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19 ABSTRACT (Continue on reverse if necessary and identify by block number)
Of a normally-sighted subjects, 3 had areas of the visual field that were "blind" to oscillating disparity (motion in depth) within the central 10 deg of vision. These stereomotion-blind areas had normal sensitivity for relative position in depth (i.e. normal stereoacuity) and normal sensitivity for front-selective sensory blindness, vergence eye movements could not be driven from within the stereomotion-blind areas, but conjugate eye movements could be driven. Vernier acuity for camouflaged bars defined by relative motion is approximately the same as vernier acuity for comparable bars defined by brightness contrast, even though receptive fields for detecting objects by motion alone are very large and sluggish. This may help to explain why helicopter pilots can make precise spatial judgements in slow low-level flight. A book has been completed that attempts to link evoked electric and magnetic fields of the human brain with human perception and cognition and with the properties of single neurons in primate brain.

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2a. OBJECTIVES

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(1) Further define the roles of the channeling hypothesis in:

(a) identifying specific visual processes; (b) understanding visual performance; (c) specifying visual parameters likely to be important in eye-hand coordination especially in aviation, and flight simulator visual displays.

(2) Motion in depth. Define the relationship between stereoscopic stimulation, vergence eye movements and motion-in-depth perception in foveal and peripheral vision.

(3) Discrimination and detection. Experimentally determine the properties of orientation and size discrimination. Test the hypothesis that the visual system contains *opponent-size* and *opponent-orientation* elements that determine size and orientation discrimination, and that these elements are involved in shape discrimination and recognition. Relate the discrimination of size and orientation to contrast detection. Model discrimination in terms of the size/orientation tuned elements postulated to explain detection.

(4) Camouflage. For camouflaged objects that are invisible except when there is motion parallax between the object and background, measure spatial discriminations and in particular the hyperacuties. Compare these data with corresponding hyperacuties for objects defined by luminance contrasts. Find whether a single visual mechanism can account for both the visibility of objects defined by motion contrast alone and also the visibility of objects defined by luminance contrast alone.

2b. STATUS OF THE RESEARCH EFFORT(i) Specific "blindness" to stereomotion in depth in perception and eye movements

Dr. H. Collewijn of the Erasmus University, Rotterdam, The Netherlands, has developed a scleral coil technique for measuring human eye movements, and is a world authority on eye movements. In a collaborative study we measured binocular eye movements to a precision of 6 sec arc (DC-100 Hz) while stimulating the two eyes with targets that oscillated in disparity so as to produce an impression of motion in depth (Regan, Erkelens & Collewijn, 1986a; Collewijn, Erkelens & Regan, 1986). First we mapped the stereomotion visual fields of six subjects using the technique described by Richards and Regan (1973). Three subjects had stereomotion "blind spots" within the central 10 deg of vision (Figs 1, 2 and 3). We confirmed that this "blindness" was specific for motion-in-depth by showing that visual thresholds for frontal plane motion and for position-in-depth were normal in the stereomotion-blind areas (Fig 4).

Then we compared stimulus-induced vergence eye movements recorded while a bar, oscillating in depth, was located in the stereomotion-blind area with vergence eye movements recorded when the bar was located in a normal area of the visual field at the same eccentricity. We found that the vergence eye movement system was blind in the affected area just like perception. A further agreement was that the conjugate eye movement system was normal in the stereomotion-blind area: frontal-plane oscillations elicited normal conjugate eye movements.

Stereomotion scotoma seem to be common in the normal population. Their importance in aviation safety and highway driving remains to be established.



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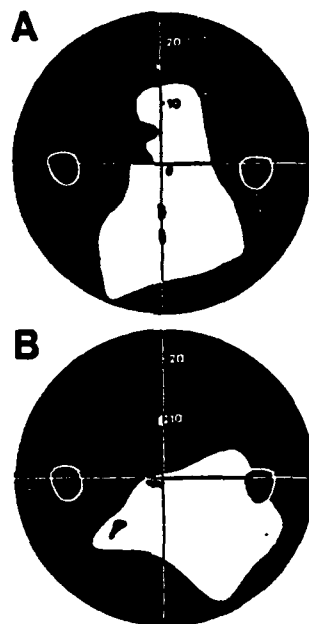


Figure 1

Visual fields for stereomotion. A - Crossed disparities. B - Uncrossed disparities. Motion in depth was seen in the white areas but not in the black areas. Dots signify areas of unstable motion-in-depth perception. The two oval areas along the horizontal meridian are the blind spots. The horizontal and vertical meridians intersect at the fovea. Numbers are eccentricities in deg. Subject D.R.

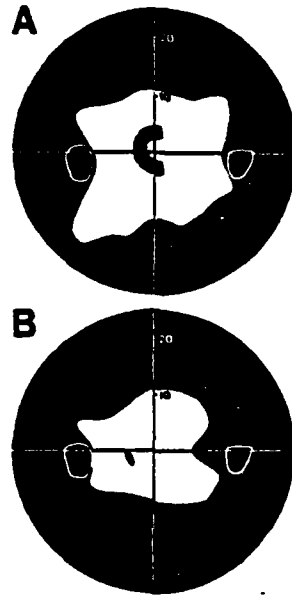


Figure 2

Visual fields for stereomotion. Subject C.E. Details as in Fig 1.

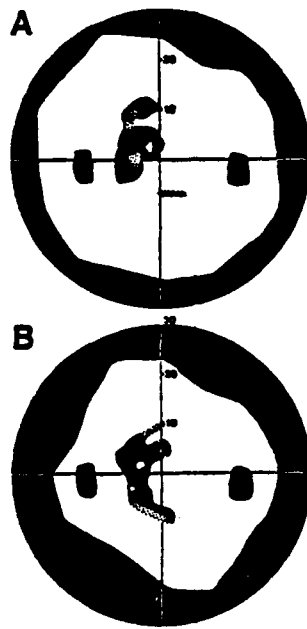


Figure 3

Visual fields for stereomotion. Subject H.S. Details as in Fig 1.

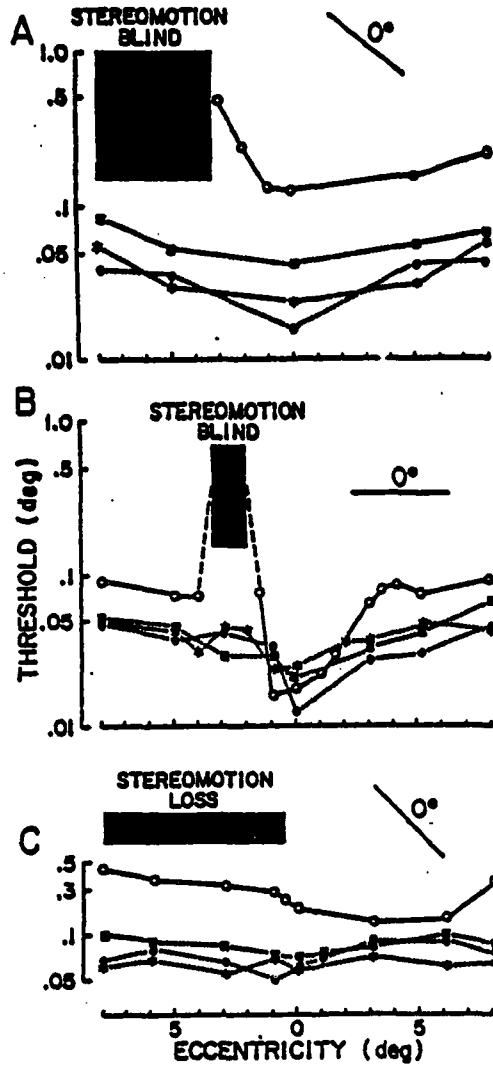


Figure 4

Thresholds for stereomotion (open circles, continuous line) and for lateral motion (filled symbols), plotted versus eccentricity along a line (see inserts) passing through both the fovea and a stereomotion scotoma. Filled circles signify left eye monocular stimulation, filled squares right eye monocular stimulation, and filled stars binocular stimulation with lateral motion. Zones of total stereomotion blindness or loss are shown black in A and B, and a zone of relative stereomotion loss is shown in C as a black zone of lesser height. Results are shown for three subjects.

(ii) Vergence eye movement responses and psychophysical sensitivity to changing-size

Vergence tracking eye movements are important for keeping a target accurately registered by the two eyes, and especially in maintaining fused binocular vision when an object is moving in depth and/or the observer is moving in depth. Thus, accurate vergence eye movement tracking is an important requirement in many real-world tasks involving eye-hand coordination. This study was concerned with the fact that when an object moves towards the eyes it produces two cues to its approach: (1) The retinal images grow larger, and (2) they move apart (Fig 5).

We explored the sufficient stimuli for producing vergence tracking, and the relation between stimulus-induced vergence eye movements and visual perception.

In this second joint study between the P.I.'s Dalhousie laboratory and Drs. Collewijn and Erkelens of Erasmus University, Rotterdam, we measured the movements of the left and right eyes using the scleral contact lens method (Regan, Erkelens & Collewijn, 1986b). We stimulated the eyes with a binocularly-fused bright solid square 1 x 1 deg in the following conditions: (a) changing-disparity alone, (b) changing-size alone and (c) changing-disparity combined with changing-size in such a way as to exactly mimic the retinal image changes produced by a real object's motion in depth. The gain and the phase of the induced eye movements were measured in each case over a range of oscillation frequencies.

Previous studies of stimulus-induced vergence eye movements were confined to the effects of change in binocular disparity. We report here the new finding that changing-size alone is also effective as a stimulus for vergence eye movements. Furthermore, vergence eye movements induced by changing-size are

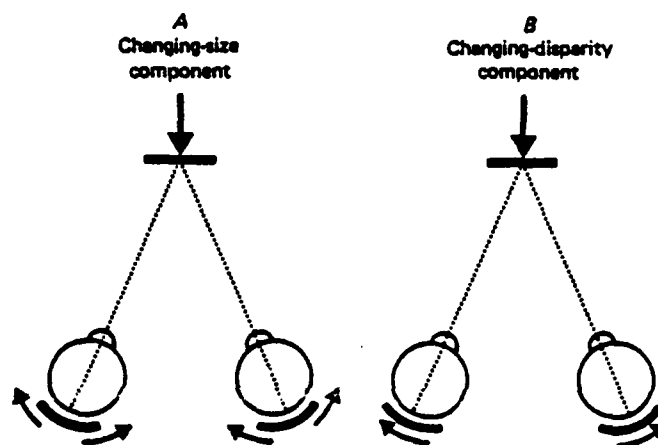


Figure 5

↓ represents a binocularly-fused, rigid, nonrotating object moving in depth directly towards an observer whose eyes maintain a constant angle of convergence. The retinal image motion caused by the object's motion is the vector sum of two components: A - a rate of increase of size; B - a translation of the images in opposite directions at velocities whose difference is equal to the rate of change of disparity.

entirely transient with no sustained component while vergence responses to changing-disparity are sustained (Erkelens & Regan, 1986).

We confirmed previous findings that vergence eye movements induced by disparity changes do not follow the stimulus smoothly, but are somewhat irregular and oscillatory. However, when the stimulus combined size change with disparity change in the ratio characteristic of a real moving object, vergence tracking was more accurate, and less noisy than when the eyes were stimulated with the disparity component alone. This improvement could be explained straightforwardly, because the vergence response to the combined stimulus could be accurately predicted by linearly adding the vergence response produced by size change alone to the vergence response produced by disparity change alone (Fig 6). We report evidence that the stabilizing influence of the changing-size system arises from its faster processing time compared with the changing-disparity system.

In order to compare eye movement responses with psychophysical responses, we used the same equipment and the same stimulus conditions that had been used several years earlier in a series of studies on motion-in-depth perception (Regan & Beverley, 1978, 1979). Fig 7 illustrates the close parallels that we found between eye movements and psychophysical thresholds. We had found previously that motion-in-depth sensation induced by changing-disparity had a sustained, i.e. lowpass characteristic (Regan & Beverley, 1979): Fig 7 illustrates the similar shape of the vergence eye movement characteristic (compare the filled black circles in A and B). Fig 7 also shows that changing-size stimulation gave similar characteristics for the vergence eye movement system (open circles in A) and for psychophysical sensitivity to motion-in-depth.

A further point brought out in Fig 7 concerns the fact that changing-size

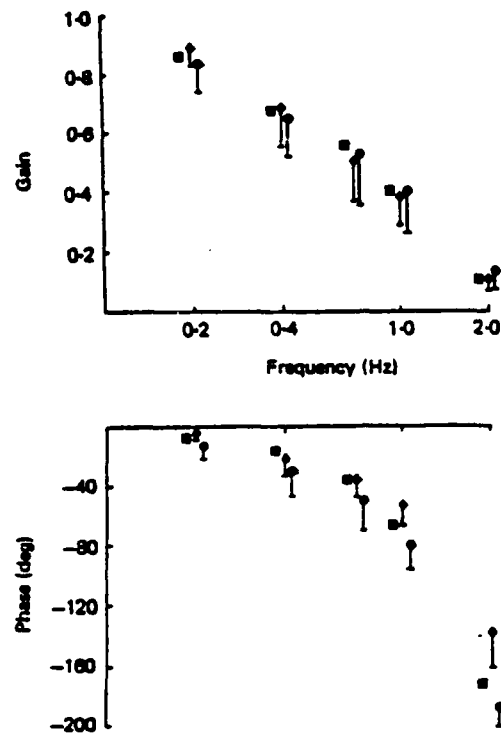


Figure 6

Gain and phase of ocular vergence responses. Diamonds plot responses induced by a combination of disparity and size changes. Circles plot responses induced by the changing-disparity component alone. Squares plot theoretically-predicted estimates for combined stimulation; these estimates were obtained by linearly adding the vergence responses induced by the disparity component alone and by the size component alone. Means and standard deviations are shown for five subjects.

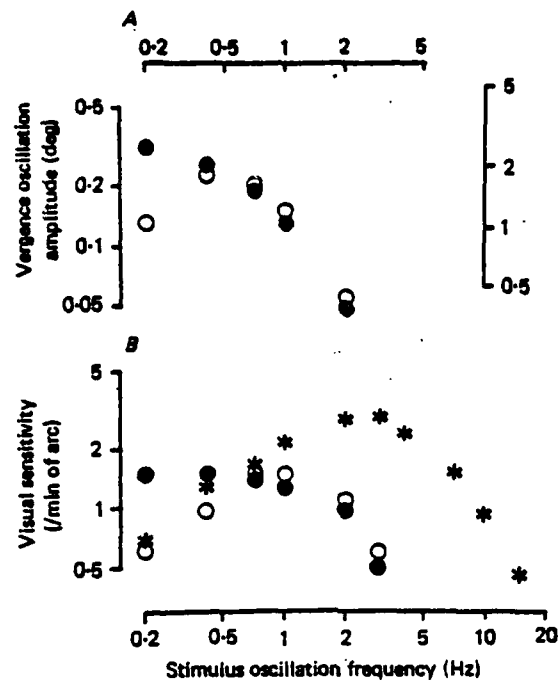


Figure 7

A - Left and right ordinates are amplitudes of vergence oscillations induced respectively by size oscillations and by disparity oscillations. Abscissae are stimulus oscillation frequencies. Open circles (continuous line) plot responses to size oscillations, and filled circles (dashed line) plot responses to disparity oscillations. (Mean of five subjects.)

B - Ordinates are psychophysical sensitivities (reciprocal of threshold). Abscissae are stimulus oscillation frequencies. Open circles (continuous line) and filled circles (dashed line) are for motion-in-depth sensation induced by oscillating size and oscillating disparity respectively. Stars (dotted line) are for oscillating-size sensation induced by oscillating size. (Mean of three subjects, computed from data in Regan & Beverley, 1979.)

stimulation can generate an impression, not only of motion-in-depth but also of changing-size. The perception is usually either one or the other, rather than a mixture (Beverley & Regan, 1979). Because the two percepts depend differently on frequency (compare stars and open circles in B), we can infer whether vergence eye movements correlate with the percept of motion-in-depth or changing size. Fig 7 indicates that vergence correlates with motion-in-depth perception rather than changing-size perception.

(iii) Necessary conditions for motion-in-depth perception

A compelling impression of motion in depth is produced by changing the disparities of two binocularly-fixated targets (Richards, 1971), and the direction of motion in depth depends on the relative velocities of the two retinal images (Beverley & Regan, 1973, 1975). However, when reference marks are removed from the visual field stereomotion-in-depth perception is completely abolished (Erkelens & Collewijn, 1985a,b). The effect is dramatic and very large indeed. With large disparity oscillations, closing one eye reveals strong motion: with both eyes open the target appears absolutely still. But when a stationary object is placed in the field of vision, strong motion-in-depth is immediately seen.

Possible explanations for this abolition include the following: (1) ocular vergence exactly tracked stimulus motion; (2) vergence changes and disparity changes, though unequal, produced equal and opposite motion-in-depth signals; (3) vergence changes, though producing no motion-in-depth signals, suppressed the signals induced by disparity changes; (4) motion-in-depth signals require relative motion.

In a third joint study, Dr. Collewijn, Dr. Erkelens and the P.I. attempted to determine the explanation for this dramatic abolition of motion-in-depth

perception. We measured binocular eye movements by means of the scleral coil technique.

Explanation (1) was rejected because vergence tracking errors were large. Explanation (2) was rejected by our finding that vergence changes do not in themselves induce a sensation of motion in depth. Explanation (3) was rejected by our finding that motion-in-depth threshold is not affected by simultaneous changes in vergence. We concluded that a change in relative disparity is required for stereomotion-in-depth perception: neither absolute motion, nor changes in absolute disparity is an adequate stimulus for the perception of motion in depth.

(iv) Periodicity in orientation discrimination

Models of human orientation discrimination must account for the following points: (1) The ability to discriminate a change of orientation is almost unaffected by a simultaneous change of contrast or spatial frequency, although the firing of orientation-tuned cortical neurons is, in general, affected by both contrast and spatial frequency (Regan & Beverley, 1985; Burbeck & Regan, 1983). (2) The substantial discrepancy between the 0.15-05 deg orientation discrimination threshold in man (Andrews, 1965, 1967; Westheimer et al, 1976; Burbeck & Regan, 1983) and the 10-20 deg bandwidths of cortical neurons and psychophysical spatial frequency channels (Hubel & Wiesel, 1968; Campbell et al, 1968; Blakemore & Nachmias, 1971; Thomas & Gille, 1979; Braddick et al, 1978; Gilinsky, 1968). (3) Orientation discrimination threshold is almost independent of contrast for contrast levels above 2-3 times threshold (Regan & Beverley, 1985). (4) Orientation discrimination shows little correlation with visual acuity (Orban et al, 1984).

It has been proposed that the sharpness of orientation discrimination can be

understood if discrimination is determined by the relative activity of two or more broadly tuned orientation-sensitive neural elements (Westheimer et al, 1976). This idea has been framed in both opponent-process (Regan & Beverley, 1985) and line-element (Wilson & Gelb, 1984; Wilson & Regan, 1984) formulations. These two formulations share the features that orientation discrimination is limited, not by the bandwidths of the broadly-selective neural elements, but by a combination of their noise levels and the shape of their sensitivity curves (specifically, by the maximum slope difference). More crucially, at least the opponent formulation of this idea can also explain why subjects do not confound simultaneous changes in orientation, contrast and spatial frequency, even though cortical neurons typically confound these stimulus parameters.

Both opponent and line element hypotheses of orientation discrimination imply that discrimination threshold will be a monotonic function of orientation if there is, in effect, an orientation-tuned element for every orientation. On the other hand, if only a few orientation-tuned elements are effective, then orientation discrimination will vary with orientation. Discrimination threshold will rise to a maximum at every sensitivity peak; minima in discrimination threshold (i.e. best discrimination) will occur between the peaks of adjacent elements.

Exploring this idea we measured orientation discrimination threshold at small (7.5 deg) increments round the clock (Regan & Price, 1986). We attempted to reduce the effective number of orientation-tuned elements by stimulating only a small (1.0 deg diameter) field located off the central fovea (1.25 deg eccentric). The subjects (one of whom was the P.I.) first performed about 40 hours of observations to ensure that thresholds had stabilized, and then the two experimental runs of 8750 trials each (about 40 hours), each comprising 350

trials at 25 orientations. Stimulus parameters were randomly interleaved.

Fig 8 shows that orientation discrimination is a periodic function of mean orientation, consistent with the idea that discrimination is determined by the relative activity of a small number (perhaps four) of broadly-tuned elements.

(v) The effect of contrast on line interval discrimination and on vernier acuity

In a joint experiment, Professor M. Morgan of London University and the P.I. found that line interval discrimination (a hyperacuity) is approximately independent of contrast for contrasts greater than about three times detection threshold. Vernier acuity, on the other hand, (another hyperacuity) shows no such plateau. Furthermore, random variations of the contrasts of the line pair does not affect line interval discrimination.

In order to explain this contrast-independence, we put forward an opponent model of line interval discrimination, proposing that line pairs are detected by "coincidence detectors" that give a strongly facilitatory (e.g. multiplicative) response for a fixed line separation, and that the relative activity of a population of such detectors determine line interval discrimination (Morgan & Regan, 1987).

(vi) Vernier acuity for bars defined by motion alone (Regan, 1986)

Some objects are perfectly camouflaged when stationary, but are clearly visible when moving: the boundaries of such an object are defined entirely by motion parallax. The ability to see and judge (distance etc) of such objects is crucial in some real-world situations including nap-of-the-Earth helicopter flight.

Real-world motion parallax commonly confounds several cues to figure-ground segregation including: (1) Different texture velocities on either side of the figure's boundary; (2) in any given interval, texture in figure and ground move

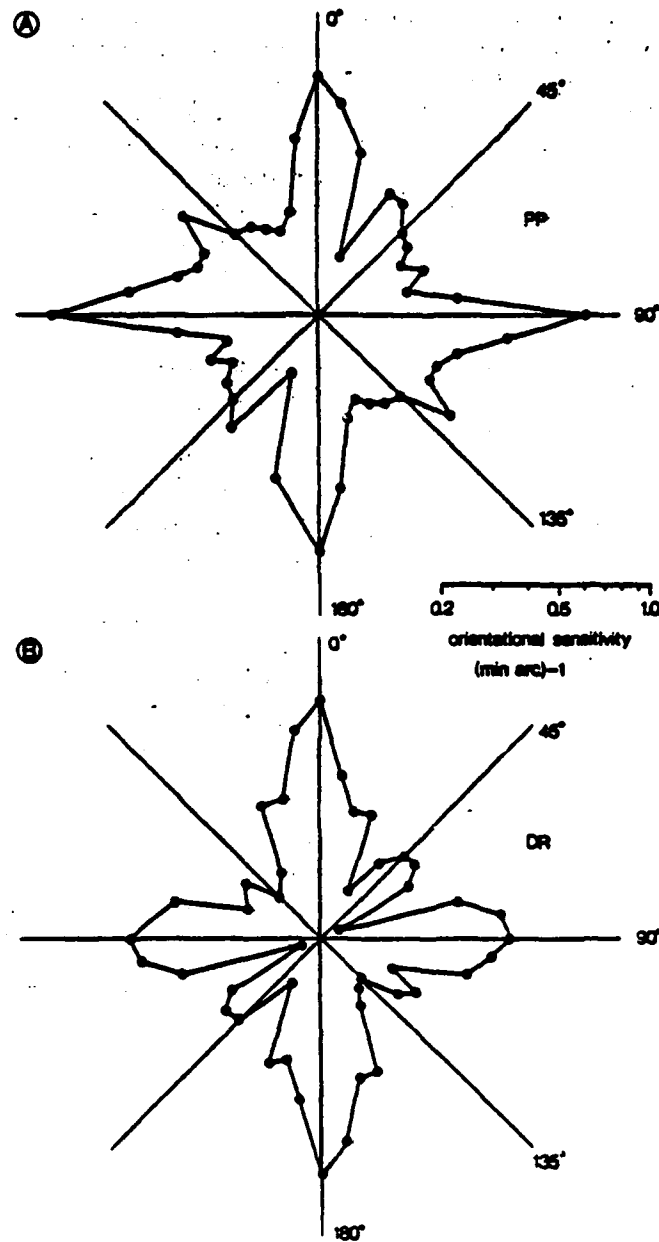


Figure 8

Orientation discrimination vs grating orientation for two subjects. The reciprocal of orientation discrimination threshold is plotted radially on a logarithmic axis, starting from 0.2 min arc^{-1} sensitivity at the origin.

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different distances (Fig 9A); (3) texture continually appears and disappears along the figure's boundary.

A 3 x 3 deg pattern of random dots was generated by computer-controlled fast hardware electronics developed for a previous study on motion-defined objects (Regan & Beverley, 1984). A bar-shaped area was perfectly camouflaged except when there was a velocity difference between the dots within and outside the bar. Cue #2 was eliminated by moving the dots within and outside the bar at equal and opposite speeds, and stabilizing the retinal image by means of a double-Purkinje eyetracker (Fig 9B). Cue #3 was eliminated by creating a completely new 1000-dot pattern eight times per second so that dots appeared and disappeared all over the screen all the time. Vernier acuity was measured by the method of constant stimuli using temporal two-alternative forced choice.

With all cues eliminated except #1, vernier acuity was 27 sec arc, comparable with the 25 sec arc intercone separation in the fovea, much less than the mean interdot separation of 360 sec arc and very much less than the estimated 7200 sec arc (2 deg) diameter of motion summation fields (Richards, 1971; Nakayama & Tyler, 1981; Regan & Beverley, 1984).

When the dots in the surround were switched off, thus producing a dotted bar defined by luminance contrast, vernier acuity was not improved beyond 27 sec arc. (When a solid bar was used instead of dots, 8 sec arc was achieved, indicating that the lower value of 27 sec arc was due to inadequate spatial sampling.)

We conclude that vernier acuity is as good for a bar defined by motion alone as for a similar bar defined by luminance. Thus the visual mechanism that achieves figure-ground segregation by motion alone is capable of a very fine spatial discrimination spite of its large summation field size (Regan, 1986).

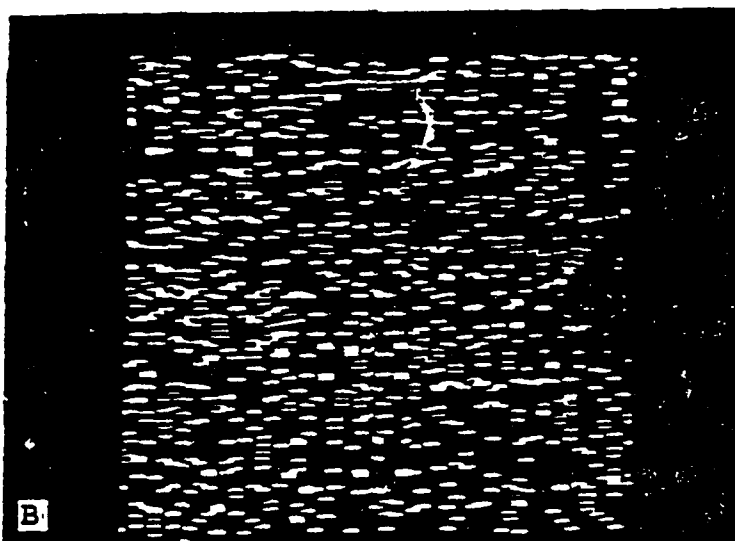
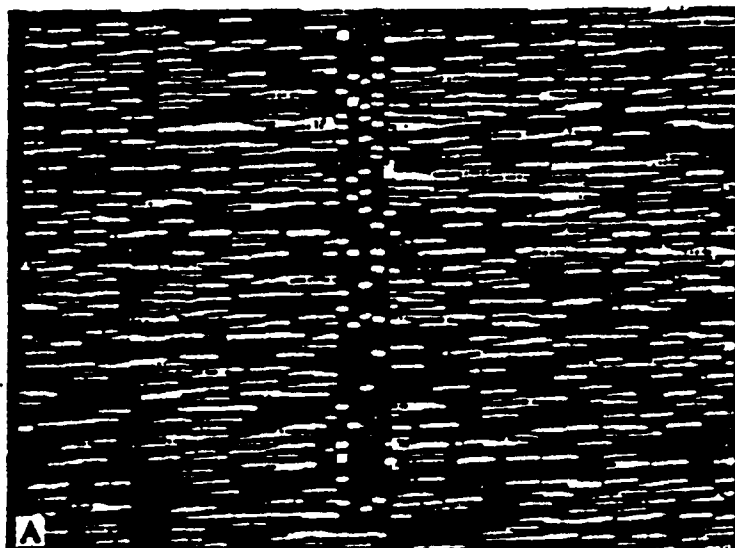


Figure 9

A - The vertical 0.2×2.0 deg bar was visible only because the dots outside the bar were moving faster than the dots within the bar. Vernier offset was very small. B - Dots within and outside the bar moved with equal and opposite velocities.



(vii) Evoked potentials in human vision research 1961-1985

To mark the first 25 years of the journal Vision Research a Jubilee Edition was published containing invited articles. Dr. H. Spekreijse and the P.I. reviewed evoked potentials in vision research over the last 25 years (Regan & Spekreijse, 1986).

(viii) Book on evoked electromagnetic responses of human brain in relation to sensation and cognition

This book attempts to link (1) our knowledge of evoked electrical and magnetic responses of the human brain to (2) sensory perception and cognition and (3) the properties of single neurons in primate brain. It covers vision, hearing, somatosensation and cognition. There are three parts: technical and mathematical aspects of recording techniques, basic research, and clinical applications. The book runs to about 1000 pages and will be published by Elsevier late 1988.

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2d. PROFESSIONAL PERSONNEL

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Joint research was carried out with H. Collewijn, M.D. (Professor of Physiology, Erasmus University, Rotterdam, Holland) and C. Erkelens, Ph.D. (Erasmus University).

2e. INTERACTIONSLectures and Abstracts

Regan D, Regan MP. Dissecting the visual and auditory pathways by means of the two-input technique. AGARD (NATO) conference on electric and magnetic activity of the CNS, Trondheim, Norway.

Regan D, Neima D. Relation between VEP and visual function in lesions of the optic nerve and visual pathway. AGARD (NATO) conference on electric and magnetic activity of the CNS, Trondheim, Norway.

Regan D. Invited talk: Acute spatial discriminations and the unconfounding of visual information. Second World Congress of Neuroscience (Satellite Symp., Manchester, England).

Regan D, Regan MP. Evoked potential processing of nonlinear processing stages in human vision. Second World Congress of Neuroscience (Satellite Symp., Manchester, England).

Regan D. Visual loss in patients with 20/20 vision. Invited lecture to the annual meeting of the Optical Society of America, Seattle, 1986.

Regan D. Computational models in human vision. Invited lecture to the Rochester University Conference on Computational Vision, 1986.

Regan D. Form from motion contrast and form from luminance contrast. Invited lecture to the American Academy of Optometry, Toronto, 1986.

Regan D. Keynote lecture on Vision in Sport. European Sports Federation of the Netherlands, 1986.

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Department of Medical Physics, University of Nijmegen, 1986.

Department of Ophthalmology, University of Amsterdam, 1986.

Department of Ophthalmology, University of Louvain, Belgium, 1986.

Department of Physics, University of Utrecht, The Netherlands, 1986.

Neuroscience Centre, London University, 1986.

Department of Physics, National Research Council, Ottawa, 1986.

Departments of Physiology and Psychology, University of British Columbia, Vancouver, 1986.

Department of Brain Science and Cognition, MIT, Boston, 1986.

Department of Psychology, York University, Toronto, 1986.

Department of Psychology, University of Toronto, 1987.

Department of Computer Science, University of Toronto, 1987.

Playfair Institute, Toronto, 1987.

Hospital for Sick Children, Toronto, 1987.

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