# THE DISSOCIATION OF SIDEWAYS MOVEMENTS FROM MOVEMENTS IN DEPTH: PSYCHOPHYSICS

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# SUMMARY

THIS ARTICLE describes a method for separately measuring thresholds for sideways motion and for motion in depth. This method is to make the two threshold percepts distinguishable by causing the timecourse of sideways motion to differ from the timecourse of motion in depth. For example, when the left and right eye's stimuli oscillate sinusoidally from sideto-side at  $F_L$  Hz and  $F_R$  Hz, depth oscillations appear to wax and wane at a frequency  $\Delta F = (F_L - F_R)$  Hz where  $\Delta F$  is independent of either  $F_L$  or  $F_R$ .

The perception of depth oscillations can be classified into three frequency regions. These are: (a) when the frequencies of sideways oscillations are less than 5 Hz in *both* eyes, depth oscillations can be seen; (b) when the frequency of sideways oscillation lies between 5 and 10 Hz in *either* eye, depth oscillations cannot be seen; (c) when the frequency of sideways oscillation exceeds 10 Hz in one eye and is less than 3 Hz in the other eye, depth oscillations can be seen.

Sensitivity to oscillations in depth falls off when depth oscillates faster than 1 Hz at most, and fails completely at 2-5 Hz.

Sideways oscillations can be seen at much higher frequencies than oscillations in depth, and up to at least 20–25 Hz.

One's ability to see oscillations in depth is reduced to an unexpectedly large degree when  $\Delta F$  is increased. This can be explained if there are several classes of "disparity detector" such that a given monocular input to a given "disparity detector" is elicited by only one direction of retinal image movement.

# INTRODUCTION

A number of recent studies on animals have described single cortical neurons which only give an appreciable response when the visual stimuli fulfil certain precisely-defined conditions. Among these conditions are that the left and right eyes view similar targets which must be moving contrast borders (edges), and that there must be some fixed disparity between the images of the target on the left and right retinae (BARLOW, BLAKEMORE and PETTIGREW, 1967; NIKARA, BISHOP and PETTIGREW, 1968; PETTIGREW, NIKARA and BISHOP, 1968). The optimal value of retinal disparity is different for different neurons.

If neurons with similar properties exist in the human brain, then they may play a role in binocular depth perception. There has, therefore, been interest in correlating the neurophysiological data with subjective observations in man. However, all single-neuron studies of disparity-specific neurons have, of necessity, used moving stimuli, whereas in most human psychophysical studies stationary stimuli have been used. There are few psychophysical studies of the dynamics of depth perception whose aim has been to describe the role of stimulus motion in binocular depth perception.

In the few studies where moving targets were used, and the dynamics of depth perception investigated, the measurement of stereoscopic depth thresholds presented a problem since the subject may use either stereoscopic cues or may detect sideways movement of the target. The problem can be avoided by restricting measurements to suprathreshold depth judgements (RICHARDS, 1972; REGAN and BEVERLEY, 1973). This article describes a way of tackling the problem of distinguishing between thresholds for movements in depth and for sideways movements. The method is to dissociate motion in depth from sideways motion. In this way depth changes can be distinguished from sideways movements.

#### METHODS

Figure 1 shows our stimulator. The subject viewed three separate patterns of random dots which he fused binocularly so that they appeared to be a single pattern. A pattern of black dots on a brightly-illuminated  $5^{\circ}$  square (Q1) was presented to both eyes. At the centre of the square was a 2° circular area devoid of dots. Both the left and right eyes saw, superimposed on the blank 2° central area, a circular target area of random dots slightly larger than 2° which always filled the central hole. However the central target seen by the left eye (Q3) was not the same as the central target seen by the right eye (Q4), although the dot patterns on the two targets were identical.



FIG. 1. Apparatus. X1, X2, X3, X4—light sources; Q1, Q2, Q3, Q4—stimulus patterns; P—polarizer; BS—beamsplitters; M1, M2—vibrators.

The diameter of the black stimulus dots was roughly 2' and they occupied roughly 10 per cent of the total stimulus area. The mean stimulus luminance was  $1.5 \log \text{ ft L} (110 \text{ cd/m}^2)$ . The distance between the stimulus planes and the subject's eye was 80 cm. Two subjects were used, DR, aged 37 yr, whose vision was corrected to 6/6 and KB, aged 24 yr, whose uncorrected vision was 6/6. Threshold settings were made by the method of adjustment. The binocular vision of both subjects was tested at the Moorfields Eye Hospital. Both subjects had appreciable stereopsis. KB had 2D exophoria at 6 m and 12 D at 1/3 m with rapid recovery and was able to converge 25 D for 1/2 m target before suppression. DR had 1° divergence R/L 1 D with good recovery at 1/3 m, no deviation at 6 m and was able to converge 18 D at 1/2 m before losing fusion, and 20 D with SV slides.

Targets Q3 and Q4 could be moved from side-to-side independently of each other by means of vibrators

M1 and M2. By critically adjusting the positions of Q3 and Q4 their mean position could be set at zero retinal disparity. This was the setting used throughout these experiments.

Also superimposed on the blank  $2^{\circ}$  central area of Q1 were a pair of nonius lines (Q2). These enabled both fixation errors and tracking to be detected with a sensitivity of roughly 0.5'.

The subjective appearance of the binocularly-fused, oscillating target can be understood as follows. Figure 2(a) (upper) illustrates how a target whose sinusoidal movement is purely sideways gives retinal images which move *in phase*. Figure 2(a) (lower) illustrates how a target whose sinusoidal movement is purely in depth gives retinal images which move *in antiphase* (180° out of phase). Figure 2(b) illustrates the target movements when the stimulus oscillated at different frequencies in the left and right eyes.

With the right eye occluded, the left eye saw target Q3 oscillate from side-to-side F times/sec as shown in Fig. 2(b). With the left eye occluded, the right eye saw target Q4 oscillate from side-to-side  $(F + \Delta F)$  times/sec [Fig. 2(b)]. When Q3 and Q4 were binocularly-fused a single target appeared to move in depth as illustrated in Fig. 2(b).<sup>1</sup> At instants when the movements of Q3 and Q4 differed in phase by 0° or 360°, the fused target appeared to move from side-to-side. As the phase difference gradually increased, the target's path became first an ellipse, then a circle, then an ellipse elongated in depth until at 180° phase the target moved along a line bisecting the subject's eyes. The target's path then became once more elliptical, circular, elliptical and finally side-to-side. This whole sequence took  $1/\Delta F$  sec and was continuously repeated. For clarity the target's path has so far been described as elliptical, circular or linear, but of course since its trajectory was changing continuously one shape continuously merged into the next.

Neither the motion of the left image nor the motion of the right image is related to  $\Delta F$ , so that the effects of changes in retinal disparity can be distinguished from the effects of changes in image position. Furthermore, the MTFs for the two stimulus parameters can be independently measured, since F and  $\Delta F$  can be independently varied.

We should emphasize that no matter how complicated the timecourse pursued by retinal disparity, both the left and right eyes viewed unvarying sinewave oscillations.



FIG. 2(a) (upper). illustrates how a target which oscillates from side-to-side gives retinal images whose positions oscillate from side-to-side *in phase*, while (lower) a target which oscillates purely in depth gives retinal images whose positions oscillate from side-to-side in *antiphase*. F—fovea;  $X_L$ ,  $X_R$ —distances from fovea to retinal image of target on left and right retinae respectively.

<sup>&</sup>lt;sup>1</sup> The case illustrated is for  $\Delta F \leq F/3$  and  $F \leq 3$  Hz.



FIG. 2(b). Upper half. Sideways displacements of the stimulus patterns (targets) Q3 and Q4.  $X_L$ ,  $X_R$ —positions of target images on left and right retinae respectively. Abscissae are time. Left eye's target oscillates at F Hz, right eye's at  $(F + \Delta F)$  Hz. Lower half. Illustration of illusiory motion in depth of the binocularly-fused target. Illusiory motion illustrated for various phase differences between oscillatory displacements of left and right eyes' targets. Plots are of retinal disparity (ordinates) vs retinal image position (abscissae).

Another way of describing the stimulus is to regard targets Q3 and Q4 to be driven at a single frequency, but that in addition the phase difference between them is continuously and progressively changing. This is in fact how we physically generated the signals F and  $(F + \Delta F)$  shown in Fig. 2. A shaft rotated a device at frequency F. This device generated a signal  $V_L = A\sin 2\pi Ft$ . Gearwheels drove a second shaft at frequency F via a stationary differential gear. The second shaft rotated a second device which generated a second signal  $V_R = A\sin (2\pi Ft + \theta)$ . The phase difference  $(\theta)$  between the two signals was determined by the angle of the differential gear. The result of rotating the differential gear clockwise was to continuously increase the value of  $\theta$ . If the differential rotated  $(\Delta F/2)$  times/sec, the first device rotated through 360 F)°/sec while the second device generated a signal  $V_L = A\sin (2\pi Ft + \theta)$ . In the present device generated a signal  $V_L = A\sin (2\pi Ft)$  while the second device rotated through a 360 F)°/sec while the second device rotated through  $(360 F + 360 \Delta F)^\circ$ /sec. This is equivalent to saying that the first device generated a signal  $V_L = A\sin (2\pi Ft)$  while the instantaneous of  $V_L$  and  $V_R$  represent the instantaneous retinal image positions of Q3 and Q4 respectively, while the instantaneous phase difference  $\theta$  [Fig. 2(b)] is proportional to their instantaneous retinal disparity.

#### RESULTS

Both subjects reported that sensitivity to depth oscillations was degraded very rapidly when the target was steadily fixated. This adaptation phenomenon is described more fully elsewhere (BEVERLEY and REGAN, 1973a, 1973b). In the present experiments its disturbing effects were minimized by fixating the target for brief periods of only 10-20 sec.

## Depth thresholds: three frequency regions

In the experiments illustrated by Fig. 3 the subject's left eye viewed a target which oscillated from side-to-side at frequency F Hz, while the right eye's target oscillated at  $(F + \Delta F)$ Hz. Peak-to-peak excursions of retinal disparity were plotted vs  $\Delta F$  in situations where



FIG. 3. Visual sensitivity to oscillations in depth for sinusoidal oscillations of stimulus targets. Upper part of each graph is a plot of threshold for depth movement (min) vs the difference frequency  $\Delta F$  Hz (where  $\Delta F$  is difference between frequencies of sideways oscillation of left and right eyes' stimulus targets). Each filled square is the mean of 10 settings; each of the four unfilled squares is the mean of less than 10 settings. Vertical bars represent  $\pm 1$  S.D. Vertical dashed lines indicate the boundaries between frequency regions W1, W2 and W3 (see text). Lower part of each graph shows the percentage of trials in which depth movements could not be seen for any amplitude of disparity oscillation. Frequency of sideways oscillation of left eye's target: 0.2 Hz (a), 0.8 Hz (b), 1.4 Hz (c), 2.2 Hz (d) and 3.0 Hz (e). Subject KB.

the subject could just see depth oscillations. The value of F was 0.2 Hz in Fig. 3(a), 0.8 Hz in Fig. 3(b), 1.4 Hz in Fig. 3(c), 2.2 Hz in Fig. 3(d) and 3.0 Hz in 3(e). Each point was the mean of 10 settings. The bars represent  $\pm 1$  S.D.

The heavy vertical black bars in Fig. 3 indicate the percentage of trials on which the subject was unable to see depth for any value of disparity. The ordinates marked 0–100 show these percentages, while stimulus frequency is plotted on the abscissa.

The psychophysical curves of Fig. 3 fall into three frequency regions.

Low frequencies. When the difference frequency  $\Delta F$  was low, the overall result of increasing F was that depth threshold progressively increased. For suprathreshold stimulation, the binocularly-fused target appeared to move in depth along a roughly elliptical path. Oscillations in depth decreased in amplitude when either F or  $\Delta F$  was increased. In this low-frequency region, the subject saw depth in practically 100 per cent of trials.

Medium frequencies. The medium frequency region can be recognized both by the profusion of black bars and by gaps in the curves (Fig. 3). These gaps signify a breakdown of depth perception. In this region depth oscillations could not be seen at all, no matter how large the changes in retinal disparity. The medium-frequency region fell within the range 1-10 Hz for  $\Delta F$ , depending on the value of F.

High frequencies. When the difference frequency  $\Delta F$  was high, oscillations in depth could be seen in practically 100 per cent of trials. The monocularly-viewed F Hz target appeared to oscillate from side-to-side, but the monocularlyviewed  $(F + \Delta F)$  Hz target appeared stationary though blurred.<sup>2</sup> The binocularly-fused target appeared to oscillate slowly in depth at frequency F. It moved along a straight line directed towards the eye which was stimulated at the high frequency  $(F + \Delta F)$  Hz. Subjective sensitivity to depth was high, and was independent of  $\Delta F$ , though strongly dependent on F.

However, depth changes could not be seen at all when the amplitude of sideways oscillations was too high. This breakdown of depth perception coincided with the point at which the appearance of the monocularlyviewed  $(F + \Delta F)$  stimulus changed from "stationary but blurred" to "oscillating sideways".



FIG. 4. Visual sensitivity for sideways movement. Thresholds (min arc) are plotted as ordinates vs the frequency of sinewave displacement of target (abscissae). Continuous line—monocular viewing with right eye occluded; chain line—binocular viewing. (a)—subject KB; (b)—subject DR.

# Sinewave oscillations of target position: sideways movement thresholds

Thresholds for purely sideways motion are plotted vs target oscillation frequency in Fig. 4. Binocular and monocular curves are shown for both subjects. For subject DR, binocular thresholds were roughly half monocular thresholds when stimulus frequency was below 0.6 Hz, but at higher frequencies thresholds differed only slightly if at all. At frequencies below 0.3 Hz, subject KB was roughly 1.5 times more sensitive when viewing binocularly, and his thresholds differed by no more than 1.2:1 when stimulus frequency was raised above 0.3 Hz.

<sup>&</sup>lt;sup>2</sup> JULESZ (1961, 1965) has reported that depth sensations can be elicited by pairing a stationary sharp pattern with a stationary pattern that has been optically blurred.

Movement sensitivity progressively fell off both at low frequencies and at high frequencies at roughly 6 dB/octave. For subject KB, the lower and upper corner frequencies were 1.8 Hz and 6 Hz respectively; for subject DR they were 0.8 Hz and 3.5 Hz (monocular viewing).

# Relative sensitivities to sideways movements and movements in depth

Subject DR could not see depth changes when the rate of depth oscillations exceeded 5 Hz, while subject KB's depth perception failed at 2 Hz. In contrast, side-to-side oscillations could be seen up to frequencies almost 10 times higher, at least 20 Hz for DR and up to at least 25 Hz for subject KB (Fig. 4).

Although depth perception was restricted to very much lower frequencies than the perception of side-to-side movements, all subjects were not necessarily less sensitive to movement in depth than side-to-side movements. This can be seen by comparing Figs. 3 and 4 for subject KB which show that as oscillation frequency was progressively reduced below 0.2 Hz, his sensitivity to oscillations in depth did not fall off as rapidly as his sensitivity to side-to-side oscillations.

In separate experiments his left and right eyes viewed targets oscillating at 0.15 Hz and 0.2 Hz respectively. The fused binocular image appeared to oscillate in depth at 0.05 Hz even when the amplitude of oscillation was so small that side-to-side movements could not be seen by monocular viewing with either eye. At a frequency of 0.05 Hz, threshold was roughly four times lower for movements in depth than for binocularly-viewed side-to-side oscillations, and roughly three times lower than for monocularly-viewed side-to-side oscillations.

However, in almost all other situations, sensitivity to depth oscillations was lower than sensitivity to sideways oscillations.

### DISCUSSION

In everyday life there are a number of visual cues which may give rise to the impression that objects extend in depth. These visual cues include the blueness and haziness of distant objects, size increases as objects grow nearer, parallax changes caused by head movements, accommodation and convergence information and differences in retinal disparity. Retinal disparity is a geometrical difference between the left and right retinal images caused by the difference between the viewing positions of the left and right eyes. By taking advantage of the fact that retinal disparity cues can, by themselves, produce an impression of stereoscopic depth (WHEATSTONE, 1838, 1852; JULESZ, 1960) it is possible to simplify investigations of depth perception by removing all cues to depth except for disparity cues. We have adopted this procedure in the present study.

Some problems of depth perception do seem more tractable when the number of stimulus parameters is so drastically reduced. On the other hand, it might be unwise to ignore the role of other cues to depth perception, exemplified perhaps by the outstanding oculo-motor coordination of some one-eyed sportsmen who can locate an object moving in depth with greater certainty, speed and precision than the great majority of their two-eyed adversaries.

## The distinction between depth thresholds and movement thresholds

The method presented in this article enables a distinction to be made between the psychophysical threshold for movement in depth and the psychophysical threshold for side-to-side movement. Figure 2 illustrates how movements of the retinal images of an object *necessarily*  occur not only when the object moves from side-to-side, but also when it moves purely in depth. Figure 2 also illustrates how pure sideways movements of a target differ from movements in depth by the fact that the retinal disparity of the target does not change during purely sideways movements but does change when the target moves in depth.

When depth and sideways movements have the same frequency we have found it very difficult to decide whether one is seeing small changes in retinal image position or small changes in retinal disparity. Thus, in threshold studies of the dynamics of binocular depth perception it is difficult to ensure that it is depth thresholds and not movement thresholds that are measured. Our method of distinguishing between the contributions to threshold perception of (1) changes in retinal disparity and (2) changes in retinal image position is to impress a qualitative difference upon the two threshold percepts. We have done this by dissociating the timecourse with which retinal disparity changes from the timecourse with which retinal image position changes.



FIG. 5. (a) and (b) show how the left and right eye's stimulus targets moved with time. Motion is sinusoidal.  $X_L$ ,  $X_R$ —positions of retinal images in left and right eyes; *t*—time; Oscillation frequency for left eye's stimulus was *F* Hz, and for right eye's stimulus (*F* +  $\Delta F$ ) Hz. (c), (d) and (e) show three ways in which retinal disparity ( $X_L - X_R$ ) can change as a function of time. In (c),  $\Delta F < F/3$ ; in (d).  $\Delta F < 3F$  or  $\Delta F > F/3$ ; in (e),  $\Delta F > 3F$ .

# Depth thresholds

One general conclusion from the data of Fig. 3 is that F oscillations of retinal disparity/ sec will produce no sensation that depth changes F times/sec unless F is less than 3-4 Hz. The exact frequency is different for different subjects, but if F exceeds this value depth perception will fail no matter how large the change in disparity. Sensitivity to depth changes will start to fall off when F exceeds, at the most, 1 Hz.

All the depth MTF's of Fig. 3 can be described in terms of three frequency regions.

The most obvious explanation for the existence of these three frequency regions would be that retinal disparity changes with time in one of three different ways. This is in fact the case [see Figs. 5(c, d and e)] though there are no abrupt transitions from one waveform to the next. However, this explanation would seem to be ruled out by our finding that the changeovers between the three stimulus waveforms W1, W2 and W3 *do not coincide* with the boundaries between the three regions of the psychophysical curves of Fig. 3 (compare the positions of the horizontal dotted lines in the graphs of Fig. 3 with the start and end of the groups of vertical black bars which signify the medium frequency region). This suggests that our finding of three frequency regions for psychophysical data is a property of the visual pathway rather than being trivially due to differences in the stimulus disparity waveform.<sup>3</sup>

One explanation for the high and medium frequency regions might be cast in terms of temporal integration which results in monocular "motion fusion". The site of this integration (fusion) would be sufficiently peripheral to be common to both motion and depth channels since we find that sideways motion of the rapidly-moving stimulus becomes evident at similar amplitudes of oscillation for which depth perception breaks down. For small oscillation amplitudes, fusion occurs at a frequency as low as 5 Hz, though for large oscillation amplitudes fusion may not occur below 10 Hz.

# Confusion of depth and sideways movement

Our findings explain why depth and sideways movement cues may be confounded in threshold studies. In some studies the illusion of movement in depth has been generated by stimulating the left and right eyes with identical targets which oscillated from side-to-side in antiphase at the same frequency, F Hz. When viewed in binocular fusion the subject saw a single target which oscillated in depth F times/sec (RICHARDS, 1972; TYLER, 1972; REGAN and BEVERLEY, 1973; REGAN and SPEKREUSE, 1970). Our present findings (Figs. 3 and 4) confirm our previous suggestion (REGAN and BEVERLEY, 1973) that thresholds measured with such a stimulus may really be movement thresholds rather than depth thresholds, particularly when the oscillation frequency exceeds some 1.5 Hz. Even for frequencies below 1.5 Hz, a further problem may be caused by errors in fixation, since depth thresholds may be lower than movement thresholds only over a narrow range of fixation disparities close to the fronto-parallel plane. For example, a fixation error of no more than  $\pm 10'$  may be sufficient to degrade depth sensitivity below movement sensitivity (REGAN and BEVERLEY, 1973).

# Model: threshold perception of sideways movements and movements in depth

In the main, the model shown in Fig. 6 can account for our findings. In Fig. 6 stage A signals retinal image position. The reduction in movement sensitivity at high frequencies is caused by temporal integration (time constant  $\tau_A$ ) at the positional (contrast) detectors of stage A. The value of  $\tau_A$  can be estimated at roughly 22 msec (KB) or 34 msec (DR) from the motion MTFs (Fig. 4). Some stage A elements are supposed to have a preferred response to retinal image movements directed from left to right; other stage A elements respond to movements in the opposite direction.

In Fig. 6 the position of a particular contour on the left retina is marked as  $x_L$  and on the right retina as  $x_R$ . Information of  $x_L$  and  $x_R$  is carried to stage B, where the retinal disparity (d) is computed. Many separate elements make up stage B, each of which responds only over a restricted range of retinal disparities.

<sup>&</sup>lt;sup>3</sup> The criteria  $3F < \Delta F$  and  $2 \Delta F < F$  adopted in Figs. 3 (c, d and e) are, within limits, arbitrary but not sufficiently so as to affect our discussion. The vertical dotted lines in Fig. 3 indicate  $3F = \Delta F$  and  $3\Delta F = F$ .

Figure 7 shows that the effect of increasing the frequency difference  $\Delta F$  between the left and right eyes' stimuli was to produce an unexpectedly large depression of depth sensitivity. The appendix shows how we predicted the effect of  $\Delta F$ . Figure 7 shows that the larger the frequency difference  $\Delta F$ , the greater the departure of experimental findings from our prediction. This means that the effect of  $\Delta F$  cannot be entirely explained in terms of the time constants of stages A and B. One way of accounting for the effect of  $\Delta F$  is as follows.



FIG. 6. Neural processing of retinal disparity information: model. Stage (a): Boxes bounded by chain lines signal retinal image position. Each box contains a population of elements (e.g.  $X_{R1}$ ,  $X_{R2}$ ,  $X_{R3}$  etc.). Each element is sensitive over a restricted retinal region. Stage (B): Boxes bounded by chain lines signal the disparity of the retinal images. Each box contains a population of elements. Each element computes retinal disparity, but the sensitivity of any given element is restricted to a narrow range of retinal disparities (centred on d1, d2, d3 etc.) Stage (C): Signals translational velocity of retinal image and hence sideways velocity of stimulus target. The graph plots attenuation vs the frequency of the target's sideways oscillations. The dotted lines and continuous lines symbolize a hypothetical segregation of disparity computers into (a) those most sensitive when the left eyes stimulus precedes the right eyes stimulus and (b) those segregation at stage (A) into positional (contrast) detectors most sensitive to targets moving from left-to-right and right-to-left respectively.

If the left and right eyes' targets oscillate at the same frequency, then the two stimuli will have some constant phase difference  $\theta$ .<sup>4</sup> Suppose that more than one mechanism underlies depth perception and that these depth mechanisms are selectively sensitive to different values of phase  $\theta$ . Now when the right and left eyes' stimuli have different frequencies, then the phase difference  $\theta$  changes continuously, passing through 360° in  $1/\Delta F$  sec. (where  $\Delta F$ Hz is the frequency difference). The result of this continuous change in  $\theta$  is that a given phase—selective mechanism will respond for only part of the time, since it is sensitive over only a restricted range of values.

Phase-selectivity can be understood as follows. Figure 2(b) shows that for some values of phase the target moves anticlockwise, and as a result both retinal images are moving right-to-left when retinal disparity is near its maximum uncrossed value and left-to-right

<sup>&</sup>lt;sup>4</sup> "The left eye's stimulus leads the right eye's stimulus by a phase of  $\theta^{\circ}$ " means that the left eye's stimulus reaches its maximum value at a fraction ( $\theta/360$ ) of a period earlier, that is ( $\theta/360F$ ) sec earlier (where F = stimulus frequency).



FIG. 7. Theoretical prediction of the effect of  $\Delta F$  upon depth threshold. The thick continuous line joins experimentally-measured values of depth threshold for different values of  $(F + \Delta F)$  with  $\Delta F$  very small (0.1 Hz). The continuous thin lines join experimentally-measured points and show the effect of increasing  $\Delta F$  for fixed values of Fequal to 1.8, 3 and 4 Hz. The dotted lines join predicted values of threshold shown as stars. Subject DR.

when disparity is near its maximum crossed value (for phase less than 180°). The situation is reversed for other values of phase (greater than 180°) when the retinal images are moving left-to-right when disparity is near its maximum uncrossed value and right-to-left when disparity is near its maximum crossed value. If one class of disparity detectors is fed entirely from right-to-left stage A (monocular) elements and a second class of disparity detectors is fed entirely from left-to-right stage A (monocular) elements, then the disparity detectors of stage B would show the required form of phase selectivity.

A possible physiological basis for such phase-selectivity of disparity detectors would be that the outputs of neurons preferentially responsive to left-right movements of the retinal image were segregated from neurons preferentially responsive to right-left movements. That binocularly-driven neurons do respond preferentially to one direction of movement seems well established in animals (HUBEL and WIESEL, 1959; 1962, BARLOW *et al.*. 1967; PETTIGREW *et al.*, 1968).

In the model of Fig. 6 the outputs of monocular left-to-right signals are (continuous lines) shown as segregated from right-to-left signals (dotted lines) right up to the disparity-computing stage. Thus the model predicts a new cyclopean effect, i.e. adaptation to the *direction* of movement in depth. Confirmation of this prediction is reported elsewhere (BEVERLEY and REGAN, 1973a, 1973b).

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#### APPENDIX

#### Prediction of sinewave thresholds for finite $\Delta F$

This calculation attempts to account for the effect of  $\Delta F$  on threshold. It is assumed that threshold can be predicted from Fig. 7. The failure of the following calculations suggest that this assumption is wrong.

The thick line in Fig. 7 is a plot of depth threshold vs target oscillation frequency  $(F + \Delta F)$ Hz when  $\Delta F$  was very small (0.2 Hz). For example, the expected attenuation when the left eye's stimulus frequency was 3.0 Hz, and the right eye's 4.0 Hz (i.e.  $\Delta F = 1.0$  Hz) is calculated as equal to the mean of the 3.0 and 4.0 Hz attenuations. These calculated points are plotted in Fig. 7 as stars (dotted lines). The number on each line is the stimulus frequency F Hz in the left eye; the value of the abscissa is the right eye's frequency  $(F + \Delta F)$  Hz. Corresponding experimentally-determined points are plotted as filled triangles (fine lines). An alternative prediction is to take the attenuation as equal to that for the higher frequency. Because threshold rises when the frequency in one eye is reduced, even this extreme prediction puts the stars no higher than the thick line, so that the predicted thresholds still disagree with the experimental points (triangles).

Abstract—Thresholds for sideways motion and for motion in depth can be separately measured when the targets viewed by the left and right eyes oscillate at different frequencies (frequency difference =  $\Delta F$  Hz). Depth sensitivity falls off when depth oscillates faster than 1 Hz at most, and fails completely at 2-3 Hz. Sideways oscillations can be seen at much higher frequencies than depth oscillations (up to at least 20-25 Hz). The unexpectedly large effect of  $\Delta F$  upon depth sensitivity suggests that there is more than one class of disparity detector such that a given monocular input to a given disparity detector is elicited by only one direction of retinal image movement.

Résumé—On peut mesurer séparément les seuils de mouvement latéral et de mouvement en profondeur quand les cibles vues par l'oeil gauche et l'oeil droit oscillent à des fréquences différentes. La sensibilité à la profondeur décroit quand la profondeur oscille à plus de 1 Hz et disparait complètement entre 2 et 3 Hz. Les oscillations latérales sont vues à des fréquences bien plus élevées (jusqu'à au moins 20-25 Hz). Cet effet important et inattendu de la différence de fréquence sur la sensibilité suggère qu'il existe plus d'une classe de détecteur de disparité, et qu'une excitation monoculaire donnée d'un détecteur donné de disparité ne se produit que pour une seule direction du mouvement de l'image rétinienne.

Zusammenfassung—Die Schwellen für die Seitwärtsbewegung und die Bewegung in die Tiefe können getrennt gemessen werden, wenn die von den linken und die von den rechten Augen geschenen Testmuster sich mit verschiedenen Frequenzen hin- und herbewegen (Frequenzdifferenz =  $\Delta F$  Hz). Die Tiefenempfindlichkeit nimmt ab, wenn die Tiefe mit einer höheren Frequenz als 1 Hz variiert wird, und verschwindet vollständig bei 2 bis 3 Hz. Seitwärtsschwingungen können dagegen bei viel höheren Frequenzen als Oszillationen in der Tiefe gesehen werden (bis zu wenigstens 20–25 Hz). Der unerwartet große Effekt von  $\Delta F$  auf die Tiefenempfindung legt nahe, dass es mehr als eine Sorte von Disparationsdetektoren gibt, dergestalt, dass ein bestimmtes monokulares Eingangssignal an einem bestimmten Disparationsdetektor nir durch eine bestimmte Bewegungsrichtung des retinalen Bildes hervorgerufen wird.

Резюме—Пороги для бокового движения и для движения в глубину могут быть измерены в отдельности, если объекты видимые левым и правым глазами осциллируют с различной частотой (различия в частоте =  $\Delta J$  гц). Чувствительносты глубинного восприятия уменьшается при осцилляцияхе глубину с частотой ревыпшающей 1 гц и совершенно исчезает при частоте осцилляций от 2 до 3 гц. боковые осцилляции могут быть видны при значительно более высоких частотах, чем осцилляции в глубину (до 20-25 гц). Неожиданно большое влияние  $\Delta J$  на пороги восприятия глубины заставляет прелполагать, что здесь имеется более одного класса детекторов диспаратности, так что данное монокулярное поступление на вход данного детектора диспаратности возникает только при одном направлении движения изображения по сетуатке.