EVIDENCE FOR THE EXISTENCE
OF NEURAL MECHANISMS SELECTIVELY SENSITIVE TO
THE DIRECTION OF MOVEMENT IN SPACE

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SUMMARY

1. Visual sensitivity to movement in depth was measured as a function of the relative distances through which the left and right retinal images moved. This relative distance (left:right ratio) provides a sensitive cue to the direction along which a target moves in three-dimensional space.

2. Gazing at a target which moved along a fixed direction in space produced a gross reduction of visual sensitivity to movements in depth along that direction. For other directions of movement, visual sensitivity was not affected.

3. Sensitivity to depth movement rapidly rose almost to the pre-adaptation level within the first 20–60 sec after removing the adapting target, but recovery was not complete until 100–300 min had elapsed.

4. Any adapting target whose left:right ratio fell within a definite range gave similar reductions of visual sensitivity to movements in depth. There were five such ranges.

5. The effects of adapting to movement in depth suggest that eight mechanisms underlie depth perception. These mechanisms are 'tuned' to the direction of movement in three-dimensional space. Four mechanisms are wholly concerned with movements along directions very close to the line which cuts midway between the eyes, and do not respond to movements whose direction departs by more than 1·5° from the preferred direction.

6. Neural mechanisms 'tuned' to different left:right ratios could provide a physiological basis for sensing the *direction* in which an object moves in three-dimensional space.

INTRODUCTION

To avoid, catch or hit a rapidly moving object are commonplace skills whose familiarity conceals an ability to sense with remarkable precision the direction in which a body moves in space. Although there is a good understanding of the various neural organizations which underlie the ability to make a number of visual judgements including orientation (Blakemore & Campbell, 1969; Gilinsky, 1968; Hubel & Wiesel, 1959), depth (Barlow, Blakemore & Pettigrew, 1967; Pettigrew, Nikara & Bishop, 1968) and the direction of sideways motion (Barlow & Hill, 1963; Wohlgemuth, 1911), the perception of motion in three-dimensional space has received comparatively little attention.

The experimental results reported below provide evidence for the existence of one neural organization that may underlie visual sensitivity to the *direction* in which an object moves in depth.

METHODS

Our subjects viewed an irregularly spaced pattern of dots with the left eye and a similar pattern with the right eye. The 2° central areas of each pattern were sinusoidally oscillated from side-to-side by Pye-Ling vibrators. When the left and right patterns were viewed in binocular fusion the 2° central area generally appeared to oscillate in depth. This stimulator has been described elsewhere (Regan & Beverley, 1973b).

The effect of altering the relative amplitudes of oscillation of the left and right targets (i.e. left:right ratio) was to change the direction of the line along which the target appeared to oscillate in three-dimensional space.

The left:right ratio was set by adjusting the relative amplitudes of the signals fed to the vibrators. By turning a logarithmic control potentiometer, the subject could vary the absolute amplitude of the retinal image movements, without altering the left:right ratio. The calibration of the control potentiometer was frequently altered without the subject's knowledge. A CRO was used to measure the amplitudes of the signals fed to the vibrators and these readings were subsequently expressed in terms of peak-to-peak change in retinal disparity.

For a given left:right ratio, the oscillation amplitude of retinal disparity was varied until the subject was just able to see the target's oscillations in depth (depth threshold).

Depth thresholds were determined over the complete range of left:right ratios. Each threshold setting was made within a brief viewing period (10 sec) in order to minimize the influence of the rapid changes in threshold discussed below. On request, the subject was allowed to use more than one 10 sec period per threshold setting. Adapted thresholds were measured after 10 min adaptation to movement in depth, with a further 30 sec adaptation between successive 10 sec viewing periods. Unadapted thresholds and adapted thresholds were not measured on the same day.

The asymmetries of Fig. 2 were confirmed while both fixation and depth tracking were monitored by means of nonious lines. Changes in ocular convergence of 0·5 min arc could be detected by this means.

Most measurements were made by the method of adjustments, but the asymmetries of Fig. 2 were also confirmed by the method of ascending and descending limits.

Stimulus patterns were transparencies located 63 cm from the eyes and trans-illuminated by diffusers placed in front of d.c.-powered fluorescent tubes (Crompton 6W 'white'). The dots were black, of diameter 2 min, and occupied roughly 10 % of the stimulus area. Mean stimulus luminance was 110 cd/m².

In order to record the time course of recovery after adaptation, the control potentiometer was ganged to a second potentiometer which gave a voltage proportional to the amplitude through which retinal disparity oscillated. This voltage was fed to a pen recorder.

A low oscillation frequency (0·8 Hz) was chosen since previous experiments (Regan & Beverley, 1973b) had shown that at higher oscillation frequencies thresholds for sideways motion were confounded with thresholds for motion in depth.

The main finding of asymmetrical adaptation to depth (Fig. 2) was confirmed on four subjects. The visual acuity of subjects K.I.B. and S.H. was 6/6 without correction and for D.R. and J.J. was corrected to 6/6.
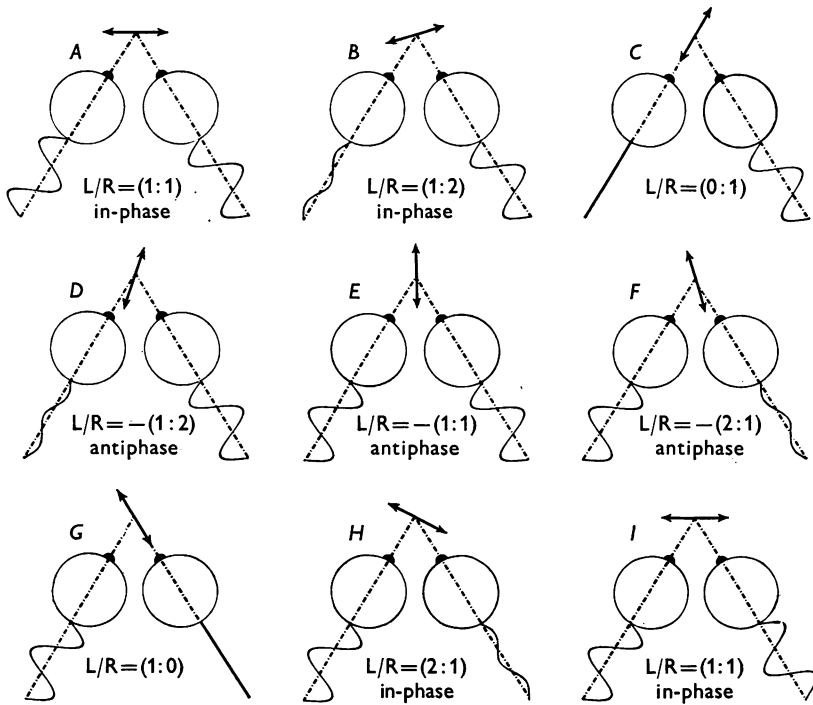

Fig. 1. Schematic diagram illustrating the motion of the images on the left and right retinae of a binocularly fixated stimulus which oscillates sinu-soidally in various directions in three-dimensional space.

RESULTS

Left:right ratio and the direction of motion in space

Fig. 1 illustrates how the effect of changing the direction along which a target moved in space could be mimicked by oscillating through varying distances the positions of the left and right retinal images.

In Fig. 1*A* to 1*I*, the directions along which a real target oscillates are represented by the heavy arrowed lines immediately in front of the eyes. In *A* the target oscillates from side to side and does not move in depth. Consequently the retinal image positions oscillate *inphase* with equal amplitudes. In *B* the target oscillates along a line directed to the left of the left eye. The left retinal image now oscillates through a smaller distance than the right, but both still oscillate inphase. In *C* the target oscillates along a line directed towards the left eye, so that the left eye's retinal image is stationary and all retinal image movement is confined to the right eye.

When the target's direction of motion is directed to any point between the eyes, the two retinal image positions oscillate in *antiphase*. In *D* the target's line of movement cuts a point between the left eye and the point midway between the eyes. The two retinal image positions therefore oscillate in antiphase, and the left image moves through a smaller distance than the right. When the target's line of motion passes midway between the eyes (*E*) the left and right retinal images have exactly the same amplitudes of oscillation. Fig. 1*F–I* show how the sequence *D*, *C*, *B* and *A* is parallelled as the target's line of motion tilts still more to the right until at *I* it is once more entirely sideways.

An important point not brought out in Fig. 1 is that the very large change in the left:right ratio going from *C* to *G* may signal only a very small change in the direction of the target's motion. In our experiments, the viewing distance was 63 cm so that the change in left:right ratios from *C* to *G* would represent a directional change of only 6°. At longer viewing distances, the same change in left:right ratio would represent a correspondingly smaller angular change. Thus, left:right ratio is a very sensitive indication of the direction of target movement for those directions within a few degrees of the line which cuts half way between the eyes.

In our experiments we did not stimulate the eyes by moving a target in depth as illustrated in Fig. 1. Instead we presented separate patterns to the left and right eyes and moved these patterns from side to side so that the resulting retinal image movements were similar to those shown in Fig. 1. Nevertheless, the significance of left:right ratio in our experiments can be visualized along the lines illustrated in Fig. 1.

The continuous lines in Fig. 2*A* and *B* provide an unadapted base line for comparison with the chain lines that represent depth thresholds measured after 10 min adaptation to motion in depth.

The impressions produced by gazing at a stimulus target were as follows. At first the target's oscillations in depth were large, but grew progressively smaller until after several minutes no movement in depth

was visible at all. At this stage the target's side-to-side movements appeared little smaller than at the start of adaptation. Although several minutes' adaptation were necessary to completely abolish the perception
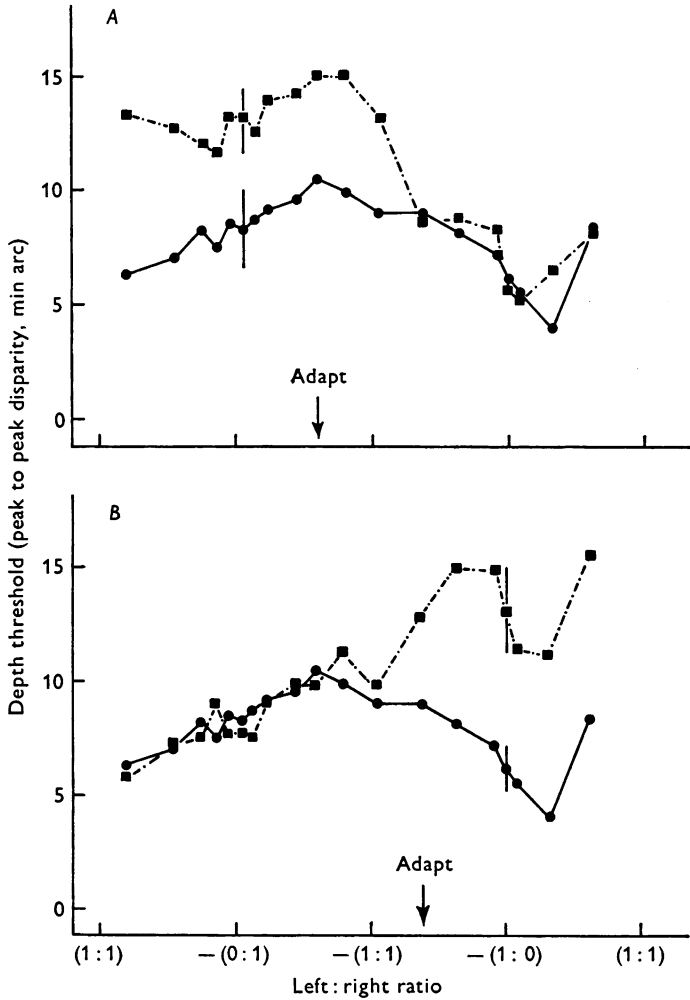

Fig. 2. Adaptation to a particular direction of movement in depth. Ordinates are psychophysical thresholds (peak-to-peak disparity in mins arc) for movement in depth. Abscissae are left:right ratios of test stimuli, i.e. the apparent direction of motion of the stimuli (see text). The continuous lines are the pre-adaptation 'base line'. The chain lines in A and B show thresholds measured after adaptation to moving stimuli with left:right ratios of $-(1:2)$ and $-(2:1)$ respectively, i.e. stimuli moving along lines directed respectively just to the right of the left eye and just to the left of the right eye. Ordinates are linear, abscissae are tangential. The bars are ± 1 s.d. (twelve settings 'base line', six settings adapted curves).
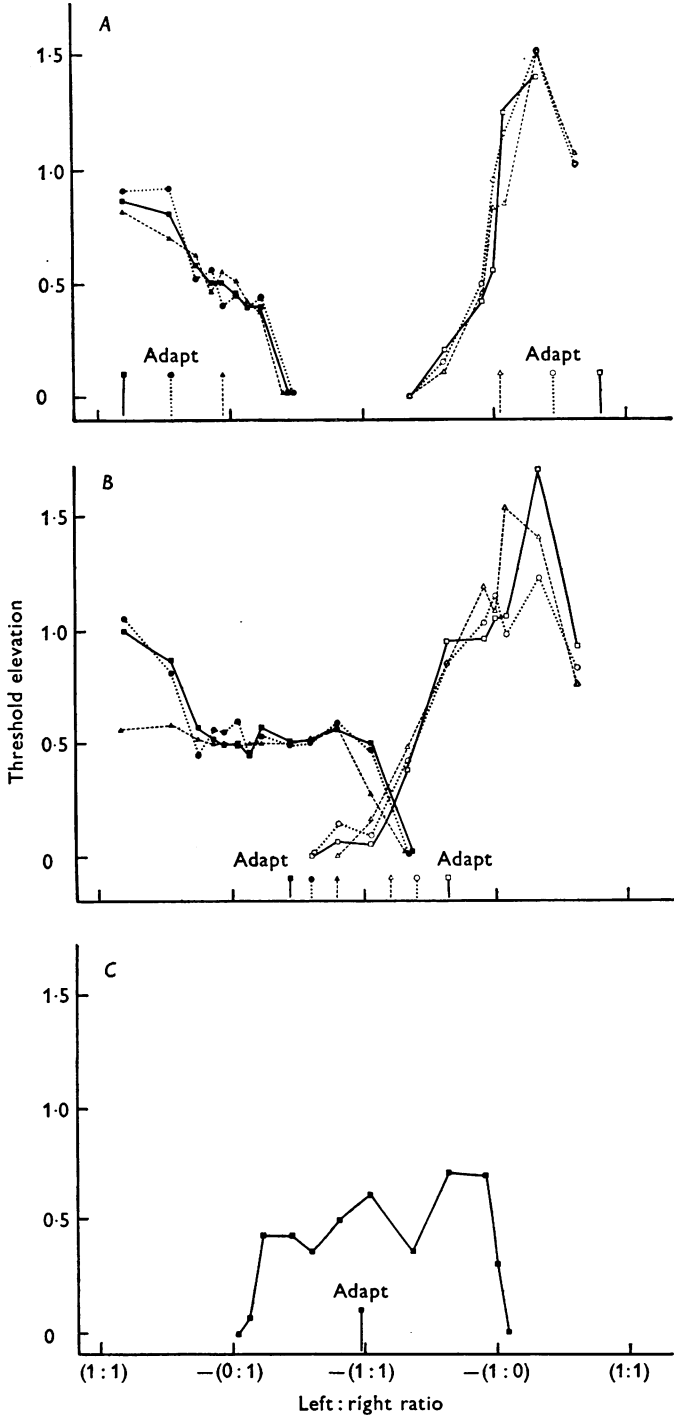
Fig. 3. For legend see facing page.

of movement in depth, a marked loss of sensitivity took place within the first few seconds of adaptation, especially for near-threshold adapting stimuli.

A subjectively striking observation was that if, after abolishing the perception of movement in depth by sufficient adaptation, the left:right ratio of the adapting stimulus were changed, then large excursions in depth became immediately visible. This finding is discussed quantitatively in the following section.

Directionally selective adaptation to motion in depth

Unadapted depth thresholds were measured as a function of left:right ratio (continuous lines, Fig. 2A and B). Threshold was highest near a left:right ratio of −(1:1). that is near the setting for which the binocularly fused target appeared to move along a line which cut midway between the eyes. The chain line in Fig. 2A is a plot of threshold versus the left:right ratio of a test target after gazing for 10 min at an adapting target which moved in depth with a left:right ratio of −(1:2). Threshold was elevated for left:right ratios plotted on the left side of the graph, but was unaffected for left:right ratios plotted on the right side. Fig. 2B shows that this asymmetry reversed after adaptation to a left:right ratio −(2:1). Threshold was now elevated for left:right ratios plotted on the right side of the graph, but was unaffected for left:right ratios plotted on the left side. In no case was threshold *reduced* for any test left:right ratio.

By referring to Fig. 1 these findings can be understood as follows. Adaptation to movement directed to the *left* of a point midway between the eyes depressed visual sensitivity for test targets which moved to the *left* of this midway point but did not depress visual sensitivity for test targets which moved more than 1–2° to the *right* of this midpoint. Adaptation to movement directed to the right of the midpoint produced a reversed effect on visual sensitivity.

Fig. 3. Fractional elevations of threshold for movement in depth caused by adapting to thirteen different left:right ratios (i.e. thirteen different directions of movement, see text). A, continuous line at left, left:right ratio (1:1·3), continuous line at right, left:right ratio (1·3:1), dotted line at left, left:right ratio (1:2·8), dotted line at right, left:right ratio (2·8:1), dashed line at left, left:right ratio (1:29), dashed line at right, left:right ratio (29:1); B, continuous line at left, left:right ratio −(1:4·3), continuous line at right, left: right ratio −(4·3:1), dotted line at left, left:right ratio −(1:2), dotted line at right, left:right ratio −(2:1), dashed line at left, left:right ratio −(1:1·3), dashed line at right, left:right ratio −(1·3:1); C, continuous line, left:right ratio (−1:1·05). The − sign indicates that the left and right eye's stimuli are in antiphase. Ordinates are linear, abscissa are tangential.

The threshold elevations shown in Fig. 2 are no more than 250%. Larger elevations, which could reach 600%, were observed when the method of ascending and descending limits was used to measure thresholds within 5 sec after removing the adapting stimulus.

Threshold elevation curves of the type shown in Fig. 2 were measured for thirteen different values of adapting left:right ratio. Fig. 3 shows these thirteen curves. Threshold elevations are plotted versus the left:right ratios of the test stimuli (ordinates in Fig. 3 are ([unadapted threshold/adapted threshold] − 1)). Only five types of threshold elevation curve were produced by the thirteen different left:right adapting ratios.
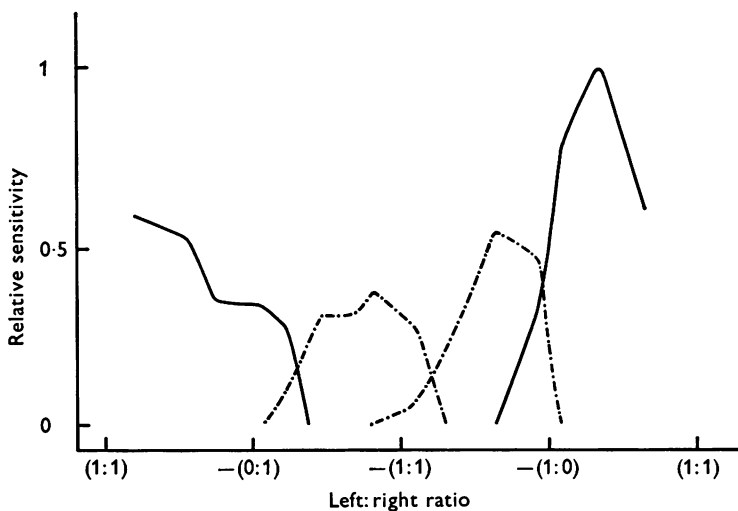

Fig. 4. Sensitivity curves of four hypothetical processes that underlie the thirteen experimentally determined curves of Fig. 3.

It is clear to informal visual inspection how the thirteen threshold elevation curves (Fig. 3) can be summarized in terms of only four sensitivity curves as illustrated in Fig. 4.

Time course of recovery from adaptation to movement in depth

Fig. 5 shows the time course of recovery after visual sensitivity had been degraded by adaptation to movement in depth. Sensitivity rose rapidly at first and almost reached the pre-adaptation level after 20–60 sec. However, sensitivity was not recovered completely until 100–300 min had elapsed. The early time course of recovery was similar to the time course of recovery of contrast sensitivity after adaptation to a high-contrast grating pattern (Blakemore & Campbell, 1969).
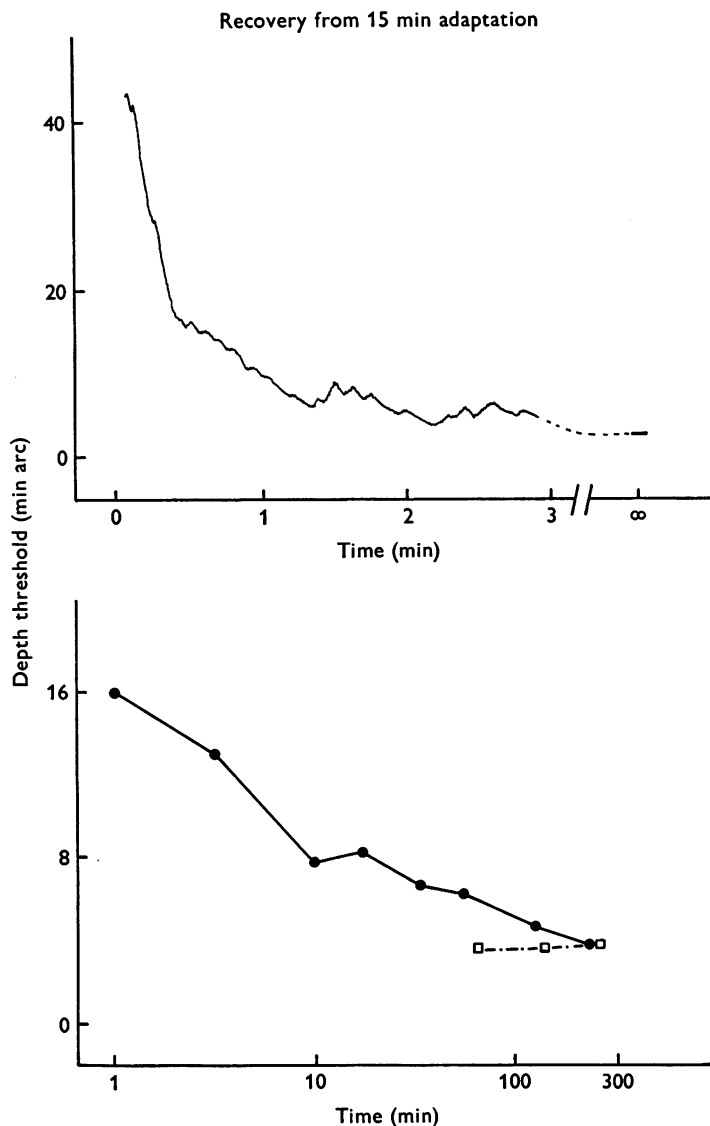
Recovery from 15 min adaptation

Fig. 5. Time course of recovery of visual sensitivity to movement in depth after 15 min adaptation to a stimulus moving in depth. *A*, recording of depth threshold versus time in mins after end of adaptation. Both axes are in linear co-ordinates. *B*, long-term recovery of stereoscopic depth sensitivity. Each point is the mean threshold set during a 30 sec test period. Continuous line, test left:right ratio identical to adapting left:right ratio. Chain line, test left:right ratio is the inverse of the adapting left: right ratio. Ordinates are linear, abscissa are logarithmic.

DISCUSSION

Adaptation to the direction of movement in three-dimensional space

Only five different curves are needed to describe the elevations of threshold for depth movement produced by thirteen different adapting left:right ratios. These five curves can be summarized in terms of the four hypothetical sensitivity functions shown in Fig. 4. This suggests that four neural mechanisms underlie visual sensitivity to depth movement, and that these mechanisms are 'tuned' in terms of left:right ratio. Since left:right ratio provides a cue to the direction of a target's motion in space, these hypothetical mechanisms might act as detectors of the direction of motion in three-dimensional space.

In the present study oscillation amplitude was proportional to maximum velocity since retinal image position was varied sinusoidally. Consequently the left:right ratio confounds the ratio of maximum *displacements* of the left and right retinal images with the ratio of maximum image *velocities*. It is, therefore, not yet clear whether the sensitivity curves shown in Fig. 4 are 'tuned' on the basis of the relative displacements of the retinal images or on the basis of the relative velocities of the retinal images.

Our results suggest that, when processing movement information, the brain does not give equal weight to all left:right ratios. The band of left:right ratios between $-(0:1)$ and $-(1:0)$ seem to be at least as important as the whole remaining range of left:right ratios (Figs. 2–4). For the 63 cm viewing distance used in the present experiments, the two central sensitivity functions of Fig. 4 were tuned to directions of movement that were respectively some 0·5 and 1·5° to the left and right of a line that bisected the eyes. The half-response widths of these tunings were roughly 1°; sensitivity was inappreciable when the direction of motion departed by more than about 1·5° from the preferred direction. Thus, the two central sensitivity functions are concerned with directions of motion close to a line that cuts midway between the eyes. Presumably at longer viewing distances the tuning, expressed in angular terms, would be even finer. The two outermost sensitivity functions of Fig. 4 are also concerned with only a restricted range of left:right ratios, though their tuning expressed in terms of angular direction is much less sharp than for the two central sensitivity functions.

One reason for the multiple sensitivity functions shown in Fig. 4 might be to provide a basis for sensitively discriminating different left:right ratios that lie at or near the crossover points of the four sensitivity functions. These crossover points are near (though not exactly coincident with) left:right ratios of $-(0:1)$ $-(1:1)$ and $-(1:0)$. As mentioned above,

these ratios correspond to directions of motion that pass through the left eye, a point midway between the eyes and through the right eye respectively. Thus the presence of four sensitivity functions might go some way to explaining the everyday, but exquisite, ability to judge the direction of movement in space of any object which looks likely to hit one's body.

The site of adaptation to movement in depth

There are three arguments to support the notion that the site of adaptation to depth movement is at or after binocular convergence. First, adaptation to a target's movement in depth is much greater than to its simultaneous sideways movement. Secondly, no test or adapting stimulus used in the present experiments had any directional bias. Since all were sinusoidal oscillations there was an exact balance between the left-to-right and right-to-left movements of each retinal image. Thirdly, monocularly indistinguishable adapting stimuli gave quite different threshold elevation curves. For example, the continuous line and the chain line to the left of Fig. 4 describe the effects of adapting left:right ratios of $+(1:2)$ and $-(1:2)$ respectively. The adapting effects of these two stimuli are clearly different, though monocularly the stimuli are identical. They differ only in the relative timing (phase) of the oscillations viewed by the left and right eyes.

Neurophysiological basis for adaptation to the direction of motion in space

One possible neurophysiological basis for the four hypothetical sensitivity functions of Fig. 4 is as follows:

There are two groups of monocular detectors of retinal image position. One group (*a*) is preferentially sensitive when the retinal image moves from right to left, while the other group (*b*) is most sensitive when the retinal image moves from left to right. Such directional selectivity has been reported as a property of single neurones in the visual pathways of animals (Barlow & Hill, 1963; Hubel & Wiesel, 1959, 1962; Pettigrew *et al.* 1968). Either left or right monocular input to a given disparity detector can be group *a* or group *b* but not both *a* and *b*. Thus, there are four possible groups of disparity detectors. Further psychophysical evidence for this subdivision is the finding that adaptation to movement in depth is selective to the phase difference between the targets viewed by the two eyes (Regan & Beverley, 1973*c*).

Each of these four groups of disparity detector is further subdivided into two. One half is selectively sensitive to motion directed to the left of centre, and the other half is selectively sensitive to motion directed to the right of centre (i.e. selectively sensitive to left-right ratios whose numerical magnitudes are respectively less or greater than unity, so that

on the abscissae of Figs. 2–4 they would be plotted respectively to the left-hand side or to the right-hand side of $-(1:1)$). In brief, four groups of disparity detectors are 'tuned' to four different directions of motion towards the head, and four further groups of disparity detector are 'tuned' to the same four directions of motion away from the head.

Adaptation to the movements of real objects in three-dimensional space

We report here that adaptation to apparent movement in depth is a striking phenomenon. A temporary but complete loss of the ability to see movements in depth over quite a large range of direction can result from gazing for a few minutes at a moving target. Given the large size of the effect it might be asked why sudden and drastic failures of the ability to judge the directions that objects move in depth are not everyday experiences.

Three possible explanations are: first, that the effect may be less striking when retinal disparity is not the only cue to depth. In everyday life the brain may be able to take advantage of size changes and the effects of head movements. A second possibility is that suitable adapting stimuli have been rarely encountered outside the laboratory until recent times when the visual experiences which accompany prolonged motorway, or freeway driving became everyday experiences.

The third possible explanation is that the experimental results reported in this article were obtained when visual cues to depth were restricted to disparity changes. Although the majority of present-day workers on depth perception have adopted this approach, there may be pitfalls in the path of these who ignore the role of all other cues to depth when attempting, as we have done, to extrapolate their findings to the perception of real objects in motion. Although Wheatstone (1838, 1852) convincingly demonstrated to the Royal Society that disparity cues alone were adequate for depth perception, one-eyed games players have since given informal but equally convincing demonstrations to their two-eyed adversaries that monocular as well as binocular cues to depth can provide a basis for judging precisely the direction in which an object moves in space.

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