positive feedback and trigger spatial winner-takes-all (WTA) mechanisms enhanced by lateral inhibition at both levels. Furthermore, the LGN membrane characteristic can switch from phasic (hyperpolarised) low-threshold Ca^{2+} bursting mode to tonic (depolarised) signal-transmission mode. Switching is triggered by feedback and amplified by intracellular intrinsic positive-feedback mechanisms in the model LGN. All positive-feedback mechanisms are subject to damping such that they remain ineffective below a certain threshold. Salient stimuli which 'attract attention' will push the system above threshold and a self-amplifying process is started which sharpens the cortical receptive fields spatially (by spatial WTA) and drives the winners in the LGN into signal transmission mode (by intrinsic intracellular mechanisms). These results predicted by the model are in accordance with LGN cell behaviour. In addition, the model predicts that cortical receptive fields should be wider during synchronised EEG than during desynchronised EEG.

◆ **Relative size perception at a distance is best at eye level**

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We studied the role of the horizon line as a source of information about the relative size of objects at a distance. Relative-size judgements (2AFC) were collected for two objects at 30.5 m and 23.8 m away from the observer to assess how performance depends on the relationship between the size of the objects and the eye level of the observer. In three experiments in an indoor hallway and in one experiment outdoors, accuracy was higher for objects in the neighbourhood of eye level. We consider these results in the light of two hypotheses: one which proposes that observers localise the horizon as a reference for judging relative size, ie on the basis of the horizon ratio, and another which proposes that observers perceive the general neighbourhood of the horizon and then employ a height-in-visual-field heuristic. The finding that relative-size judgements are best around the horizon implies the use of information independent of distance perception in perceiving size.

◆ **Visual acuity affected by size perception based on convergence cue**

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Increasing (or decreasing) the convergence angle can shrink (or expand) the perceived size of an object without changing its retinal size (Oyama, 1974 *Perception & Psychophysics* 16 175–182). Here we address the question whether such a change in perceived size affects visual acuity. We investigated the effects of perceived size on the legibility of letters, using a telestereoscope consisting of four mirrors to control the observer's convergence angle while keeping the size of the retinal image constant. The targets were photocopies of ordinary Japanese books containing both types of Japanese characters, kana and kanji. The former is a phonetic character and simpler than the latter. Letters were printed in black on white paper. First, we demonstrated that letters do become more legible (illegible) as perceived size expands (shrinks), although their retinal size does not change. Then, we measured the size of the convergence angle at which letters became legible. The 'threshold' size of the convergence angle was obtained for several retinal sizes (0.1 to 0.2 deg) of letters, and for kana and kanji, respectively.

Four subjects participated in the experiment. The result shows that the threshold convergence angle for legibility decreases as the retinal size of letters decreases, so that the minimum retinal size of legible letters depends linearly on the convergence angle. The results implicate contributions from higher levels of the visual system to the determination of visual acuity.

◆ **Neurophysiological contributions to luminance and chromatic mechanisms in a hyperacuity task**

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We recently reported (paper presented at ARVO 1997) psychophysical evidence as to contributions of luminance and chromatic mechanism in a hyperacuity task, namely detection of small displacements. Achromatic or chromatic (430, 550, 690 nm) edges were presented on white or chromatic (550 nm) backgrounds, and displacement thresholds measured as a function of luminance contrast. Above 3% (achromatic detection threshold), all conditions yielded nearly identical contrast/threshold curves; we believe a luminance mechanism to be responsible. In chromatic conditions, below 3% contrast, large (> 100 s arc) displacements were detectable; presumably chromatic mechanisms are responsible. We have now carried out equivalent physiological experiments. Data were consistent with cells of the magnocellular (MC) pathway underlying the luminance mechanism. Opponent S-cone or parvocellular (PC) cells became responsive to displacements in the chromatic conditions. S-cone cells were very responsive to the 430 nm edge, and responded at low contrasts matching the psychophysical thresholds. L, M-cone opponent cells were responsive to the 690 nm edge, but less so than was expected from the psychophysical data. Our data suggest MC-cells underlie a luminance hyperacuity mechanism. Additional factors (eg cell numerosity) may have to be considered for chromatic spatial mechanisms.

◆ **Relevant image features for Vernier acuity**

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The extraction of relevant image features is a key part of discrimination learning (E Gibson, 1969 *Principles of Perceptual Learning and Development*) and the identification of those features is necessary for the understanding of observer performance. Two mechanisms are thought to limit Vernier acuity judgments: orientation-selective and local-sign mechanisms (Waugh and Levi, 1993 *Vision Research* 33 539–552; Beard et al, 1997 *Vision Research* 37 325–346). The linear component of relevant image features can be determined for a Vernier task by adding external noise to the image and then averaging the noises separately for the four types of stimulus/response trials.

The Vernier stimulus consisted of two short, dark, horizontal lines presented within low-contrast white noise. Two spatial separations were tested: nearly abutting and a wide horizontal separation. The task was to determine if the target lines were aligned or offset in the vertical direction. The noises were averaged separately for the groups of trials, corresponding to each of the four possible stimulus/response combinations (eg, stimulus = offset, response = aligned). The sum of the two 'not aligned' images was then subtracted from the sum of the 'aligned' images to obtain an overall image. We then computed a weighted average of adjacent pixels, smoothing the image and fostering visualisation of the relevant feature pattern. Our image analysis supports the view that as the vernier line separation narrows, oriented features play a larger role in the Vernier discrimination.

◆ **A dynamic type of Vernier acuity in the visual prediction of motion trajectory**

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The purpose of the experiment was to analyse a dynamic type of Vernier acuity in the visual prediction of the trajectory of linear apparent motion. The subjects were shown a single moving dot, which moved from the left end to the right end of a CRT. The change in dot position between two successive frames was 0.15 deg. Midway through the trajectory the dot moved behind an amodal occluding square, thus being invisible in this area. The vertical position where the dot re-emerged from behind the occluding square was varied, with 14 conditions for deviations both above and below the 'correct' locus of straight movement. A unit step of the deviation was 0.029 deg. There were three SOA conditions (13 ms, 21 ms, and 26 ms). In a 2AFC paradigm, the subjects had to report on which of two presentations the dot reappeared in the 'correct' position.

We applied Probit analysis to fit a cumulative normal distribution to the result of each SOA condition and each deviation direction. We defined a value giving 75% correct response as

a threshold value. Within each SOA condition, there was no difference between the threshold for deviations above or below the correct position, nor did threshold values between three SOA conditions show significant differences (ANOVA). We compare and discuss Vernier-acuity thresholds with and without amodal occlusion of the locus.

◆ **Vernier image processing: model and experiments**

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Earlier we proposed a model for visual processing of the optical image of Vernier targets (1996 *Perception* 25 Supplement, 115–116) based on Fourier analysis of the image. Our model comprises blurring of the thin Vernier bars by the optical point-spread function followed by calculation of the two-dimensional Fourier spectrum. In our model the processing area for Fourier analysis (the receptive field size) is 5 min arc. For a Vernier target, the contrast energy in the low-spatial-frequency range is different in different orientations, and magnification of the Vernier shift changes the orientation of the oblique Fourier components. To test the model, we carried out experiments in which the stimuli were Vernier lines with additional line distractors orthogonal to the orientation of the oblique Fourier components. Thresholds for detecting Vernier displacements were determined by a 2AFC paradigm and compared with model predictions. The results are consistent with our modelling of Vernier performance as a measurement of oblique components of the 2-D Fourier spectrum.

◆ **Separation discrimination in the presence of flanking lines**

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The presence of flanking stimuli decreases sensitivity in many visual tasks. Earlier we showed that size perception depends on the distance between objects (Bondarko and Danilova, 1996 *Perception* 25 Supplement, 94). Now we suggest that flanks not only decrease sensitivity, but also lead to misperception of size. To test this hypothesis we studied the perception of spatial interval for a set of separations from 6 to 33 min⁻¹ in the presence of two vertical flanking lines.

The method of constant stimuli was used in a temporal 2AFC paradigm. Reference stimuli were two vertical lines with separation S , either with or without two symmetrical external flanking lines. The distance to the flanking lines varied from $\frac{1}{4}S$ to $3S$ in steps of $\frac{1}{4}S$. The test stimuli were just two lines. The first stimulus in the pair could be either the test or the reference. Observers had to report whether the distance between the two central lines in the first stimulus were smaller or larger than the distance in the second stimulus. Probit analysis was used to estimate the threshold and the point of subjective equality (PSE).

We found that the PSE implied overestimation by up to 10% of the spatial intervals for the smallest distances to the flanking lines. Increasing distances to the flanking lines finally led to slight underestimation. The strength of the illusion depended on the order of presentation of the reference and test stimuli. Thresholds increased for the smallest distances to flanking lines. Our results confirmed the hypothesis that flanks can induce distortions in size perception. We suggest that our experimental situation could be considered as a one-dimensional case of geometrical visual illusions such as the Ebbinghaus illusion.

◆ **Adjustment of collinearity of laterally moving, vertically separated lines reveals compression of subjective distance as a function of aperture size and speed of motion**

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We have investigated the effects of the size of the aperture and the speed of motion of a pair of laterally moving vertical lines on the precision with which subjects were able to adjust the spatial position of these moving lines so as to achieve subjective collinearity. The reference line moved laterally across the whole computer display (14.4 deg) while the upper line (that was vertically separated from the reference one by 0.64–2.56 deg) appeared in a central aperture of varying horizontal width (0.62–1.9 deg). In each trial subjects shifted the aperture line leftwards and/or rightwards until it seemed collinear with the ‘permanently’ moving line. In order to achieve *subjective* collinearity the aperture line had to be shifted towards the direction of motion from the position that would have satisfied *physical* collinearity. The size of these shifts (up to 0.124 deg) was a monotonically increasing function of the speed of motion and a monotonically decreasing function of the diameter of the aperture. The results point to the compression of subjective space-time as a monotonically decreasing function of the spatiotemporal availability of

the aperture stimulus. The longer the exposure of the aperture stimulus, the more its perception 'caught up' the initial delay compared with the perception of the moving reference stimulus. We may postulate a relative acceleration of establishing subjective conscious representation with increasing temporal availability of the stimulus. Similarities with the Fröhlich effect and tandem effect are discussed.

◆ **The misperception of the direction of a feature added on a moving line is eliminated with static cues**

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It has been reported earlier that a feature (a gap or a dot) added on an oblique line which is translating vertically behind a horizontal rectangular aperture (we call this the basic display), appears to slide along that line while the perceived direction of the line is horizontal. Castet and Wuerger observed that, when the aperture is a visible circular outline, the perceived 'sliding' of the dot is significantly reduced compared to the conditions where the aperture is invisible. They suggested that the misperceived direction of the dot in the invisible-aperture condition might be due to a lack of static cues. To investigate this hypothesis further we ran a similar experiment in which the aperture was a rectangle. Subjects had to report with an adjustable arrow the direction of the dot added on the line. Results showed that the sliding effect completely disappeared when the rectangular aperture was visible (white outline) compared to the condition where the aperture was invisible. We hypothesised that better performance is obtained when the outlined aperture is rectangular rather than circular because of additional vertical cues. Therefore, in a second experiment using the basic display mentioned above, we tested how a single static dot affects the 'sliding' effect. The static dot was either vertically aligned or not, with the dot placed on the moving line. Results showed that the sliding effect was significantly reduced but not eliminated when the static dot was aligned vertically with the moving dot, compared to the conditions where the static dot was not aligned vertically with the moving dot (or where there was no static dot at all). This suggests that static features providing alignment information are optimal for eliminating the misperception of the direction of a moving feature.

ORIENTATION

◆ **Discrimination between plaids: Do oriented filters combine dichoptically?**

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Two oblique gratings combine perceptually to form a chequerboard appearance under monoptic presentation but not under dichoptic presentation (Georgeson and Meese, 1996 *Perception* 25 Supplement, 121), suggesting an early combination process. Combining processes that operate over orthogonal orientations are also observed in complex pattern discrimination tasks (Olzak and Thomas, 1991 *Vision Research* 31 1885–1898). We ask here whether the interactions observed in discrimination tasks occur before or beyond the site of binocular interaction.

Observers discriminated between two patterns that differed slightly in their spatial-frequency content. On each trial, one of the two patterns was presented. Observers judged which stimulus had been presented on a 1–6 confidence scale. In control conditions, the stimuli were single sinusoidal gratings near 3 cycles deg⁻¹, and were always presented monoptically. In test conditions, a second component was added to the first in each stimulus. The second component was either presented to the same eye as the first component (monoptic presentation), or to the other eye (dichoptic presentation). The second component was either a mask of exactly 3 cycles deg⁻¹, or varied to give a second cue to discrimination. Second cues either varied with the first (both components lower frequency or both higher) or varied in opposite sign (high with low). Rivalry was eliminated by using low contrast (10 × threshold) and small (1.2 deg) patterns. Our results suggest that the combination processes we observe occur beyond the site of binocular combination and differ from those mediating the percept.

◆ **The detection of orientation of small objects**

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Visual information processing in primate cortex is based on a highly ordered representation of the surrounding world. In addition to the retinotopic mapping of the visual field, systematic

variations of the orientation tuning of neurons are described electrophysiologically for the first stages of the visual stream. On the way to understanding the relation of position and orientation representation, in order to give an adequate account of cortical architecture, it will be an essential step to define the minimum spatial requirements for detection of orientation. We addressed the basic question of spatial limits for detecting orientation by comparing computer simulations of simple orientation filters with psychophysical experiments in which the orientation of small lines had to be detected at various positions in the visual field. At sufficiently high contrast levels, the minimum physical length of a line whose orientation can just be resolved is not constant when presented at various eccentricities, but covaries inversely with the cortical magnification factor. A line needs to span less than 0.2 mm on the cortical surface in order to be recognised as oriented, independently of the actual eccentricity at which the stimulus is presented. This seems to indicate that human performance for this task approaches the physical limits, requiring hardly more than approximately three input elements to be activated, in order to detect the orientation of a highly visible line segment. Combined with the estimates for receptive field sizes of orientation-selective filters derived from computer simulations, this experimental result may nourish speculations of how the rather local elementary process underlying orientation detection in the human visual system can be assembled to form much larger receptive fields of the orientation-sensitive neurons known to exist in the primate visual system.

◆ **Orientation channels in the peripheral visual field**

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Peripheral vision has been modelled as a coarser version of foveal vision. Thus visual behaviour elicited by, say, a 2 cycles deg^{-1} grating imaged foveally would be reproduced in the periphery by a lower spatial frequency (say 1 cycle deg^{-1}). Tuning for orientation is broader at a low than high spatial frequency (Snowden, 1992 *Vision Research* 32 1965–1974). Taken together this leads to the surprising prediction that, given a particular spatial frequency, tuning for orientation is narrower for peripheral viewing! In this study it has also been found that orientation tuning broadens with increasing temporal frequency, but the opposite relationship has been reported for peripheral vision (Sharpe and Tolhurst, 1973 *Vision Research* 13 2103–2112).

Orientation bandwidths were measured by the method of selective adaptation following the procedures and analysis techniques described by Snowden (1991 *Proceedings of the Royal Society of London, Series B* 246 53–59). The results show that orientation bandwidths did indeed narrow as a stimulus was imaged more peripherally, so that its bandwidth in the peripheral retina could be half that of the fovea. However, at a greater eccentricity, bandwidths broadened once more. The results were not influenced by the contrast of the adaptation pattern eliminating visibility as a possible explanation. Increasing temporal frequency broadened orientation bandwidth at all eccentricities.

◆ **The tilt illusion and the orientation bandwidth of primary level filters**

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Models for pattern discrimination can be applied successfully to simple orientation discrimination tasks. However, the mechanisms underlying long-range spatial effects, such as the tilt illusion, are not well understood. The magnitude of the tilt illusion and its sensitivity to the polarity of the inducers were measured by means of tests with varying orientation bandwidths. The orientation tuning bandwidth of the primary-level filters, whose peak frequency is 1.7 cycles deg^{-1} , was estimated in a 2AFC orientation-discrimination task. The luminance distribution of the stimulus was jointly normal. First, the orientation bandwidth of a single elongated test stimulus was increased by reducing its length-to-width ratio from 7.5 : 1 to 1.5 : 1. The orientation discrimination performance rapidly decreased after the ratio became less than 3.5 : 1, which is in good agreement with the estimates of the shape of the filters (Wilson, 1986 *Vision Research* 26 453–469). These optimally shaped stimuli were used as inducers in the tilt illusion experiment.

Six 20° tilted inducers were added around the test stimulus at the radial distance of 1.25 deg. When the length-to-width ratio of the test stimulus was varied as in the first experiment, the magnitude of the tilt illusion increased after the ratio was less than 3.5 : 1. However, the precision of the orientation discrimination when compared to the first experiment did not change. Changing the polarity of the inducers did not affect the illusion. The results suggest that the tilt effects of the inducers are not mediated by the primary-level filters. Rather, strengthening of the tilt illusion as the orientation bandwidth of the test stimulus increases suggests that long-range interactions between second-order orientation mechanisms might underlie the described phenomena.

◆ **Stages of orientation coding assessed by the tilt aftereffect**

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We investigated orientation coding via the spatial-frequency tuning of the tilt aftereffect (TAE). In the single-adaptation condition, subjects adapted to single gratings of 1 or 8 cycles deg^{-1} , 40% contrast, tilted 15° clockwise or anticlockwise from vertical; in two double-adaptation conditions the 1 and 8 cycles deg^{-1} gratings were superimposed at opposite orientations ('plaid' condition) or at the same orientation ('parallel' condition). Test gratings of 1, 2, 4, and 8 cycles deg^{-1} , 20% contrast, were presented for 150 ms in an interleaved staircase procedure that measured the TAE by nulling it, hence making a tilted test grating appear vertical. Initial adaptation was for 3 min, topped up for 2 s between test presentations.

Results from the single-grating condition indicated broad spatial-frequency tuning of the TAE, since the effect was still strong when tested three octaves away from the adapter. In the parallel condition, the TAEs were around the average of those reported in the single condition. Negligible TAEs were found in the 1 + 8 cycles deg^{-1} plaid condition, indicating that opposing adaptations had effectively cancelled each other out. These findings strengthen the suggestion of Olzak and Thomas (1992 *Vision Research* 32 1885–1898) that orientation is encoded via an integrative mechanism which pools or sums the outputs of different spatial-frequency channels, and further imply that much of the adaptation responsible for the TAE occurs at this later broad-band stage.

◆ **Enhancement of orientation discrimination with stimuli in apparent motion**

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Form and motion have been considered to be analysed separately in different streams of the visual system and then recombined at a later stage of computation of forms in motion. Nevertheless, motion analysis is required in visual tasks like breaking of camouflage and this suggests that motion mechanisms respond directly to form attributes.

This second possibility was investigated by using stimuli in apparent motion, consisting of two frames in which a target element segregates by an orientation gradient from a texture background of uniformly oriented line elements. Frame-duration thresholds for target-orientation discrimination were measured to assess if they depend on: (1) whether the target is static or moving horizontally (left/right); (2) whether the target is oriented in parallel or orthogonally to the direction of motion; (3) the amount of dynamic noise present in the background texture (dynamic jitter). Thresholds for direction of motion discrimination were also measured as a function of orientation and dynamic jitter.

Thresholds for orientation discrimination were lower for a moving than for a static target. Thresholds for orientation discrimination were lower than those for discrimination of motion direction. Thresholds for orientation and direction discriminations were lower when the target was oriented orthogonally to the direction of motion. Dynamic noise interfered only at high levels of background jitter. These results suggest that orientation discrimination occurs before motion-direction discrimination on the basis of a directionally selective mechanism also responding to form attributes. Form discrimination is likely to be enhanced by the motion component carried by contour motion processing similar to that involved in second-order motion which cannot specify direction of motion at its absolute threshold.

◆ **Centre-surround tuning of orientation detectors in human vision**

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We present a new psychophysical method to study the tuning of orientation detectors in the human visual system. The stimulus consists of a sequence of sinusoidal gratings of random orientations and spatial phases (but of fixed spatial frequency) shown at a high presentation rate (30 Hz) in 60 s long trials. The gratings are seen through a circular aperture. The subject's task is to report, as fast as possible, by pressing a key, when the presence of a horizontal grating is seen embedded in the stimulus sequence. The data are analysed by calculating the distribution of orientations present in the stimulus sequence at different times [before] the key was pressed. Similar experiments can be done by asking the subject to detect vertical and oblique orientations. In these experiments we used 100% contrast, a 3 deg diameter circular aperture, and spatial frequencies ranging from 1 to 4 cycles deg^{-1} .

The resulting orientation-tuning profiles have a 'centre-surround' (or Mexican hat) shape in the orientation domain. These findings are consistent with the idea of fast 'lateral inhibition'

between orientation detectors. The centre-surround profiles may explain systematic errors in visual angle judgments, such as the perceptual expansion of acute angles and the contraction of obtuse angles, the tilt aftereffect, and the effects observed in the Zöllner, Hering, Ponzo, and Poggendorff illusions.

TEMPORAL VISION AND VISUAL MEMORY

◆ Implicit learning of temporal discriminations in perception

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We measured the temporal accuracy of signal transfer in the brain by means of periodic pulse stimuli in various sensory modalities using an adaptive threshold algorithm. Trains of supra-threshold signal pairs in 0° or 180° phase shifts appeared, and the subject indicated whether the signals of each pair in a train were simultaneous or not at various nominal frequencies of the pairs. The signals were spatially separate flashes of light, clicks, tactile pulses, or combinations thereof in intermodal comparisons. Temporal discrimination thresholds involving one signal in central photopic vision and the other in audition or tactile presentation to the finger tips did not exceed frequencies from 3 to 8 Hz, and in vision alone the average synchronism thresholds were about 10 Hz (SOA 0.05 s with 0.008 s pulses). The practice derived from 9 experimental sessions during 6 weeks improved temporal accuracy by factors ranging from 1.2 to 2.0 on the average in a sample of 33 naive subjects (university students), although no explicit feedback was given. The practice effect was lasting, for the average performance decrement was only 9% in 7 months. Thus, a considerable temporal modifiability must exist in the brain because a large learning effect was found in the simple temporal synchronism discrimination tasks.

◆ Temporal integration and the masking effect of spatiotemporal noise

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In computer-generated spatiotemporal noise every stimulus frame contains a new static noise sample. The spectral density of white spatiotemporal noise is calculated by multiplying the squared rms contrast of noise by the product of the noise check area and the exposure duration of each noise check. When the exposure duration of each noise check is gradually increased, the spectral density of spatiotemporal noise increases, reaching its maximum when noise becomes static. In static spatial noise both stimulus and noise checks have the same duration. The signal-to-noise ratio is known to be constant at detection threshold. Detection thresholds should thus increase in proportion to the spectral density of spatiotemporal noise, which increases with the duration of the noise checks. We measured detection thresholds for stationary cosine gratings embedded in spatiotemporal noise. The exposure duration of the noise checks was increased from one frame duration to the total exposure duration of the stimulus grating. Noise was thus gradually transformed from spatiotemporal to static spatial noise. The contrast energy threshold increased in proportion to the spectral density of spatiotemporal noise up to a noise check duration found to be equal to the integration time for the stimulus grating without noise. After this, energy thresholds remained constant in spite of the increase in the spectral density of spatiotemporal noise. This suggests that the masking effect of spatiotemporal noise increases with the duration of noise checks up to the critical duration marking the saturation of the temporal integration of the signal.

◆ Flicker sensitivity as a function of eccentricity

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We determined DeLange curves with and without external temporal noise at eccentricities of 0–70 deg by measuring flicker sensitivity at 1–45 Hz for sharp-edged M-scaled spots with an equi-luminous surround. Without noise, flicker sensitivity at high frequencies increased with eccentricity but remained unchanged at low frequencies. In strong noise, flicker sensitivity was independent of eccentricity. The only exception was 70 deg where sensitivity was reduced at 1–3 Hz with and without noise. The data at each eccentricity are well described by our flicker-sensitivity model (Rovamo et al, 1996 *Vision Research* 36 3767–3774) comprising (i) low-pass filtering by the modulation transfer function (MTF) of the retina, (ii) filtering in direct proportion to temporal

frequency by the high-pass MTF of the retina and subsequent neural visual pathways, (iii) addition of white internal neural noise, and (iv) detection by a temporal matched filter. When interpreted in the context of the model, our results mean that while the high-pass filter and the magnitude of internal noise remained unchanged across eccentricities, the bandwidth of the low-pass filter increased with eccentricity and at 70 deg eccentricity the efficiency of the detecting mechanism in the brain was reduced at 1–3 Hz. The increase in the bandwidth of the low-pass filter is in agreement with the eccentricity-dependent changes in the retinal function as revealed by the electroretinogram (ERG).

◆ **Investigating the time-course of task-dependent perceptual grouping**

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At what stage do factors such as task experience and expectation interact with the perception of whole objects? Recent work (Freeman, 1995 *Perception* 24 Supplement, 134; 1996 *Perception* 25 Supplement, 51) suggests that perceptual grouping of ambiguous 1-Whole/2-Wholes stimuli is dependent upon learning and task predictability, as inferred from changes in performance in a Whole-Whole/Whole-Part shape matching paradigm. Thus, subjects seemed able to offset the effect of a stimulus parameter known to influence perceived grouping, in order to see the grouping they had been trained to see or were expecting to see. In the present research the timing of these interactive processes was investigated, with the use of backward masking to take a snapshot of visual processes at different stages in their development.

Stimulus and task-context factors were found to interact even at the shortest masking interval (50 ms), suggesting that top-down knowledge constrains perceptual grouping processes from an early stage onwards. A simple model of the development of 1-Whole and 2-Whole percepts implies two further conclusions. First, task and stimulus factors both seem to work by modifying the rate of development of the alternative percepts. Second, and counter-intuitively, it appears that, given the appropriate task-context and stimuli, it is possible to group the stimulus in several different ways at once. These results shed light on issues concerning the nature of perceptual grouping, and the process by which our experience of objects is brought to bear on our selection of functional perceptual groups.

◆ **A signal-detection model of visual short-term memory performance for random block patterns**

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On the basis of signal-detection theory, we have formulated a model that accurately explains performance on a visual short-term memory task involving random block patterns. The model assumes that the internal response of an observer for detecting a change in any given element of the block pattern is noisy and has a Gaussian-shaped distribution. On this basis we can calculate the likelihood that an observer correctly or falsely identifies a change in the pattern after a certain time interval (ISI). Using this likelihood, we can then predict the likelihood that an observer correctly identifies a whole pattern as having changed or not as a function of the number of elements that changed in the pattern. We have previously shown (Cornelissen and Greenlee, 1993 *Perception* 22 Supplement, 46) that memory performance declines when changes occur in pattern elements located on the perimeter of the pattern. Therefore the model also incorporates a circular symmetric 'memory field' that shows a Gaussian-shaped decline of memory performance from the point of fixation. The model has three parameters: d' (detectability of a change), λ (criterion level), and the standard deviation of the Gaussian of the memory field.

In the experiments we performed, block patterns made up of 50 light and 50 dark randomly arranged elements (0.5 deg checks) were briefly (200 ms) shown. In a forced-choice task, subjects judged whether two sequentially presented (with ISIs of 1, 3, or 10 s) block patterns were the same or different. Task difficulty was varied by varying the number of elements in the patterns that changed on 'different' trials. The model is able to accurately predict memory performance at the three different ISIs for various levels of pattern differences (changes in 1, 2, 4, 8, 16, 20, and 50 out of 100 elements).

◆ **Visual memory for multiple Gabor targets**

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Visual memory for spatial frequency in stationary Gabor targets was measured as a function of interstimulus interval (ISI 2 or 8 s), number of targets (2, 3, or 4), and pre-cueing versus post-cueing of the critical target. The width of the Gabor and the initial and final spatial frequency were varied to eliminate confounding variables such as number of cycles, apparent contrast, and initial or final spatial frequency. A signal-detection analysis was employed, in which the subject was required to determine whether the spatial frequency of a selected Gabor target was the same or different over the ISI. The data were analysed by plotting d' as a function of spatial-frequency difference.

The results show only small and inconsistent decreases in d' as a function of the ISI. There was little change in d' in any condition except certain 3 and 4 target post-cueing conditions, where its magnitude was halved. It was expected that pre-cueing should be superior to post-cueing because, although the Gabor displays are the same, effectively only one pre-cued target needs to be retained over the ISI. However, the expected effect did not always occur. In some spatial-frequency conditions, discrimination performance was maintained even for the most difficult condition (4 targets, 8 s ISI, post-cueing). It is concluded that there is a durable representation of stimulus spatial frequency in visual memory. Under optimum conditions, 2–4 targets can be remembered for 8 s with minimal change in d' .

TEXTURE AND IMAGE SEGMENTATION

◆ **Figure–ground assignment of stereo-defined contours affects the ease of symmetry and translation detection**

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When figure–ground assignment reverses for a given contour, convexities along it become concavities, and vice versa. Baylis and Driver (1995 *Journal of Experimental Psychology: Human Perception and Performance* 21 1323–1342) examined the possible implications of this effect for the perception of symmetry between contours. Using contrast reversal to determine figure–ground assignment, they argued that the ease of detecting symmetry between two contours depends on whether convexities along them match following figural assignment. However, their results might be attributed to the contrast polarity of individual edges instead. We used random-dot stereograms to vary figure–ground assignment for edges while holding contrast polarity constant. By placing the areas on either side of each contour at various depth planes, conditions were created in which the convex parts yielded for related contours either matched or mismatched following figural assignment. Particular depth arrangements which yielded matching convex parts for symmetrical contours yielded mismatching parts for translated contours, and vice versa. The results confirmed that the relative ease of symmetry-detection versus translation-detection depends on the convex parts yielded for each contour following figural assignment. These findings suggest that the perception of symmetry between contours arises only after they have been assigned to a figure on one of their sides, and is based on a higher-level interpretation of each contour in terms of convex parts, rather than lower-level properties of the image.

◆ **Contrast polarity affects performance after figure–ground coding**

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Gilchrist et al (1997 *Journal of Experimental Psychology: Human Perception and Performance* 23 464–480) proposed that some aspects of grouping are relatively insensitive to variations in contrast polarity between the elements to be grouped. We assessed the contrast-polarity sensitivity of grouping in a visual search experiment. Display elements were corner-brackets arranged at the vertices of regular polygons (see Donnelly et al, 1991 *Journal of Experimental Psychology: Human Perception and Performance* 17 561–570), either aligned with polygon sides (strong-grouping condition), rotated through 20° (weak-grouping condition), or rotated through 180° (open condition). The background was grey; on same-contrast-polarity trials, elements were either all white or all black; on opposite-polarity trials, each element was white and black. The task was to detect a target element rotated 180° with respect to the others. With weak grouping present, opposite contrast polarity slowed reaction times dramatically: they were as slow as those to open displays. A second experiment in which display elements were pacmen showed that the contrast-polarity effect on

performance is modulated by figure-ground relations: the dramatic effect of contrast polarity in the weak-grouping condition disappeared, presumably because search focused on the uniform grey illusory surface. These results suggest that grouping operates automatically to produce figure-ground coding of displays, but that contrast polarity differences within a figural surface affect the output of these codes to systems concerned with perceptual discriminations.

◆ **Image segmentation by local temporal phase differences**

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Previous research has shown that flickering elements can be grouped on the basis of temporal phase differences. We investigated the spatial and temporal parameters that permit temporal phase segmentation. The stimulus consisted of a regular square lattice of Gaussian spots modulated in luminance against a background of 54 cd m⁻². Subjects identified one quadrant which was modulated 180° out of phase to the other quadrants. The modulation threshold was found for temporal frequencies between 4 and 30 Hz. Four Gaussian spot sizes with standard deviations from 0.05 to 0.43 deg were used: lattice spacing was proportional to dot size.

We found that detection of phase differences between large spots failed at about 10 Hz. However, for the smallest dots the task was possible at frequencies of 30 Hz. Furthermore, the elements at the border of the quadrant were necessary and sufficient for maximal sensitivity. Using solid quadrants modulated at 15 Hz, we found that the maximum separation between the flickering quadrants lies between 0.5 to 1.0 deg. The results suggest that there are two systems that use temporal phase for segmentation. The first system operates below 10 Hz, where phase can be consciously followed and integrated over a large area. The second system operates at higher frequencies but only within confined regions of the visual field. Image segmentation for stimuli modulated at high temporal frequencies is not determined by long-range phase synchronisation. We suggest that detection may be mediated by a second-order nonlinearity.

◆ **Separation of figure from ground as an adaptive image processing**

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We define the separation of figure from ground as a visual-attribute-dependent and task-dependent representation of sensory information in higher-level visual processes. A computer model for adaptive segmentation of 2-D visual objects (Dudkin et al, 1995 *Proceedings of SPIE* 122) was developed in these studies. The description and separation of figure from ground are implemented by spatial frequency filters and feature detectors performing as self-organising mechanisms. The simulation of control processes caused by attention (top-down), and lateral, frequency-selective, and cross-orientation inhibition (bottom-up) determines the adaptive image processing.

The first stage is the estimation of input image produced by the analysis of the spatial brightness distribution by algorithms calculating the vector of primary descriptive attributes. These results provide the synthesis of control processes based on several algorithms, each of which transforms descriptive attributes into separate control parameters. The creation of two primary descriptions: 'sustained' (contours) and 'transient' (fragments with homogeneous intensity), and the selection of feature-detection operators are governed by the complete set of control parameters. The primary descriptions allow formation of the intermediate image description in which similar elements are grouped by identical brightness, colour, spatial position, curvature, and texture according to Gestalt concepts. To divide the image into basic areas and to extract fragments which belong to a putative figure, all these descriptions are combined into the final integrated image representation. The model has been tested on various images.

◆ **Summation of contrast in perceived form from texture**

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The relative contrast of two superimposed triangles formed by truncated sinusoidal gratings determines which appears more salient. We have previously reported that the saliency of one triangle is selectively enhanced by superimposing a third grating of similar frequency but different orientation. We now ask how the contrasts of the three gratings combine to determine saliency.

Stimuli were two superimposed isosceles triangles, formed by overlaying sharply truncated patches of a sinusoidal grating, one at 1.5 cycles deg⁻¹ tilted +45°, the other at 6 cycles deg⁻¹, tilted -45° from vertical. The sharpest-angle apexes pointed in opposite directions (left or right).

Contrasts of the gratings were initially adjusted to yield equal performance when observers chose whether the more salient target pointed left or right following a brief (400 ms) monocular exposure. In each test condition a third grating of vertical orientation (spatial frequency 1.5, 3, or 6 cycles deg^{-1}) was added to the entire stimulus at one of six contrast levels ranging from near threshold to $10 \times$ threshold. The point of equal saliency was re-determined from psychometric functions by varying the contrast of one triangle in a 2AFC staircase procedure.

The saliency of each triangle was enhanced when the third grating was matched in frequency, but no effect occurred when the third grating differed by an octave (eg was 3 cycles deg^{-1}). Beyond some threshold value of the third grating contrast, the contrast needed to reinstate equal saliency was found to be inversely proportional to the contrast of the third grating. Our results are in agreement with the characteristics of higher-level mechanisms that mediate spatial-grain and/or pattern contrast discrimination, and suggest that form-from-texture mechanisms sum component contrasts linearly over a wide range of orientations within a narrow frequency band.

◆ **Are angles transformed into blobs in early vision?**

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When textures used in visual segmentation experiments are composed of angle elements, these angles seem to be transformed into 'blobs' at early stages of visual processing ('blob hypothesis'; see Meinecke and Kehler, 1994 *Perception & Psychophysics* **56** 326–334). These blobs can be imagined as ellipses in which the angles are embedded. Thus, ellipses/blobs are more or less elongated depending on the width of the underlying angle.

We tested the blob hypothesis in a psychophysical experiment using two experimental conditions with angle textures. In condition A, subjects had to detect a target texture, in which the resulting blobs had a well-defined orientation, within a background texture, in which the blobs had a less-well-defined orientation. Condition B was identical, except that the target elements became the background elements and vice versa.

If angles are really transformed into blobs in early vision, then condition A should yield a better performance than condition B, because it is much easier to detect ellipses among circles than circles among ellipses (Treisman and Gormican, 1988 *Psychological Review* **95** 15–48). Our results replicated this asymmetry and thus support the blob hypothesis.

In a simulation study, in which Gabor filters were used as the input layer in a spatial filter model, we tried to gain a better understanding of the underlying mechanisms. The simulation indicated that the experimentally observed asymmetry might be due to particular features of the target textures, leading to higher Gabor target responses in condition A than in condition B, whereas background responses were very similar in both conditions.

◆ **Configuration saliency revealed by dichoptic masking**

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We studied suprathreshold spatial integration by testing the saliency of multi Gabor element configurations in dichoptic masking conditions. Dichoptic presentations allows for a competition between spatially overlapping suprathreshold stimuli that involve nonoverlapping receptive fields in the first stage of visual filtering.

Different spatial configurations of Gabor patches ($\sigma = \lambda = 0.12 \text{ deg}$) were presented to one eye (target) together with a bandpass noise presented to the other eye (mask). After a short rivalry period (128 ms) in which a dominance of one eye was established, a probe (a randomly positioned small rectangle of reduced contrast in the target) was presented for an additional detection period (80 ms). Probe detection performance was measured (2AFC) by finding the mask contrast leading to 75% correct response.

We find that textures of randomly oriented patches are more dominant than uniform textures where the effect decreases and even reverses with decreasing of contrast. For suprathreshold (1-D) contours, however, we find that smooth collinear contours are more dominant than 'jagged' ones, regardless of contrast. These findings suggest principles underlying an early lateral integration mechanism based on contrast-dependent inhibitory and excitatory connections. This mechanism could be based on iso-orientation surround (2-D) inhibition and collinear (1-D) facilitation, with inhibition being more effective at high contrasts.

◆ **A comparison of electrophysiological and psychophysical threshold detection in texture segregation**

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The salience of targets in preattentive tasks depends on local feature gradients between the target and the surrounding background. We have developed an electrophysiological method to isolate texture-segregation-specific components in the human visual evoked potential (tsVEPs). We report here on threshold estimates of orientation-based texture segregation, comparing psychophysical and electrophysiological measures.

Eight visually normal subjects participated in the experiment. In a 4AFC task, subjects indicated the position of a single patch that differed in orientation from a homogeneously oriented background. Orientation gradients ranged from 5° to 90° ; orientation threshold was estimated with a best PEST procedure. In further experiments VEPs to the onset of 'orientation chequerboard' patterns with orientation gradients ranging from 0° to 90° were recorded from an Oz-Fpz derivation. Orientation threshold was estimated in two steps. First, the VEP to the 0° condition was subtracted from all other VEPs to isolate tsVEPs. Second, tsVEP amplitudes were determined by cross-correlation between the tsVEP to any given orientation and the 90° condition.

We found, first, that the electrophysiological threshold derived from the overall mean tsVEPs was considerably higher than the psychophysical threshold of the orientation gradient, $16.1^\circ \pm 1.0^\circ$. Thus the pool of neurons contributing to the VEP signal must be larger or more strongly activated in order to elicit a significant tsVEP than to subserve psychophysical performance. Second, we found that the amplitudes of tsVEPs above threshold increased monotonically with increasing orientation gradient of the chequerboard patterns, suggesting that the tsVEP may have its neural correlate in orientation-contrast-dependent neurons similar to those found in monkey and cat striate cortex.

COLOUR

◆ **Perceptual salience of borders between coloured regions**

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Difference measurement is a little-used but potentially valuable method for studying suprathreshold vision. We used it to investigate the perceptual salience of borders between adjacent uniformly coloured regions. In these experiments, the observer viewed pairs of colours C_1, C_2 presented simultaneously in two rectangles, sharing a common border, centred on a neutral background. On each temporal 2AFC trial, the observer saw two colour pairs (C_1, C_2) and (C_3, C_4), and was asked to judge which of the two colour borders was more salient (stronger). In a single condition of the experiment, the colours C_1, C_2, C_3, C_4 were drawn from a set of ten colours constrained to lie along a fixed line segment in *LMS* space extending from the neutral background point (NBP) in a particular direction in *LMS* colour space.

Let D_i denote the distance of C_i from the NBP in *LMS* space. A difference measurement model accounts for such data if and only if there is an increasing 'scale' $f(D)$ such that (C_1, C_2) is judged more salient than (C_3, C_4) precisely when $f(D_2) - f(D_1) > f(D_4) - f(D_3)$. For each of three observers and eight directions, we found that estimated functions $f(D)$ were concave, resembling power functions with exponents between 0.64 and 1.

◆ **Spatial integration of objectively equiluminous chromatic gratings**

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Contrast sensitivity functions for achromatic and chromatic gratings tend to be band-pass and low-pass in shape, respectively. Our aim was to test whether spatial integration contributes to the shape difference found at low spatial frequencies. We measured binocular chromatic contrast sensitivity as a function of grating area for objectively equiluminous red-green and blue-yellow chromatic gratings. Chromatic contrast refers to the Michelson contrast of either of the two chromatic component gratings presented in counterphase against the combined background. Grating area (A) varied from 1 to 256 square cycles (Af^2) at spatial frequencies (f) of 0.125–4.0 cycles deg^{-1} . We used only horizontal gratings at low and medium spatial frequencies to minimise

the transverse and longitudinal chromatic aberrations due to ocular optics. At all spatial frequencies studied, chromatic contrast sensitivity increased with grating area. A_c was found to be constant at low spatial frequencies ($0.125-0.5$ cycles deg^{-1}) but decreased in inverse proportion to increasing spatial frequency at $1-4$ cycles deg^{-1} . Thus, spatial integration depends similarly on spatial frequency for achromatic (Luntinen et al, 1995 *Vision Research* **35** 2339-2346) and chromatic gratings, and differences in spatial integration do not contribute to the shape difference of the respective contrast sensitivity functions.

◆ **On the validity of colour vision tests in the field: a practical assessment**

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We found a surprisingly high incidence of tritan-like (blue-yellow) symptoms in population samples from southern Africa. However, these results could be false positives because the test (The City University Colour Vision Test: CUCVT) was not administered under the prescribed illuminant (CIE Illuminant C). We therefore assessed the robustness of the test in order to estimate the true tritan rates in our data and to assess its usefulness under field conditions. First, we administered the test to normal young people under three illuminances (600, 300, and 150 lux), and three spectral distributions (C, reduced short wavelength, and reduced long wavelength). In addition, two viewing distances were used: the standard (14 inches) and double the standard. At the normal viewing distance, no errors were induced by reducing the illuminance or by changing the spectral distribution. However, at 28 inches, both illuminance and spectral changes induced tritan errors. Second, we assessed a sample of old people (over 65), first, under the prevailing illuminant; second, under Illuminant C; and third, under Illuminant C with increased intensity. In all cases, the old people in the sample made large numbers of tritan responses, but the frequency of tritan errors decreased under Illuminant C and decreased even more under enhanced illuminance. Thus, for normal young people at the prescribed distance the test is robust, but at increased distance the test is vulnerable to deviations from the prescribed illuminant. Further, older people can present as having tritan-like problems unless the illuminance is increased above the standard.

◆ **Do linguistic categories affect colour perception? A comparison of English and Turkish perception of blue**

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Cultural relativists adduce the variation in colour categories across languages as prima facie evidence for linguistic relativity (language affects thought). However, there have been very few experiments that have gone beyond this observational level to assess the extent and the nature of linguistic differences on colour categorisation and perception. Here, we report experiments comparing English and Turkish speakers using a colour-grouping task and same-different tasks aimed at redressing this lack. Turkish categorises the blue region with two basic colour terms (lacivert 'dark blue' and mavi 'blue') whereas English has a single basic term. In experiment 1 subjects sorted a representative set of 65 colours into groups on the basis of their perceptual similarity. Native Turkish speakers were significantly more likely than native English speakers to form two distinct blue groups corresponding to the two basic blue terms of Turkish. In the same-different tasks we sought for possible categorical effects: enhanced discrimination across category boundaries and/or reduced discrimination within categories. For successive presentation, Turkish speakers were more accurate than English speakers in judgments of colour pairs that fell on opposite sides of the lacivert-mavi boundary. However, for simultaneous presentation, there was no difference between the two language groups. The results suggest that there are detectable effects of linguistic categories on colour cognition, but the locus of the effect may be in memory rather than perception.

◆ **Highly accurate measurements of human colour vision parameters with application to diagnostics**

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A new method for measuring a wide spectrum of parameters describing a subject's colour vision is presented. It is based on a portable visual colorimeter, 'Spectr-3M', designed in our laboratory and has several useful features: (1) it enables testing over a wide area of the chromaticity diagram; (2) it allows the use of continuously changing colour stimuli; (3) the measurement accuracy is high; (4) the testing procedure is fast and comfortable, minimising the effects caused by prolonged testing and increasing the reliability of the data.

Using this method we have revealed significant deviations from the CIE 1931 standard colorimetric observer in the colour perception of several subjects previously attested by the Rabkin and Ishihara charts as having normal perception. The data obtained by our method are more informative than results obtained with the Nagel anomaloscope, revealing not only general features of colour perception defects (as the anomaloscope), but allowing more detailed characterisation, including even small deviations from the CIE 1931 standard observer.

◆ **A study of the Abney effect in some colour atlases: designing opponent variables and hue functions**

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The Abney effect in colour-appearance systems (Munsell, NCS) means that the lines for identical apparent hue (at constant lightness) do not coincide with the straight lines for constant dominant wavelength. The curvature of constant-hue lines in chromaticity diagrams reflects the fact that cone signals are nonlinear functions of the rate of photon absorption. The most widely used nonlinear intensity-response function in vision is the Naka-Rushton function, which in an intermediate range can be approximated by a square-root function. Our purpose has been to study the Abney effect in the Munsell and NCS colour atlases in order to develop a mathematical-physiological description on this basis, designing the redness-greenness and yellowness-blueness perceptual variables and the perceptual hue function in each colour system. The description is applicable to both biological and machine-vision systems.

◆ **Vertical visual-field differences in schematic persistence for colour information**

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The functional specialisation in the upper and lower visual fields is related to the distinction between far and near vision, and may parallel differences between the ventral and dorsal processing streams. Here, we studied possible differences in colour processing. According to postulates of Previc (1990 *Behavioral and Brain Sciences* 13 519–575), we expected longer persistence and an advantage in colour classification for stimuli presented in the upper visual field. Performance was tested in a modified partial-report task to estimate duration of schematic persistence for colour and verbal information. The targets were letter strings—either red, yellow, blue, or green—presented in three combinations: (a) nonsense strings, (b) congruent colour-words, and (c) incongruent colour-words. Eight targets were simultaneously presented in a circular array for 60 ms. After a variable interstimulus interval (ISI, 0–900 ms), a coloured marker was briefly displayed pointing to one of the original target positions, and the participants had to report whether the colours of target and marker were identical or not. The responses were analysed separately for upper and lower visual-field presentations. The verbal content of the targets did not affect performance. There were no differences in performance between the two visual fields. However, analyses of both accuracy and reaction latencies showed significant interactions between visual field and ISI, ie performance decreased at a slower rate in the upper visual field. These results suggest longer schematic persistence for colour stimuli presented in the upper visual field.

◆ **Masking effects induced by perceptual colour components**

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Signals from the three types of cone photoreceptors are generally thought to be combined into two opponent-colour components and an achromatic component. Here we have chosen the cardinal directions Ach (achromatic axis), Cr1 (reddish-greenish axis) and Cr2 (bluish-yellowish axis) defined by Krauskopf to build a colour image coding scheme based on features of the human visual system. In order to design the optimal perceptual quantisers, we studied the perception of colour at different spatial frequencies, measuring the effect of a colour masking signal on the perception threshold for achromatic or chromatic sine-wave gratings. Three cases were considered to describe these interactions.

First, we measured the masking effect of each colour component by itself. For the two chromatic components, we observed a pedestal effect for low masking contrasts and threshold rises for higher masking contrasts. Second, we studied interactions between the two colour axes. With colour masking signals composed of Cr1 and Cr2 components, thresholds for Cr1 stimuli

dropped at low contrasts of the Cr2 component of the masking signal. This effect disappeared for high Cr2 masking contrasts. This was true at all contrasts of the Cr1 component of the masking signal. Thresholds for Cr2 stimuli were not modified by Cr1 masking. Finally, interactions between the chromatic and achromatic components were more complex. We observed a strong modification of the achromatic contrast-sensitivity function when a Cr1 masking sine-wave grating was added. When the achromatic frequency was lower than the colour masking frequency, the threshold rose. However, when the achromatic frequency was higher than the colour masking frequency, there was a significant pedestal effect. The global effect is a shift of the achromatic contrast sensitivity function. With a Cr2 masking signal, no significant modification of the achromatic contrast-sensitivity function was observed.

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◆ **The effects of chromatic conditions for transparency**

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When two rectangles overlap crosswise like a letter X, we perceive them as transparent in certain conditions. Perception of transparency is constrained by the luminance and chromatic relations of the overlapping and non-overlapping areas and the background, but not necessarily by their physical transmission profiles. In this study, we investigated the relation between luminance and chromatic mechanisms for the percept. Using two crossed rectangles (2 deg × 8 deg), we measured the ranges of chromaticity and luminance of the overlapping area (2 deg × 2 deg) that allowed the percept of transparent layers.

We found that the 'transparency' luminance range was shifted by the intensity of the background. When the two rectangles were isochromatic and isoluminant (10 cd m⁻²) on a dark background, the overlapping area had to be around 0.3 log units brighter than the rectangles. When the background was D₆₅ white (60 cd m⁻²), the luminance range for transparency was lower than the luminance of the rectangles. When the two rectangles differed in colour, however, the 'transparency' range of the overlapping area varied around the luminance of the rectangles. Transparency was perceived best when the colour of the overlapping area was on the additive mixture chromaticity line of the two rectangles. We discuss how the background influences the appearance of transparency and how the chromatic mechanism is effective in transparency.

◆ **Luminance and colour cues in perceptual transparency**

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A series of experiments was carried out to determine the dependence of the perception of transparency on colour relationships in a four-region pattern comprising two non-overlapping regions, an overlapping region, and a background. The proportion of trials where the pattern was perceived as transparent, and the relative layering in depth of the two perceived surfaces, were determined as a function of the luminance of colour of the overlapping region while those of the non-overlapping regions were kept constant. It was found that perceptual transparency could arise from displays where the four regions were isoluminant but different in colour. The function obtained for isoluminant colour-varying patterns was quite similar to that obtained for isochromatic luminance-varying patterns. In both types of patterns, the background condition strongly affected perceptual transparency and perceived depth order in a similar way. These results suggest that perceptual transparency for both the isochromatic and the isoluminant pattern was specified in a common manner by contrast relations in a certain region of the image, and was not always constrained by the physics of transparency. The dependence of perceptual transparency on the contrast relation may be accounted for by mechanisms incorporating the filling-in process associated with antagonistic luminance and opponent-colour responses.

◆ **Elementary colour perception in hue judgment**

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The ratios of psychological elementary colours perceived in chromatic colour papers with a variety of hues were measured by a paired comparison method. Stimulus sets were composed of two colour papers with hues between two of four elementary colours, but on either side of one elementary colour. Five students observed stimulus sets comprising two colour papers under

approximately 1000 lux D_{65} illumination, and they chose the one which caused the stronger elementary colour percept. The results showed that the sum of the ratios of two elementary colours in a colour whose hue is located between them was less than 100%. This result was the same for every hue condition.

This shows that observers underestimated psychological elementary colours, consistent with previous studies (Sakata, 1996 *Perception* 25 Supplement, 100) which showed that the sum of black and white was less than 100% in the perception of greys. If elementary colours are processed simultaneously from the whole colour percept, their sum would be 100%. The result of these experiments strongly shows that psychological elementary colours are processed independently from the inputs of the three cone systems and the rod system, and they are integrated to form the whole colour percept after each process.

◆ **Surface colour matching under conditions of multiple illuminants**

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Most theories of colour constancy assume a flat coloured surface and a single homogenous light source. Natural situations, however, are 3-dimensional (3-D), are hardly ever restricted to a single light source, and object illumination is never homogenous. Here, two special cases of secondary light sources with sharp boundaries were simulated on a computer screen: a house-like 3-D object with colour patches in sunlight and shadow, and a Mondrian-type pattern with a coloured transparency covering some of the colour patches. Subjects made 'paper'-matches between colour patches in light and shadow and between patches under the transparency and without the transparency. Matching did not depend on whether the simulated lighting condition was natural (yellow light, blue shadow) or artificial (green light, magenta shadow). Patches under a coloured transparency produced lightness constancy but subjects could not discount chromaticity shifts induced by the transparency. The number of context patches (2 vs 6) made no difference, and it made no difference whether the transparency covered the Mondrian completely or only partially. These results indicate that subjects were not able to use local contrast cues at sharp illumination boundaries to discount for the illuminant.

◆ **A method for measuring apparent illumination**

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Knowledge of perceived illumination is very important for almost all experimental investigations in colour science. We consider here a method for measuring apparent illumination based on the perceptual phenomenon of fluorescence. The underlying hypothesis is that the minimal illumination level at which a patch begins to look fluorescent exactly corresponds to the respective chromatic component of the apparent illumination in the scene. We report results of three experimental studies: (1) measurements of apparent illumination for a flat mondrian presented on a screen and mondrians made of paper presented in a specially designed box with controlled illumination observed monocularly; (2) measurements of apparent illumination in a 'rich' 3-D scene; (3) measurements to test the linearity of the subjective illumination space.

The results confirm the basic hypothesis of the relation between fluorescence phenomena and perceived illumination and demonstrate that the proposed method gives reliable and accurate values for each of its chromatic components (errors were in the range 4%–10%), eg for paper mondrians there was a strong correlation between the level and colour of illumination and the fluorescence. In the case of mondrians presented on a screen in darkness the measured apparent illumination was found unstable, however, as would be expected given that the context of such a scene is insufficient for a unique solution of the photometric problem. In the second experiment we found that the measurement results remain constant when the context of a 'rich' 3-D scene is changed and that they follow the changes in illumination conditions. In the third experiment we found that the linear relation $f = f_1 + f_2$ holds for the measured apparent illumination (f) produced by combining of two other apparent illuminations (f_1, f_2).

◆ **Radial asymmetry in the sensitivity of the blue mechanism**

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In the human retina, the density of blue cones is lower along the nasal horizontal meridian (Curcio et al, 1991 *Journal of Comparative Neurology* **312** 610–624) than along the other cardinal meridians, but this finding might reflect interpolation between widely spaced data points rather than actual radial asymmetry. Available psychophysical data on the sensitivity of the blue mechanism do not address this question.

In the present study, subjects had to detect a blue test stimulus (wavelength range at half-amplitude 425–480 nm, diameter 24 min arc) presented against yellow background (wavelength above 550 nm, 200 cd m⁻²). The test stimulus was flickering at 5.7 Hz around a mean level of 3 cd m⁻² within a Gaussian temporal window with a time constant of 0.2 s. Foveal and parafoveal sensitivity was measured along the vertical and horizontal meridians. Radial asymmetry in the sensitivity of the blue mechanism was observed, in that the known foveal insensitivity also involved part of the nasal horizontal meridian. The dip in the sensitivity map at the fovea was narrower along the vertical than along the horizontal meridian. While these data are in good agreement with the blue-cone density map, the dip in sensitivity is wider than the depression in the density of blue cones at the fovea. Both screening by yellow pigment and effects of stimulus size might contribute to this discrepancy.

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◆ **Implication of the yellow pigment in dichoptic colour mixing**

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Working with colours generated from the three primaries, we found earlier that blue made it difficult to obtain dichoptic mixtures, producing chromatostereopsis and alternation effects which disappeared with increasing eccentricity (1 deg 3 min) or decreasing intensity of the blue component. The unanswered question was: is it true that mixtures with a strong blue component can never be obtained centrally as some authors claim? Therefore, we returned to this subject, using the same methodology and analysing the role that the yellow pigment (YP) would play.

First, the samples that previously produced the aforementioned effects were tested, confirming that chromatostereopsis stopped before the alternation. Immediately after that, identical samples were observed through low-density yellow filters that were superposed until both effects ceased. Since the density of the YP of the four participating observers had been previously measured, it was possible to calculate the necessary increase for each one of them, observing that the increment became smaller as the mixtures were displaced towards longer wavelengths.

This behaviour indicates a possible function of YP: the attenuation of the blue cone signal to make it compatible with signal from the red and green cones. As the YP varies among observers, this might be the reason why some sources mention that these mixtures can be obtained. If this hypothesis is accepted, this should not be interpreted as a variation in the number of blue receptors through the macula, a variation not necessarily observed in physiology.

◆ **Genetic studies of macular pigment**

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One of the major functions suggested for macular pigment is to protect the retina. However, a tenfold variation in pigment level is observed in the general population, which cannot be explained by other factors, such as age, sex, race, eye or skin colour (Bone and Sparrock, 1971 *Vision Research* **11** 1057–1064). We aim to examine the role of genetic factors in this variation. In our first experiments (Alexander and Moreland, 1996 *Perception* **25** Supplement, 105) we used colour matching to examine pigment levels in 23 local families. The highest correlation was seen for the father/child relationship where a linear regression accounted for 25% of the variance ($p < 0.01$); no significant relationship was observed for mother/child, grandparent/grandchild, or, as expected, for the control parent/parent plot.

These families, and a few new ones, have been retested by a motion photometry paradigm, with a foveal 2 deg field and an extrafoveal annular field at 5 deg eccentricity. In the tests, a grating of alternating bars (460 nm and 580 nm) moves horizontally across the field at 14 Hz. The subject adjusts the luminance of the 580 nm bars for minimum perceived motion. The difference in setting between the two fields is used to measure the subject's pigment level. Analysis of preliminary data shows no significant correlation for any of the relationships but further analysis is in progress.

◆ **Difference in perceived colour between painted chips and CRT images**

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The inducing effect of blue in colour assimilation on a CRT screen is so strong that pale blue apparently veils the stimulus pattern (Miyamoto and Hasegawa, 1996 *Perception* 25 Supplement, 105). A similar tendency can be observed on painted paper, but this effect is not so marked. This led us to try colour matching between coloured papers and colours reproduced on a CRT screen. In both conditions the shapes (square) and the sizes (35 cm × 35 cm) were the same. They were displayed in the centre of a 155 cm × 155 cm gray (Munsell value 5, 22 cd cm⁻²) square with 10 cm wide white fringe (74 cd cm⁻²). The task was to adjust the colour on the CRT screen to match the coloured chip which was inside an illuminated box at a viewing distance of 180 cm in a dark room. Twenty-four colours were tested. Matched blues and other blue hues were slightly more saturated than object colours, but differences in chromaticity coordinates (*u'*/*v'*) were not statistically significant. This result is opposite to the prediction because it suggests a less bluish impression in the film-colour mode. By contrast, luminance in matched blues was lower than that of the object. This means that the brightness effect increased. An additional experiment in which the stimulus size was larger and the illuminating condition was changed to a light room produced the following results: (i) no meaningful difference in chromaticity coordinates could be seen; and (ii) the luminance of matched colours increased with size and in the lighter viewing condition. These facts show that the bluish colours on the CRT screen do not change their perceived chromaticity or spread spatially. The only difference was the subjective brightness increase in the condition when the room was dark. The strong effect of the blues in assimilation on the screen, therefore, does not depend on the colour identification process itself, but on the combined effect of luminosity and visual frequency response.

◆ **Development of blue–yellow and red–green discriminations in infants during the first year of life**

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Colour discrimination was investigated in infants aged 4–14 months. 250 healthy subjects and 80 subjects with slight defects in basic visual functions (the risk group) participated. A coloured toy was moved in front of the subject and disappeared behind a screen, reappearing after 2–3 s at the other side. Sometimes when the toy was hidden, the experimenter replaced it with another one that differed only in colour: yellow was replaced by blue or vice versa (Y/B switch), or red by green or vice versa (R/G switch). The form and size of the toy remained constant. The emotional reaction of surprise showed whether the infant discriminated these colour pairs. The brightness of the stimuli was slightly varied make sure that the infant reacted to the change in colour rather than brightness. About 75% of healthy 4–5-month-olds showed good expressive reactions to the Y/B switch, and practically all children did so at 7–8 months. The discrimination of red and green develops more slowly: only at 12 months did practically all children show good reactions to the R/G switch. In all children, Y/B discrimination preceded R/G discrimination. The mean difference between the numbers of children discriminating these two pairs was 7.6%. The infants of the risk group were as good as their healthy age-mates in Y/B discrimination, but performed significantly less well on R/G: the mean difference between the numbers discriminating the former but not the latter was 17.0%. Possible reasons for the retardation of chromatic discrimination in the risk group are discussed.

EVOKED POTENTIALS AND BRAIN IMAGING

◆ **Afferent vs efferent motion evoked potentials: Relationship to dynamic visual performance**

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Visual evoked potentials (VEPs) were elicited by a computer-generated random-dot kinematogram in which a Landolt ring target moved from monitor centre to the right in front of a stationary background. Motion contrast was varied in terms of percentage of moving pixels within the ring (100%, 50%, 30%, 20%, 10%). Subjects indicated one of four gap locations (left, right, upper, lower) while fixating a small dot which was either screen centred (afferent task) or centred within the moving Landolt ring (efferent task). Correctly reported gap locations and reaction times were recorded as well as N2-amplitudes and N2-latencies. Decreasing contrast lead to decreased correct responses, decreased N2-amplitudes, and increased reaction times which were

linearly correlated with increased N2-latencies. While these effects were obtained for both the afferent and efferent tasks, they were significantly stronger for the latter. At 10% motion contrast, efferent reaction times and peak N2-latencies were as much as 370 and 100 ms greater, respectively. To determine whether the stronger efferent effects were due to differences in retinal afference between the two conditions, a third stimulus was employed in which the retinal image motion of the efferent task was simulated in the absence of eye movements (stationary fixation point and Landolt ring on a leftward moving background). The effects on performance and N2-latencies and amplitudes obtained fell between those of the two initial conditions. Implications of these findings for the processing of afferent vs efferent dynamic visual stimuli and their relationship to VEPs are discussed.

◆ **Altered functions of visual brain areas: review of recent evidence from blind human subjects**

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We investigated the functional role of human visual brain areas deprived of visual information. To this end, we recorded brain activity elicited by auditory and somatosensory stimuli in blind human subjects. Activity was recorded in the 'Attend' condition, in which subjects detected occasional deviant stimuli presented among repetitive standard stimuli and in the 'Ignore' condition, in which subjects did not attend to the stimuli.

The results indicate that in the early-blinded subjects, event-related potential (ERP) topography elicited by deviant auditory and somatosensory target stimuli is posterior to that in the sighted (Kujala et al, 1995 *Experimental Brain Research* **104** 519–526). This suggests involvement of posterior brain areas in auditory and somatosensory processing in the blind humans. For the auditory modality, activated areas were located with magnetoencephalography (MEG), which indicates involvement of extrastriate occipital areas in detection of auditory targets (Kujala et al, 1995 *Experimental Brain Research* **103** 143–146). Visual-cortex plasticity was further studied in subjects who had lost their vision after childhood in order to clarify whether these cross-modal changes are specific to visual deprivation of early onset. In that study, auditory ERP topographies of late-blinded, early-blinded, and sighted subjects were compared. Comparison of posterior topography of ERPs elicited by deviant target stimuli in both early-blinded and late-blinded subjects with that in the sighted subjects suggests visual-cortex involvement in auditory processing even in late-onset blindness (Kujala et al, 1997 *Psychophysiology* **34** 231–216). Preliminary MEG recordings in one late-blinded subject provided further support for posterior generators (parietal-occipital) in auditory processing.

◆ **Visual evoked potentials to gratings and noise**

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Visual evoked potentials were recorded in a study of the spatial-frequency characteristics of the human visual system. Stimuli were gratings with and without superposition of white noise. Evoked potentials were recorded in normal subjects from different areas of the occipital cortex, from the temporal and parietal lobes, according to the 'ten-twenty' electrode system. A set of black-and-white sine-wave gratings was used with eight different spatial frequencies in the range 0.45 to 14.4 cycles deg⁻¹. The gratings were presented with binary quasi-white noise or with a uniform grey field with mean luminance equal to that of the noise. The amplitudes of the N1, P1, N2, and P2 response components were compared under the two stimulation conditions. Changes in the form of responses as well as changes in spatial-frequency characteristics were found when white noise was superimposed. The results obtained are discussed in terms of the presence and location of matched filtering in the visual system.

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◆ **Spatial-frequency characteristics of different areas of human cortex**

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We recorded visual evoked potentials in normal subjects from different areas of the occipital cortex, from the temporal and parietal lobes according to the 'ten-twenty' electrode system. Stimuli were black-and-white sine-wave gratings with eight different spatial frequencies in the range 0.45 to 14.4 cycles deg⁻¹, presented at four different temporal frequencies (1, 2, 4, 8 Hz).

Stimulation was either contrast-reversal or onset. VEPs were analysed both by component analysis and by Fourier transformation.

Spatial characteristics were measured from the dependence of the amplitudes and latencies of the main response components (N1, P1, N2, P2) on the contrast and spatial frequency of the gratings. The characteristics obtained in the occipital lobe are in accordance with earlier experimental data [Regan, 1989 *Human Electrophysiology* (Amsterdam: Elsevier)]. When the temporal frequency of stimulation was increased, the maximum of the spatial-frequency curves shifted to lower spatial frequencies. However, we found differences in the spatial-frequency characteristics of different cortical areas. The results are discussed in terms of differences in the spatial and temporal tuning of the receptive fields of neurons in these areas.

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◆ **Task-dependence of texture-segregation-specific VEP components**

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Recently, texture-segregation-specific components have been isolated in the human visual evoked potential (tsVEPs). As tsVEPs are characterised by a negative peak near 200 ms they occur between luminance-contrast responses (P100) and cognitive responses (P300). The aim of this study was to estimate the temporal overlap of tsVEPs and cognitive VEP components by directing a task to either visual or auditory stimuli.

Eight visually normal subjects participated in the experiment. Horizontal and vertical line segments were arranged to yield either an 'orientation chequerboard' stimulus or two fields with homogeneous orientations. As auditory stimuli, two tones with different pitches were presented through headphones. Auditory and visual stimuli were temporally uncorrelated, which allowed off-line isolation of VEPs and AEPs by appropriate averaging from the same raw data. VEPs and AEPs were recorded from an array of 13 electrodes ranging from frontal to occipital positions. tsVEPs were isolated under two conditions, where the subjects detected the presence of (a) the orientation chequerboard, or (b) the higher pitch by pressing a button.

It was found that (1) tsVEPs could be isolated under both tasks; (2) tsVEPs were strongly modulated by the task; (3) the task-specific modulation occurred in the same time domain as the tsVEP itself, but showed a different topography; (4) AEPs were less modulated by the task. The data suggest that an additional task concerning the gradient content of texture stimuli may modulate the resulting tsVEPs. This may partially account for the interindividual variability in recent tsVEP data, as a comparable task may be introduced tacitly by the subjects.

◆ **Visually evoked magnetic field induced by ring motion aftereffect**

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Motion aftereffect (MAE) is a negative aftereffect caused by prolonged viewing of visual motion: after gazing at a moving grating for a while, a stationary image will appear to move in the opposite direction (Ashida and Osaka, 1995 *Vision Research* 35 1825). Evoked magnetic field (magnetoencephalogram: MEG) was measured when a human subject observing ring MAE in which concentric circles appear to contract continuously after viewing continuously expanding rings. The diameter of the stimulus was 20 deg with fixation point in the centre. The magnetic evoked field (80 averagings at a latency of 190 ms) was measured from 37 points over the occipital and parietal areas (MagneSQUID biomagnetometer, BTi) while the subject was observing stationary rings after an adaptation period of 2 s at low spatial frequency (4 cycles deg⁻¹, 4 Hz). The luminance profile was sinusoidally changed across rings. MRI image fitting (sagittal, coronal, and axial view) for each of four subjects, and dipole estimates obtained for equal magnetic field contours (with value of goodness of fit greater than 0.98) from the right brain hemisphere suggest that the main loci subserving MAE lie in the surrounding region over the lateral occipitotemporal areas in the human brain, close to area MT. This is in good agreement with another study with fMRI-based MAE measures [Tootell et al, 1995 *Nature (London)* 375 139] in which a clear increase in activity in these areas was observed when subjects viewed MAE.

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◆ Neuroimaging analysis of visual motion

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The evoked magnetic field (magnetoencephalogram: MEG) was measured in human subjects observing random-dot motion. 600 random dots generated with VSG2/3 (Cambridge Research Systems) moved at about 10 deg s⁻¹ (either in the 45° or the 135° direction). The motion frame (5 s) was followed by a stationary frame on a screen (projected from Barcodata 3100 projection system) subtending a visual angle of about 20 deg × 20 deg. Six subjects observed the motion frame presented in the left visual field. The magnetic evoked field (80 averagings) was measured from 37 points over occipital, temporal, and parietal areas (Magnes SQUID biomagnetometer, BTi) of the right brain hemisphere. Dipole estimates based on equal magnetic field contours (190 ms after motion frame onset with value of goodness of fit greater than 0.95) and MRI image fitting (sagittal, coronal, and axial view) for each subject suggest that the main loci subserving motion perception lie in the surrounding region over occipital, temporal, and parietal junction areas in the human brain close to area MT.

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◆ The characteristics of VEPs associated with the accuracy of recognition of facial emotion

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While investigating the timing of the N180 wave of human VEPs, we found earlier that correct recognition of facial emotions was characterised by the primary activation of the right fronto-central regions followed by the immediate involvement of the left ones.

The aim of the present study was to analyse the relations between the parameters of the N400 wave, its regional and hemispheric specificity, and the accuracy of emotion recognition. Twenty healthy right-handed subjects and thirty-two untreated psychiatric patients with mild cognitive dysfunction were instructed to recognise the emotional expression of sad, neutral, or laughing faces presented for 80 ms on a computer screen. The amplitude and peak latency of the N400 response were found to be closely related to the accuracy of recognition. In healthy subjects the main difference between error and correct recognition manifested itself in decreased amplitude and shortened latency of the N400 response in frontal and central zones of the left hemisphere ($p < 0.001$). Compared to healthy subjects, the patients demonstrated both poor recognition and decreased latency and amplitude of the N400 response in the left frontal regions ($p < 0.0001$). The results suggest that activation of the left fronto-central regions plays a principal role in the final stages of facial emotion identification.

◆ Differential activation to faces, degraded faces, and their inverted counterparts

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We investigated electrophysiological correlates of activation to faces, pointillised faces (degraded to a degree still allowing face perception), and their inverted counterparts. Evoked magnetic fields to the four stimulus categories were recorded by 122-channel magnetoencephalography (MEG) in six subjects. Simultaneously recorded 64-channel EEG provided visual evoked potentials in four subjects.

Analysis of the onset, peak latencies, and the signal strength of the face enhanced N170 response indicated the following. (1) In general, the MEG and EEG recordings supported each other. (2) Degrading the images delayed both the onset and peak latencies. Degrading the upright faces increased activity in some subjects, but activity to the degraded inverted faces was lower in all subjects. (3) Inversion delayed the onset latency of both the original and degraded faces by 4–10 ms on average. A similar shift was found for the peak latency of the inverted original face images. However, their pointillised counterparts peaked on average 26 ms later when inverted. The signal amplitude also reflected a differential effect of inverting original vs degraded faces; whereas original faces evoked larger responses in all six subjects, the signal to inverted degraded faces decreased in four subjects. The findings suggest that the analysis of both the onset (100–120 ms) and peak activity (150–170 ms) is important for understanding face processing. The effect of inversion on the evoked responses was found to be different for the original and pointillised faces.

- ◆ **Non-linear interactions in cortical responses to bilateral vs unilateral visual field stimulation**
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Stimuli in different parts of the visual field can be perceived as independent entities and as conjoined wholes. It is of interest to determine whether there are cortical representations of the left and right hemifields which remain as independent entities when both hemifields are stimulated simultaneously and/or whether they interact to form a conjoined representation. We examined whether cortical processing of visual stimuli depends on whether they occur in isolation in one hemifield (unilaterally) or simultaneously in both hemifields (bilaterally).

Visual evoked potentials of six normal subjects were recorded from 128 scalp sites. Wedge-shaped chequerboard stimuli, extending 1–4 deg eccentricity, were presented to quadrants of the visual field. Stimulus duration was 250 ms; the stimulus onset asynchrony was random, 500–750 ms. The evoked potentials revealed multiple peaks of activity with different surface topography. Prominent deflections occurred around 80, 120–180, and 230 ms.

The response to bilateral stimuli was compared with the sum of the responses to unilateral stimuli. On the basis of the multichannel recordings, nonlinear interactions were characterised as either (a) modulations (same generators, but different amplitude) or (b) interactions originating from different generators. Modulation occurred at 230 ms, the response being suppressed for the bilateral case. At 120–180 ms, the field patterns suggested that at least some of the sources of the interaction effect are different from the source of the bilateral response. Underlying generators of the evoked responses and the interaction effects were further explored with the use of an equivalent current dipole model.

- ◆ **Comparison of human occipital cortical activation to lower and upper visual field stimuli**
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We compared cortical responses to lower and upper quadrant and full hemifield stimuli (90° and 180° sectors of circular checkerboards) measured from 15 healthy subjects with a Neuromag-122® whole-scalp neuromagnetometer. The 0.2 s stimuli were presented once every second, while the subjects fixated a black dot in the centre of the screen.

The first evoked responses, peaking at 70 ms in the contralateral hemisphere, were stronger for lower than for upper field stimulation (13/15 subjects, LVF; 11/15 RVF). The sources of the evoked responses, modelled as equivalent current dipoles, clustered around the calcarine fissure, with a trend for stronger sources after lower than after upper field stimulation (on average 12% LVF; 40% RVF; ns).

Attention-related visual processing may be enhanced in the lower compared with the upper visual field (Rubin et al, 1996 *Science* 271 651–653). Although our data showed a strong tendency to larger responses for lower than for upper visual field stimuli, this difference was not significant for source strengths, mainly because of different source depths for upper and lower field stimuli. However, the marked similarity of source current directions for full hemifield and lower quadrant stimuli (15°–35° upwards from the horizontal axis, viewed from back, compared with directions 15°–25° downwards for upper field stimuli) suggest that visual input from the lower field is preferred already at early stages of the human visual system.

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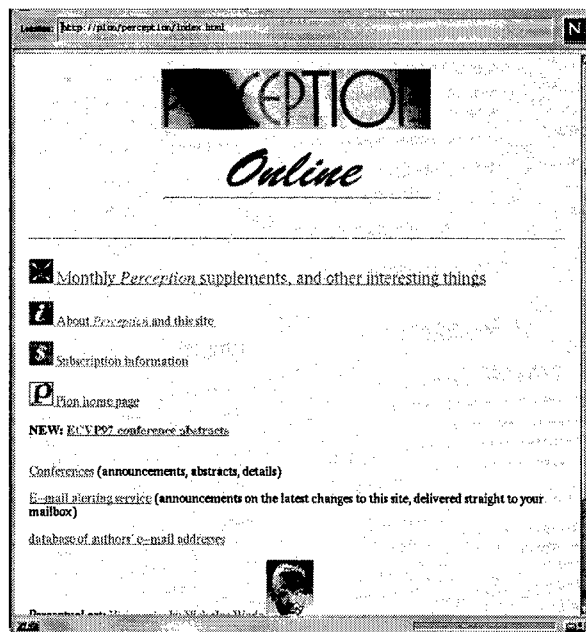
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