Stereopsis: A Dynamic Approach.

by

K. I. Beverley.

Thesis submitted for the degree
of Doctor of Philosophy at Keele
University.

1975.

ABSTRACT.

An angular disparity between the left and right retinal images is sufficient to elicit a sensation of stereoscopic depth. Hitherto, few studies of the dynamics of this effect have been reported.

Some experiments are described which show how a subject's ability to utilize disparity cues in detecting a target's movement is affected by the frequency of the target's oscillation. Also discussed is whether these dynamic characteristics of binocular depth perception differ for stimuli located in front of, behind, or near the plane of fixation, and the differing effects of sinewave, squarewave and pulsed movements. The results of threshold experiments are compared with the results of suprathreshold (matched depth) experiments.

A new method is described for the isolation and the separate study of the effects of side to side movements and changes in retinal disparity on the perception of movement in depth. This method is to cause the timecourse of motion in depth to differ from the timecourse of the side to side movements of the retinal images. Some experiments which were performed using this method are described. Both sinewave and squarewave stimulation were used. A model is propounded which will account for the findings of these experiments.

Two methods are described for generating a stimulus which appears to move in a specific direction in three-dimensional space. These methods are to alter the relative amplitudes of, or the relative phase differences between, the movements of the targets seen by the left and right eyes. The effects of adapting to such stimuli are reported. A model which will account for the findings of these experiments is discussed.

FOREWORD.

This thesis reports an attempt to investigate some of the characteristics of the binocular perception of stimuli that move in depth.

There are several possible cues that an observer can use to estimate how far away an object is. These cues include (a) accommodation - the adjustment of the shape of the eye's lens necessary to bring an object into focus; (b) convergence - how far the eyes must converge to bring an object into the region of binocular single vision; (c) retinal disparity - the images on the left and right retinae of a single object will have different positions; (d) motion parallax - when the head is moved, two objects at different depths will move by differing amounts; (e) size - the size of the retinal image of an object increases as the object approaches; (f) interposition - nearby objects can occlude more distant objects, but not vice versa; and (g) texture - the texture of a regularly marked object becomes denser as the object recedes. These cues will have differing effects upon the perception of depth. Furthermore, the cues will interact with each other.

To simplify the investigation of the mechanism of depth perception, only the effects of changing retinal disparity are considered in this thesis. This limits the extent to which the findings can be applied to the general problem of how human beings perceive an object moving in depth.

I would like to thank Dr. D. Regan, my supervisor, for all the help and advice that he has given me, for managing to put up with all my faults, and for acting as a subject in many of the experiments. I am grateful to my wife, Jo, for helping me type this thesis, for correcting many of the errors therein and for acting as a subject in many of the experiments. Further thanks must go to my other subjects, Margo Young, John Jolley and Simon Hakill. I am indebted to Professor D. M. MacKay for the help he has given me and the facilities that he made available in the Department of Communication; to Robert Cartwright, who gave me much technical advice when I needed it, and to the Science Research Council which generously supported me for three years, enabling me to carry out this research.

CONTENTS.

1/ INTRODUCTION.

One consequence of the fact that man's eyes are separated by a distance of a few centimetres is that the left and right eyes have different views of three-dimensional objects. Thus, there is an angular disparity between the left and right retinal images of an object which is either in front of or behind the point at which one is looking. Although in everyday life many visual cues contribute to the sensation of depth, it has long been known that an angular disparity between the left and right retinal images is sufficient to elicit a sensation of stereoscopic depth (Wheatstone, 1838, 1852), even when there are no monocular cues to depth at all (Julesz, 1960). This phenomenon has been the subject of many recent studies using psychophysical (Julesz, 1961, 1965, 1971; Ogle, 1950; Blakemore, 1970A; Bough, 1970; Richards, 1970, 1971), single-unit (Hubel and Wiesel, 1970; Barlow, Blakemore and Pettigrew, 1967; Nikara, Bishop and Pettigrew, 1968; Pettigrew, Nikara and Bishop, 1968; Blakemore, 1967, 1970B)and evoked potential (Regan and Spekreijse, 1970; Fiorentini and Maffei, 1970; Regan and Beverley, 1973E) techniques.

The single-unit studies (on animals) have described single cortical neurones which only give an appreciable response when the visual stimuli fulfill 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 unique disparity between the images of the target on the left and right retinae. The optimal value of retinal disparity is different for different neurones. If neurones 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. One possible approach is through evoked-potential experiments in man, which can give both subjective observations and also objective data concerning the workings of populations of neurones (Regan and Beverley, 1973E). Another approach is put forward in this thesis.

A major problem in the attempt to correlate single-unit with psychophysical data has been the fact that all single-neurone studies of disparity-specific neurones have, of necessity, used moving stimuli, whereas in most human psychophysical studies, stationary stimuli have been used. There are only a few psychophysical studies of the dynamics of depth perception whose aim has been to describe the role of stimulus motion in binocular depth perception (e.g. Tyler, 1971; Richards, 1972; Regan and Beverley, 1973A).

One way of investigating the dynamics of binocular depth perception is to measure how psychophysical sensitivity to oscillations in retinal disparity depend on the frequency of oscillation. This has been experimentally achieved by presenting a target to the left eye which oscillates from side to side at a frequency FHz. while presenting to the right eye an identical target which also oscillates from side to side at FHz.. The two targets are then fused in binocular vision. If the two targets oscillate in phase then the fused target appears to move from side to side at FHz.; if the targets oscillate in antiphase, then the subject experiences a compelling illusion that the fused target appears to oscillate backwards and forwards in depth at FHz.. Such antiphase movements have been used in attempts to find how psychophysical sensitivity to oscillations in depth is affected by the frequency of oscillation (e.g. Richards, 1972).

Chapter 3 describes some experiments which show how a subject's ability to utilize disparity cues in detecting a target's movement is affected by the frequency of the target's oscillation. Experiments on whether the dynamic characteristics of binocular depth perception differ for stimuli located in front of, behind or near to the plane of fixation were performed, as this might have some bearing on Richards' (1970, 1971) suggestion that there are three pools of disparity detectors maximally responsive to crossed, uncrossed and near-zero disparities. The differing effects of sinewave, squarewave and pulsed movements are discussed. Finally, the results of threshold experiments are compared with the results for suprathreshold (matched depth) measurements.

If a change in retinal disparity is necessary to elicit the illusion that a target moves in depth, then there must necessarily be a sideways movement of one or both retinal images at the same time. As a result, it is difficult to be certain, in threshold studies, whether the subject is using purely stereoscopic cues rather than cues related to the sideways motion of the targets on the two retinae. Some authors (Richards, 1972) have overcome this problem by using suprathreshold depth measurements (e.g. matched depth paradigms) however it is uncertain whether results from these measurements can be extrapolated to threshold.

What is required is a method for isolating and separately measuring the ways in which side to side movements of the retinal image(s) and changes in retinal disparity contribute to the resulting perception of a change in depth. In other words, we wish to treat side to side movements and changes in retinal disparity as two distinct stimulus (input) variables for the visual system in the situation where the visual system's output is a single quantity - a change in perceived depth. The idea is to isolate and separately study monocular and binocular information processing in binocular depth perception.

In all binocular depth experiments so far described, the side to side movements of the retinal image(s) and the changes in perceived depth were at the same frequency, and therefore, were difficult to distinguish when the movements were small (as at threshold). However, it is not necessary that this should be so. If the target seen by the left eye oscillates from side to side at frequency FHz., and the target seen by the right eye oscillates from side to side at a slightly different frequency GHz. (where $G = F + \Delta F$), then, provided that fusion can be maintained, oscillations in depth can be seen with amplitude waxing and waning ΔF times a second. This can be understood by considering that the positions of the left and right retinal images oscillate at frequency F but that the relative phase of these oscillations is modulated at frequency ΔF. In this context relative phase corresponds to retinal disparity. Since ΔF is independent of both F and G, the timecourse of sideways motion will differ from the timecourse of motion in depth, and the threshold functions for the two stimulus parameters can be independently measured.

Chapter 4 describes some experiments which were performed using this method. Both sinewave and squarewave stimulation were used. A model which will account for the findings of these experiments is discussed in Section 4:4.

Stationary objects can appear to be in motion if objects moving in one direction are first viewed for some time. The direction of the illusory motion is opposite to the direction of movement of the first viewed objects. This aftereffect of seen motion has been cited as evidence for the presence of directionally-selective motion detectors in the human visual system (Wohlgemuth, 1911). According to this explanation, the human visual system contains motion detectors that respond preferentially to a retinal image that is moving in a specific direction. The "preferred" direction differs for different motion detectors. The particular detectors that are excited by a moving stimulus provide a physiological representation this thesis, further psychophysical evidence for such mechanisms is reported.

One method for generating a stimulus which appears to move in a specific direction in three-dimensional space, is to view identical targets which oscillate sinusoidally from side to side in the two eyes. If the relative amplitude of stimulus oscillation seen by the left and right eyes (L/R ratio) is varied, the fused target appears to oscillate along a specific direction in space. If the relative phase difference between the oscillations viewed by the left and right eyes is altered, the fused target appears to orbit in depth, the direction of motion being different for phase differences of less than 180° and for phase differences greater than 180°.

The effects of adapting to a stimulus with an amplitude difference between the two eyes' stimulus oscillations is reported in Section 5:3. The effects of adapting to a stimulus with a phase difference between the two eyes' stimulus oscillations is reported of the direction of movement. The balance between the outputs of detectors with different "preferred" directions is upset when all detectors with the same "preferred" direction are selectively fatigued, and this imbalance produces an illusion of movement. Motion-sensitive neurones of a type that could be responsible for this effect have been found in the rabbit (Barlow and Hill, 1963).

It is possible that there are directionally-selective mechanisms in the human visual system other than those selectively responsive to the direction of sideways motion. In particular, there may be disparity-sensitive mechanisms selectively responsive to the direction of motion in depth. Binocularly-activated neurones which respond only when disparity is changing in a particular direction have recently been found in cat (Pettigrew, 1973). Regan and Beverley (1973E) have reported some electrophysiological evidence for such mechanisms in man. In Sections 3:6:2, 4:3:1 and 4:4:3 of in Section 5:4. The timecourse of recovery from adaptation is discussed in Section 5:2. A model which will account for the findings of these experiments is discussed in Section 5:5.

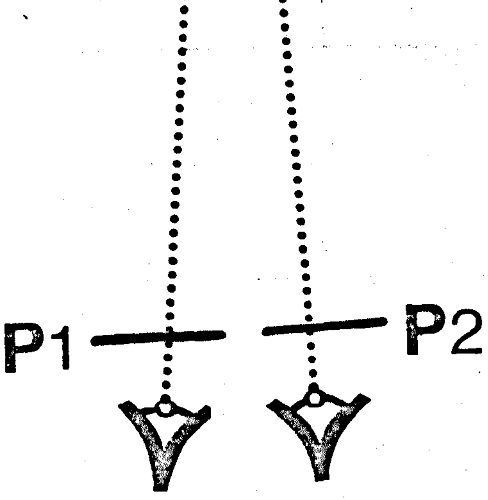
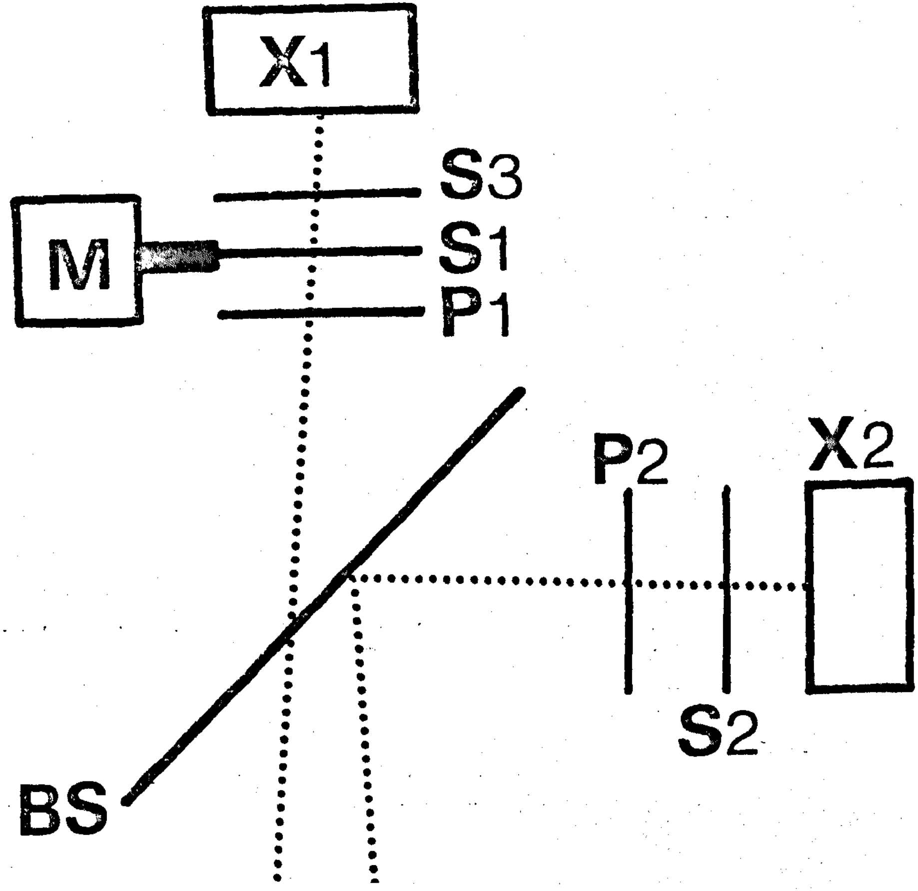


Figure 1. Schematic diagram of Apparatus 1. X1,X2 - fluorescent tube light sources; S1,S2,S3 - stimulus transpar~~a~~encies; P1,P2 - polarizers; BS - beam splitter; M - vibration generator. Movement of the vibration generator moves stimulus transpar~~a~~ency S1 and hence changes the stimulus disparity.


X1
S3
M
S1
P1
BS
P2
S2
X2

2/ METHODS.

2:1. Apparatus.

2:1:1. Apparatus 1 - Single Vibrator.

A schematic diagram of Apparatus 1 is shown in Fig. 1.

X1 and X2 are aluminium boxes which were light-tight except for a 10cm. square aperture on one side. This aperture was covered with an opalescent glass sheet (screen). Behind the aperture four 6 watt, 22cm. long, fluorescent tubes were mounted equidistant from each other. When the tubes were on, the screens were evenly illuminated. The luminance of the screens was 110cd/m^2.

The stimulus transparencies were mounted in front of these screens. Figs. 9A and B show the two sets of stimulus transparencies that were used with Apparatus 1. All the transparencies were photographically produced on "Kodalith Ortho Film Type 3", an extremely high contrast negative film. A negligible amount of light was transmitted through the black parts of the stimulus transparencies and less than 10% of the light was absorbed by the transparent parts.

Stimulus transparencies S2 and S3 were cemented (using perspex cement) to 10cm. square by 0.3cm. thick clear perspex plates which were mounted about 3cm. in front of their respective luminous screens. The optical distance from the plane of the transparencies to the subjects' pupils was 75cms..

Transparency S1 (which was either a disc 3.3cm. in diameter, or an opaque bar 2.6cm. high by 0.15cm. wide) was mounted on one end of a steel (and hence opaque - see below) rod of about 0.04cm. diameter. The steel rod extended from the centre of transparency S1, horizontally to the left, beyond the edge of the luminous screen. The other end of the steel rod was mounted on the shaft of a (horizontal) "Pye-Ling" vibration generator (M)(vibrator). By applying a voltage to the vibrator, the steel rod, and hence transparency S1, could be moved to and fro in a horizontal direction. Transparency S1 could be moved through a total distance of about 0.5cm..

Stimulus transparencies S1 and S3 were arranged in such a way that the emulsion sides of the transparencies were face-to-face and separated by no more than 0.1cm.. From the viewing distance of 75cm., and when viewed by the left eye alone, both transparencies appeared to lie in a single plane. As this was the situation during an experiment, it was felt that the difference of 1 part in 750 between the viewing distances of transparencies S1 and S3 was negligible.

A 10cm. square sheet of "polaroid" (P2) was mounted in front of transparency S2. A second 10cm. square sheet of "polaroid" (P1), with its polarising direction at 90° to that of P2, was mounted in front of transparencies S1 and S3.

A 30cm. by 20cm. beam-splitter (BS) was mounted so that transparencies S1, S2 and S3 appeared exactly coincident. * To facilitate aligning the transparencies, (a) the vibrator (M)(and hence transparency S1) was mounted on a micrometer which enabled alignment of transparencies S1 and S3; ** (b) transparency S2 was

---

* A disparity of 10 sec. arc is detectable. At a viewing distance of 75cm., this corresponds to 0.004cm.. Coincidence of the transparencies to better than 0.002cm. was therefore required.

** This had an additional advantage in that the micrometer movement could be used to move the vibrator (and hence transparency S1) a precisely determined distance horizontally. This caused a static disparity to occur between transparency S1 and the corresponding part of transparency S2. When the transparencies were viewed in mounted on an adjustable optical bench saddle which was also mounted on a micrometer. This enabled transparency S2 to be aligned with transparencies S1 and S3; (c) the beam splitter (BS) was mounted in an adjustable mount to permit a coarse alignment between the three transparencies.

The subject wore a pair of ophthalmic trial frames containing two sheets of "polaroid" (P1 and P2), one in front of each eye, such that the left eye viewed transparencies S1 and S3 only, and the right eye viewed transparency S2 only. Prescription lenses could also be inserted in the trial frames, if necessary.

The whole apparatus was contained in a large, light-tight box. All (non-optical) surfaces were coated with matt black paint. At one end of the box there was a slit, 10cm. wide and 5cm. high. The subject sat, more or less in the dark, in a curtained cubicle so that he could view the transparencies through the slit.

The subject rested his chin on a chin-rest, which was adjusted so that his eyes were in the same horizontal plane as the centres of the transparencies, and the viewing distance was 75cms.

When the subject's eyes were correctly converged on the fixation plane of black dots, he saw two black nonius lines (15min. arc long by 1 min. arc wide) as a single line. In fact the upper half of the line was seen by the left eye and the lower half by the right. These lines were to assist the subject in maintaining a steady convergence. A deviation of convergence of less than 0.5 min. arc could be detected by this means.

---

binocular fusion this static disparity caused the central disc (Stimulus 1 Fig. 9A) or the right hand bar (Stimulus 2 Fig. 9B) to stand out in depth. The amount by which the central disc or the right hand bar stood out in depth (either in front of, or behind the rest of the stimulus) could thus be preset by adjustment of the micrometer movement.

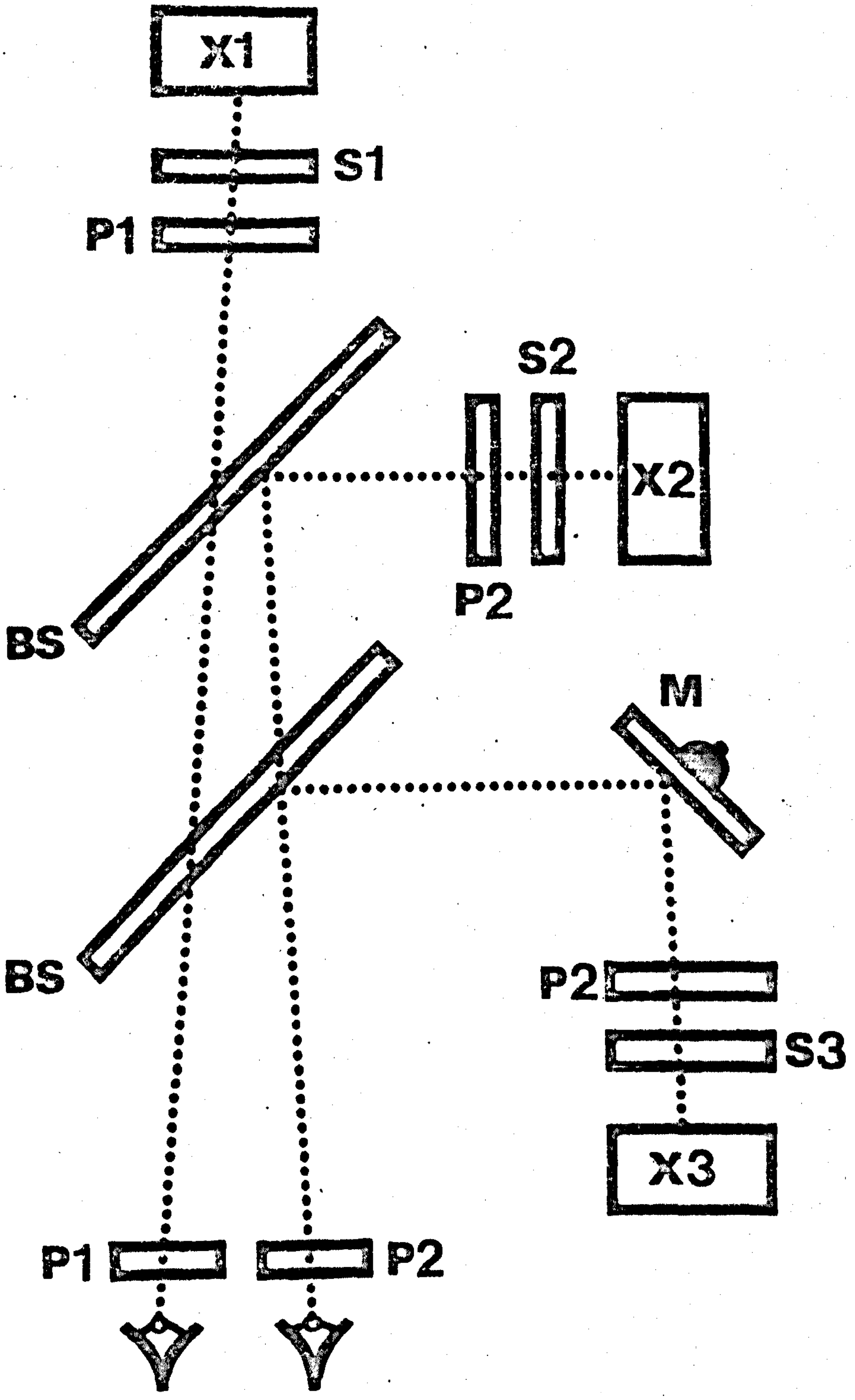


Figure 2. Schematic diagram of Apparatus 2. X1,X2,X3 - fluorescent tube light sources; S1,S2,S3 - stimulus transparencies; P1,P2 - polarizers; BS - beam splitter; M - front surface mirror mounted on a pen motor. Rotation of the mirror deflects stimulus transparency S3 and hence changes the stimulus disparity.

The electronic apparatus for the generation and control of stimulus movements, and for the recording of the subjects' responses was the same for all three sets of optical apparatus and is described in Section 2:1:4.

Apparatus 1 was used for two sets of experiments. At the conclusion of these experiments certain shortcomings in the apparatus were evident. The main problem was the opaque rod which extended from the left hand side to the centre of the stimulus. This rod, although very thin, was nonetheless clearly visible. As it did not appear to move, either in depth or from side to side, it was unlikely to have affected the experimental results. Its very presence was, however, "distracting" and this was considered unsatisfactory.

A second problem was that the vibrator could only move transparency S1 through a horizontal distance of 0.5cm. (corresponding to a change in disparity of about 24 min. arc). This restricted measurements to within Panum's fusional area.

In order to overcome these shortcomings, a new apparatus was constructed.

2:1:2. Apparatus 2 - Moving Mirror.

A schematic diagram of Apparatus 2 is shown in Fig. 2.

X1, X2 and X3 are aluminium boxes which were light-tight except for a 10cm. square aperture on one side. This aperture was covered with an opalescent glass sheet (screen). Behind the aperture four 6 watt, 22cm. long, fluorescent tubes were mounted equidistant from each other. When the tubes were on, the screens were evenly illuminated. The luminance of the screens was 110cd/m^2.

The stimulus transparencies were mounted in front of these screens. Fig. 9C shows the stimulus transparencies that were used with Apparatus 2. All the transparencies were photographically produced on "Kodalith Ortho Film Type 3", an extremely high contrast negative film. A negligible amount of light was transmitted by the black parts of the stimulus transpar~~a~~encies and less than 10% of the light was absorbed by the transpar~~a~~ent parts.

All three stimulus transpar~~a~~encies were cemented (using perspex cement) to 10cm. square by 0.3cm. thick clear perspex plates which were mounted about 3cm. in front of their respective luminous screens. The optical distance from the plane of the transpar~~a~~encies to the subject's pupils was 63cm..

A 10cm. square sheet of "polaroid" P1 was mounted in front of transpar~~a~~ency S1. Additional sheets of "polaroid" P2 with optical axes at 90° to that of P1 were mounted in front of transpar~~a~~encies S2 and S3.

A surface-silvered mirror (M) was mounted on a "Devices" pen motor in the optical path between transpar~~a~~ency S3 and the right eye. By applying a voltage to the pen motor, the mirror could be rotated through a small angle. This caused the image of transpar~~a~~ency S3 to shift from side to side on the right retina. The image could be moved through a distance corresponding to an apparent shift of 1.5cm. in the position of transpar~~a~~ency S3. This was equivalent to a change in disparity of 82 min. arc.

Two 30cm. by 20cm. beam splitters (B.S.) were mounted so that transpar~~a~~encies S1, S2 and S3 appeared exactly coincident .* To facilitate aligning the transpar~~a~~encies (a) Stimulus S2 was mounted on a micrometer which enabled alignment of transpar~~a~~encies S2 and S3; (b) transparancy S1 was also mounted on a micrometer. This enabled transpar~~a~~ency S1 to be aligned with transpar~~a~~encies S2 and S3; (c) both beam splitters were mounted in adjustable supports to permit a coarse alignment between the three transpar~~a~~encies.

---

* A disparity of 10 sec. arc is detectable. At a viewing distance of 63cm. this corresponds to 0.004cm.. Coincidence of the transpar~~a~~encies to better than 0.002cm. is therefore required.

The subject wore a pair of ophthalmic trial frames containing two sheets of "polaroid" (P1 and P2), one in front of each eye, such that the left eye viewed transparency S1 only, and the right eye viewed transparencies S2 and S3 only. Prescription lenses could also be inserted in the trial frames if necessary.

The whole apparatus was contained in a large, light-tight box. All (non-optical) surfaces were coated with matt black paint. At one end of the box there was a slit, 10cm. wide and 5cm. high. The subject sat, more or less in the dark, in a curtained cubicle so that he could view the transparencies through the slit.

The subject rested his chin on a chin-rest, which was adjusted so that his eyes were in the same horizontal plane as the centres of the transparencies, and so that the viewing distance was 63cm..

When the subject's eyes were correctly converged on the fixation plane of black dots, he saw two, black, nonius lines (15 min. arc long by 1 min. arc wide) as a single line. In fact the upper half of the line was seen by the left eye and the lower half by the right. These lines were to assist the subject in maintaining a steady convergence. A deviation in convergence of less than 0.5 min. arc could be detected by this means.

The electronic apparatus for the generation and control of stimulus movements, and for the recording of the subject's responses is described in Section 2:1:4.

Apparatus 2 was used for several experiments. Although the shortcomings of Apparatus 1 had been overcome, there were still some deficiencies in the new apparatus. Firstly, it was difficult to preset a static disparity between transparency S3 and the corresponding part of transparency S1. A D.C. voltage had to be applied to the pen motor to achieve this. This voltage changed slowly with time, however, as the current through the pen motor caused it to heat up.

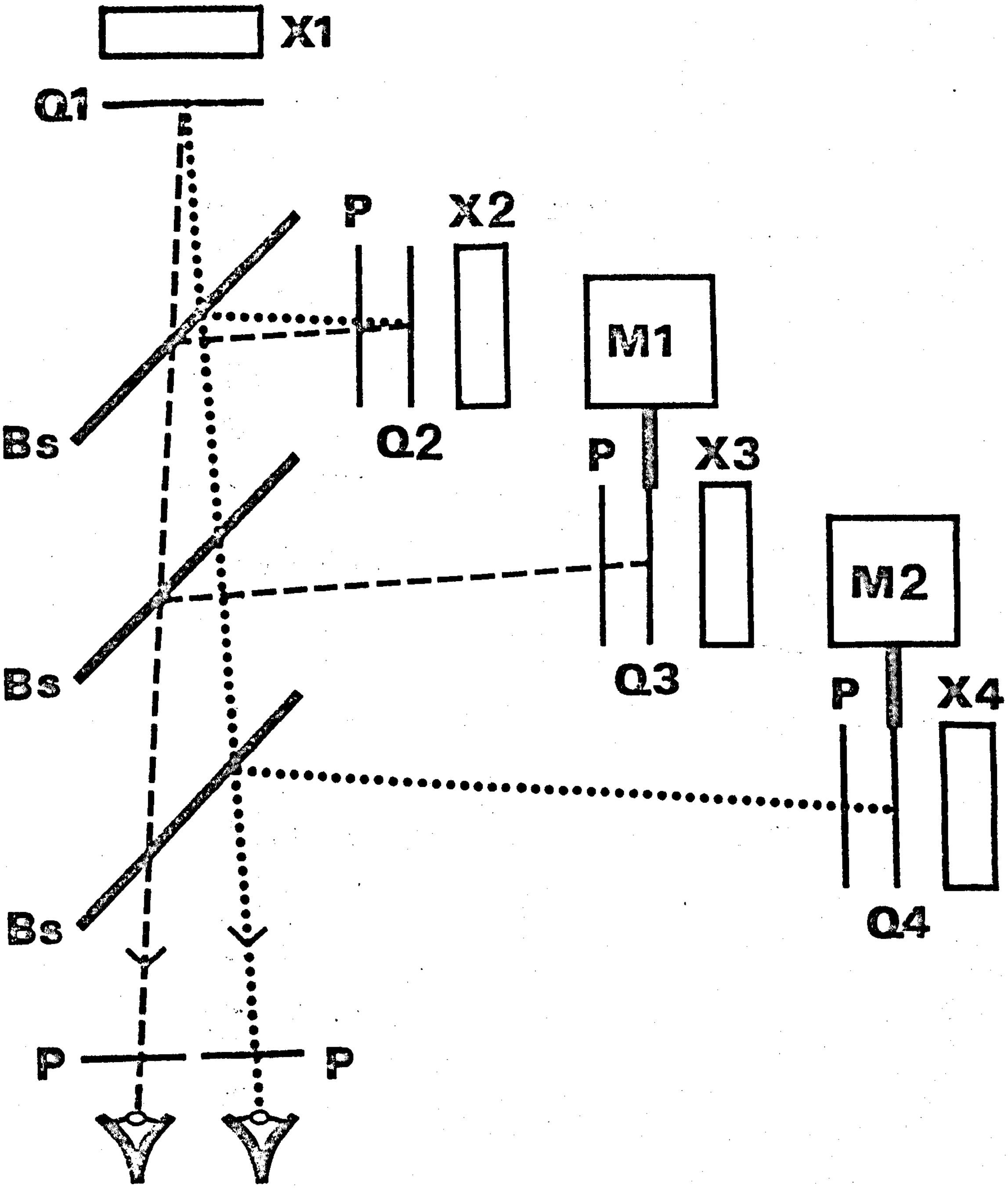


Figure 3. Schematic diagram of Apparatus 3. X1,X2,X3,X4 - fluorescent tube light sources; Q1,Q2,Q3,Q4 - stimulus transparencies; P - polarizer; Bs - beam splitter; M1,M2 - vibration generators. Movement of M1 and/or M2 moves stimulus transparencies Q3 and/or Q4 and hence changes the stimulus disparity.

Although this was not serious, it meant that it was necessary to reset the static disparity every half hour or so.

A second problem was that the pen motor had a large (8cm. by 6cm.) mirror mounted on it. Although the mirror was very light (it was in fact a microscope cover slip with one surface aluminised) it still had a substantial moment of inertia. This meant that although a reasonably linear frequency response could be achieved with sinewaves (up to 20Hz. +0, -1dB.) the response to squarewaves was not very good (monitored with a photocell). The squarewave response was acceptable below about 3Hz., however. It was not possible to perform some experiments with the moving mirror since they would have required the use of ~~demanded~~ squarewaves of up to 20Hz. in frequency.

A third point was that with both Apparatus 1 and Apparatus 2, one eye saw one transparency (with virtually 100% contrast) whilst the other eye saw two (with a maximum contrast of 50%). It was felt that it would be better if the contrast in both eyes was about the same.

A fourth point was that with both Apparatus 1 and Apparatus 2, the stimulus moved in only one eye. For some experiments, however, it was necessary to be able to move stimuli in both eyes independently.

A new apparatus was, therefore, constructed to overcome these shortcomings.

2:1:3. Apparatus 3 - Twin Vibrators.

A schematic diagram of Apparatus 3 is shown in Fig. 3.

X1, X2, X3 and X4 are aluminium boxes which were light-tight except for a 10cm. square aperture on one side. This aperture was covered with an opalescent glass sheet (screen). Behind the aperture four 6 watt, 22cm. long, fluorescent tubes were mounted, equidistant from each other. When the tubes were on, the screens were evenly illuminated. The luminance of the screens was 110 cd/m^2.

The stimulus transparencies were mounted in front of these screens. Figs. 9D and E show two sets of stimulus transparencies that were used with Apparatus 3. Two further sets of stimulus transparencies were also used with Apparatus 3. These sets were the "negatives" of the transparencies shown in Figs. 9D and E. All the transparencies were photographically produced on "Kodalith Ortho Film Type 3", an extremely high contrast negative film. A negligible amount of light was transmitted by the black parts of the stimulus transparencies. Less than 10% of the light was absorbed by the transparent parts of the stimulus transparencies.

Stimulus transparencies Q1 and Q2 were cemented (using perspex cement) to 10cm. square by 0.3cm. thick, clear perspex plates, which were mounted about 3cm. in front of their respective luminous screens. Stimulus transparencies Q3 and Q4 were cemented (using a clear iso-cyanate glue) to two 8cm. by 6cm. by approximately 0.02cm. microscope cover slips. The two cover slips were mounted on the shafts of two (horizontal) "Pye-Ling" vibration generators (M1 and M2) (vibrators). By applying a voltage to one vibrator, the corresponding stimulus transparency could be moved to and fro in a horizontal direction. Transparencies Q3 and Q4 could each be moved through a total distance of about 0.5cm.. The optical distance from the planes of all four transparencies to the subject's pupils was 63cm.. This meant that a change in disparity of about 60 min. arc could be achieved.*

---

* With Q3 at its extreme left position and Q4 at its extreme right position, the disparity will be +0.5cm.. With Q3 at its extreme right position and Q4 at its extreme left position, the disparity will be -0.5cm.. A change in disparity of 1cm. (about 60 min. arc) is thus possible.

A 10cm. square sheet of "polaroid" (P) was mounted in front of transparency Q3. A second 10cm. square sheet of "polaroid", with its optical axis at 90° to the first sheet, was mounted in front of transparency Q4. When the "negative" sets of stimulus transparencies were used, two sheets of "polaroid" were mounted in front of transparency Q2 so that the upper (white) bar was polarized with its optical axis parallel to that of transparency Q3, and the lower (white) bar was polarized with its optical axis parallel to that of transparency Q4. When the positive sets of stimulus transparencies shown in Figs. 9D and E were used, transparency Q2 was unpolarized. Stimulus transparency Q1 was always unpolarized.

Three 30cm. by 20cm. beam splitters (Bs) were mounted so that transparencies Q1, Q2, Q3 and Q4 appeared exactly coincident. * To facilitate aligning the transparencies, (a) both vibrators (M1 and M2)(and hence transparencies Q3 and Q4) were mounted on micrometers which enabled alignment of transparencies Q3 with Q1, and Q4 with Q1; (b) transparency Q2 was also mounted on a micrometer. This enabled transparency Q2 to be aligned with transparencies Q1, Q3 and Q4; (c) all three beam splitters (Bs) were mounted in adjustable supports to permit a coarse alignment between the four transparencies.

The subject wore a pair of ophthalmic trial frames containing two sheets of "polaroid" (P), one in front of each eye, such that the left eye viewed transparencies Q1 and Q3 and the right eye viewed transparencies Q1 and Q4. When the positive sets of stimulus

---

* A disparity of 10 sec. arc is detectable. At a viewing distance of 63cm. this corresponds to 0.004cm.. Coincidence of the transparencies to better than 0.002cm. is therefore required.

transparencies shown in Figs. 9D and E were used, transparency Q2 was unpolarized, and thus could be seen by both eyes. When the "negative" sets of stimulus transparencies were used, transparency Q2 was polarised so that the left eye saw the upper (white) bar, and the right eye saw the lower (white) bar. Prescription lenses could also be inserted in the trial frames, if necessary.

The whole apparatus was contained in a large, light-tight box. All (non-optical) surfaces were coated with matt black paint. At one end of the box there was a slit, 10cm. wide and 5cm. high. The subject sat, more or less in the dark, in a curtained cubicle so that he could view the transparencies through the slit. The subject rested his chin on a chin rest, which was adjusted so that his eyes were in the same horizontal plane as the centres of the transparencies, and so that the viewing distance was 63cm..

In the experiments where the "negative" transparencies were used, when the subject's eyes were correctly converged on the fixation plane of white dots, he saw two white nonius lines (15 min. arc long by 1 min. arc wide) as a single line. In fact, the upper half of the line was seen by the left eye and the lower half by the right. These lines were to assist the subject in maintaining a steady convergence. A deviation in convergence of less than 0.5 min. arc could be detected by this means.

The electronic apparatus for the generation and control of stimulus movements, and for the recording of the subject's responses is described in Section 2:1:4.

Apparatus 3 was used for several experiments. The major shortcomings of Apparatus 1 and Apparatus 2 had been overcome. Static disparities between transparencies Q3, Q4 and Q1 could be easily preset by adjustments of the micrometers upon which the vibrators, and hence transparencies Q3 and Q4, were mounted. The transient response of the vibrators was adequate for the purpose

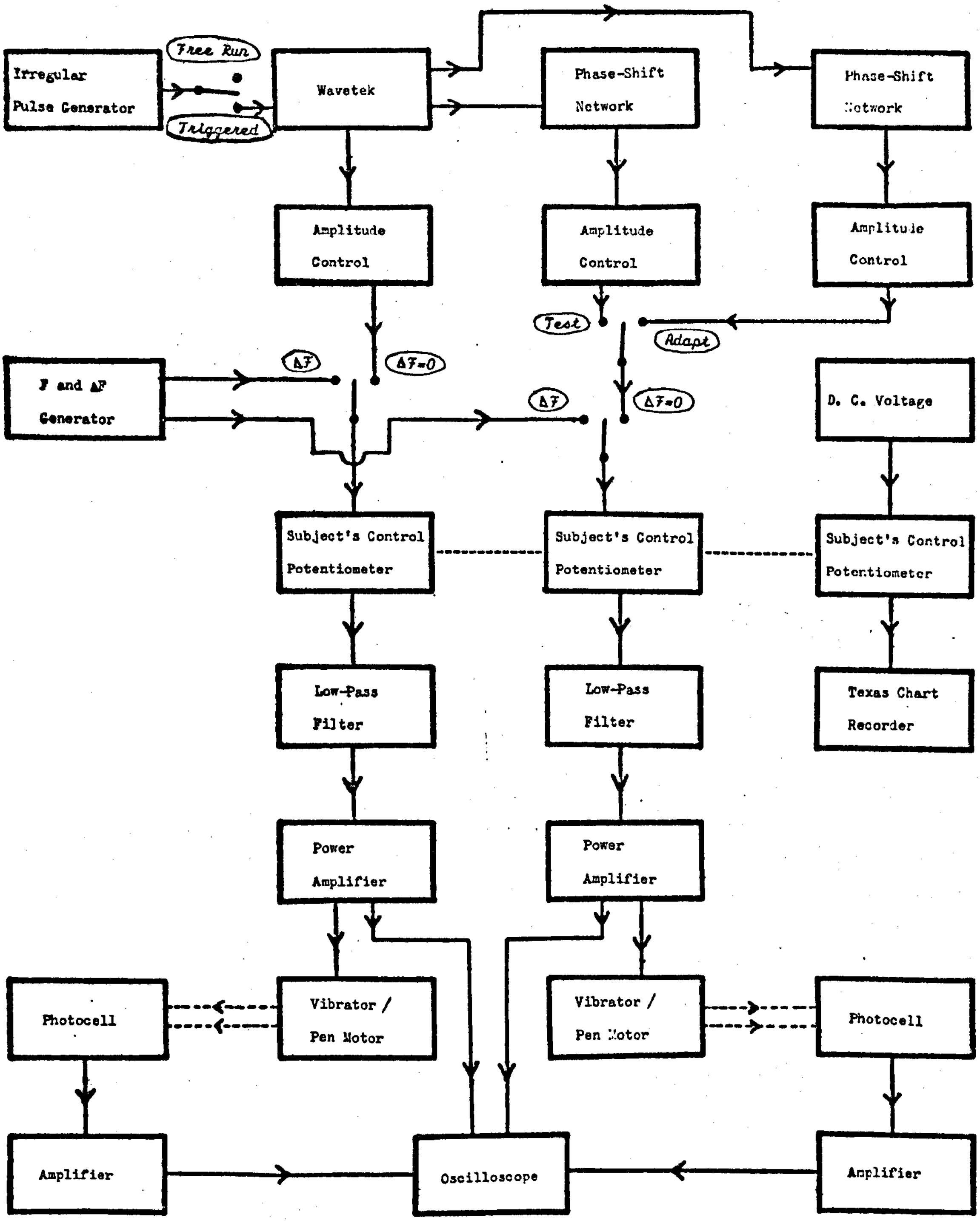


Figure 4. Schematic diagram showing the electronic equipment used to generate the stimulus movements and to record the responses of the subjects.

(see Section 2:1:6). The contrast of the stimuli seen by both eyes was the same. Finally, the stimuli could be moved quite independently in either eye.

2:1:4. Ancilliary Apparatus.

A schematic diagram of the ancilliary apparatus used to generate the stimulus movements and to record the subject's responses is shown in Fig. 4.

The irregular pulse generator consisted of four astable multivibrators running at different frequencies. The outputs from these astable multivibrators were summed and fed to a Schmitt trigger, and thence to a monostable multivibrator with a time constant which could be varied between 100 milliseconds and 4 seconds. The output from the monostable was differentiated and fed to the trigger input of the Wavetek. The sum of the four uncorrelated squarewaves caused the Schmitt to trigger at irregular intervals in a sequence that repeated after 16 triggerings (approximately 20 seconds). The monostable ensured that the output pulses were separated by at least a minimum interval (usually twice the duration of the output pulses of the Wavetek - see below). The trigger pulses to the Wavetek were sufficiently irregular for the subject not to be able to know when the next stimulus movement would occur.

The Wavetek was a "Wavetek" model 112 signal generator, which either could be triggered by the irregular pulse generator, or could be set to oscillate continuously. The Wavetek was used to generate variable frequency sinewaves or squarewaves, or when externally triggered, variable duration pulses. Three, constant-amplitude outputs were available from the Wavetek; one output being 180° out of phase from the other two.

One output from the Wavetek was fed to a variable-gain operational amplifier (741 - OPA)(amplitude control) the output of which could be connected to one gang of the subject's control potentiometer. This permitted the experimenter to alter the calibration of the subject's control potentiometer at any time during an experiment, thus ensuring that the position of the knob on the subject's control potentiometer provided no clue as to the amplitude of the stimulus oscillations.

The two other outputs of the Wavetek (180° out of phase with each other) were both connected to two phase-shift networks. Since these networks were only used with sinewave stimulus oscillations at a single frequency (0.8Hz.), simple resistance/capacitance networks were used to generate a phase shift of 90° (at 0.8Hz.). By switching the inputs to the networks, phase shifts of 0°, 90°, 180° or 270° relative to the third output of the Wavetek, could be obtained. By mixing these phase-shifted signals and by varying the amplitude of each, a signal whose phase could be varied between 0° and 360° was obtained. *

The variable phase signals from the two phase shift networks were fed to two variable-gain operational amplifiers (741 - OPA) (amplitude control). The outputs from either of these amplitude controls could be connected to a second gang of the subject's control potentiometer. This permitted the experimenter to switch between two signals of different phase (see below) or to switch between two signals of different amplitude (see below) or to switch between signals differing both in amplitude and phase (see below). The experimenter could also use the amplitude controls to alter the calibration of the subject's control potentiometer.

---

* For example, zero signal at 0° phase + 3 volts at 90° phase + 4 volts at 180° phase + zero signal at 270° phase results in a 5 volt signal with a phase of 143.2°.

The F and ΔF generator is described in Section 2:1:5.

A D.C. voltage could be connected to the third gang of the subject's control potentiometer. The output voltage from the potentiometer varied linearly with the position of the potentiometer, and was fed to a chart recorder. The chart recorder thus recorded the position of the subject's control potentiometer as the subject set the depth threshold.

The outputs of the other two gangs of the subject's control potentiometer were fed to two low-pass filters. These were single-stage resistance/capacitance networks with $F_T \mathrel{\hat{=}} 100$Hz., designed to limit the rate of change of input voltage to the power amplifiers and so reduce overshoot.

The power amplifiers were modified "Tobey/Dinsdale" D.C. power amplifiers. They could produce an output of ± 10V D.C. at up to 3A. Their output impedance was less than 0.1Ω. Their frequency response was limited by the preceeding low-pass filters.

The vibrator/pen motors were either "Pye-Ling" vibration generators or "Devices" pen motors. They converted the output voltages of the power amplifiers into stimulus movements.

The motion of the stimuli could be monitored by means of two photocells. These were pin photodiodes, the outputs of which , after amplification, could be displayed on an oscilloscope.

During experiments, the motion of the stimulus was monitored by displaying the outputs of the D.C. amplifiers on a "Tektronix type 502A" oscilloscope. These voltages (which had previously been calibrated using the photocells - see Section 2:1:6) were used as the experimental measure of the subject's threshold.

In the experiments of Sections 3:1 and 3:4, the Wavetek was set to "free-run" and sinewaves with frequencies in the range 0.1 to 20Hz. were generated. In the experiments of Sections 3:2 and 3:5

the Wavetek was set to "free-run" and squarewaves with frequencies in the range 0.1 to 10Hz. were generated. In the experiments of Sections 3:3 and 3:6 the Wavetek was triggered by the irregular pulse generator. Pulse durations in the range 7 milliseconds to 1 second were set on the Wavetek and the time between pulses was set by the irregular pulse generator. In all the experiments of Chapter 3 anti-phase outputs from the Wavetek were connected via the experimenter's amplitude controls to the subject's control potentiometer and thence, via the low-pass filters and the power amplifiers, to the vibrator/pen motor. In some experiments a single vibrator was used (Apparatus 1), in others a single pen motor was used (Apparatus 2) and in others two vibrators were used (Apparatus 3). The subjects' settings were recorded from the oscilloscope which was set to monitor the outputs from the power amplifiers.

In the experiments of Chapter 4 the outputs from the F and ΔF

generator (see Section 2:1:5) were connected to the subject's control potentiometer. Thereafter, the electronic equipment was the same as used in the experiments of Chapter 3.

In the experiments of Chapter 5 the Wavetek was set to free run and a sinewave of frequency 0.8Hz. was generated. One output from the Wavetek was connected via the experimenter's amplitude control to one gang of the subject's control potentiometer. The other outputs from the Wavetek were connected to the phase shift networks and thence to the experimenter's amplitude controls. The output from either of these could be connected to a second gang of the subject's control potentiometer. One of the phase shift networks and the corresponding amplitude control was preset before each experiment to give the phase shift and oscillation amplitude for the adapting stimulus. The other phase shift network and corresponding amplitude control was varied during each experiment to provide the test stimulus. In the experiments of Sections 5:2 and 5:3, the phase shifts were only set to 0° or 180°. In the experiments of Section 5:4 phase shifts in the range 0° to 360° were used. In the experiments of Sections 5:2 and 5:3, the relative stimulus oscillation amplitude between the left and right eyes (L/R ratio - see Section 5:1) was varied by the experimenter throughout each experiment by altering the amplitude controls. In the experiments of Section 5:4, the L/R ratio was preset before each experiment and remained constant throughout that experiment. In the experiments of Section 5:2, a D.C. voltage was connected to the third gang of the subject's control potentiometer. The output voltage from the potentiometer was recorded on a chart recorder. This enabled a permanent recording to be made of the position of the subject's control potentiometer throughout the experiment (i.e. the subject's threshold setting). In all the experiments of Chapter 5, the electronic equipment following the subject's control potentiometer was the same as used in the experiments of Chapter 3.

The non-commercial electronic equipment was powered by two "Advance" 12V, 3A stabilised power supply units connected so as to give ± 12V with respect to earth.

Each of the 12 fluorescent tubes was run off a 250V D.C. power supply unit, with a 12E14 valve in series (to compensate for the negative resistance characteristic of the fluorescent tubes). The current through the fluorescent tubes (and hence the light output) was maintained at a constant value throughout all the experiments by adjusting the bias of the valves.

The static disparities of the stimulus transpar~~a~~encies could be preset at the beginning of an experiment by one of two methods. Either the stimulus transpar~~a~~ency was physically moved by means of a micrometer adjustment, or a D.C. voltage could be added to the stimulus waveforms produced by the Wavetek (see Sections 2:1:1, 2:1:2 and 2:1:3). In the latter case, the resulting D.C. outputs

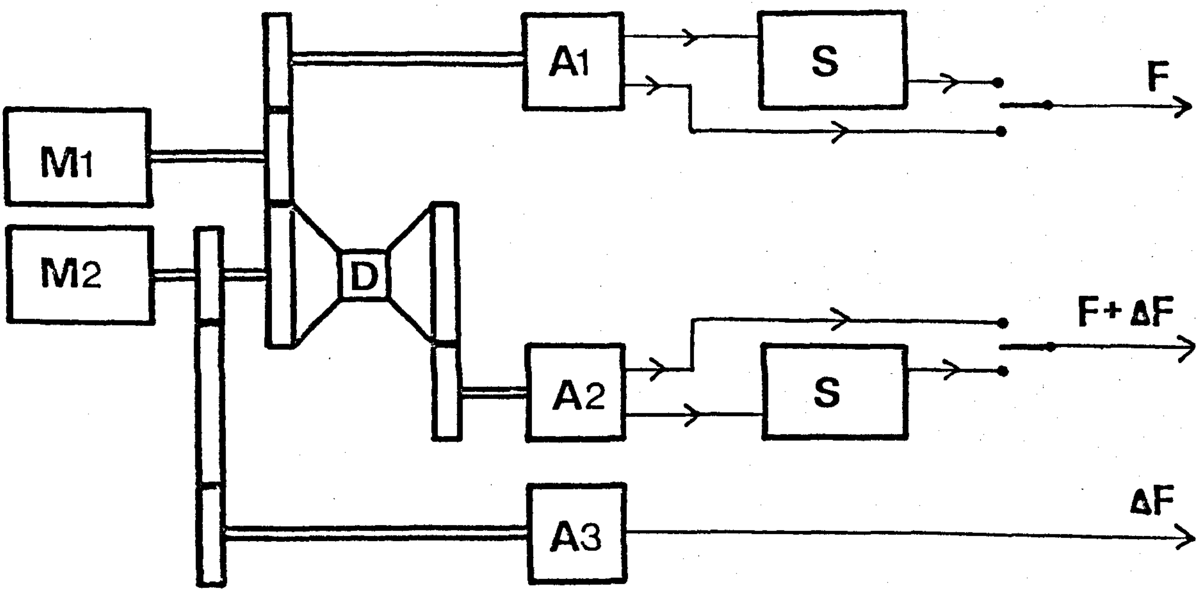


Figure 5. Method of generating signals whose frequencies differ by a variable amount (ΔF). M1, M2 - high-stability, variable-speed motors; D - differential gear; A1, A2, A3 - alternators; S - sinewave to squarewave converter.

from the power amplifiers produced constant mean displacements of the stimulus transparencies (i.e. static disparities).

2:1:5. Method of Generating ΔF.

The principle of the method used to generate signals whose frequencies differ by a precisely-controlled amount has been previously described (Regan, 1970; Regan and Cartwright, 1970).

A schematic diagram of the apparatus is shown in Fig. 5.

A high-stability variable-speed motor (M1) drives an alternator (A1) directly and a second alternator (A2) through a differential gear (D). The speed of motor M1 sets the frequency (FHz.) of the sinusoidal output from alternator A1. A second, high-stability,variable-speed motor (M2) drives a third alternator (A3) directly and also turns the differential gear D. The speed of motor M2 sets the frequency (ΔFHz.) of the sinusoidal output from alternator A3. The frequency of the sinusoidal output from alternator A2 is set by the speed of both motors and is (F+ΔF)Hz..

For example, if the speed of motor M1 is 600 r.p.m. and the speed of motor M2 is 60 r.p.m. (both motors rotating in the same direction) then in 1 second,alternator A1 will have rotated 10 times (i.e. F = 10Hz.), alternator A3 will have rotated once (i.e. ΔF = 1Hz.), and alternator A2 will have rotated 10 times due to M1 plus 1 additional time due to the rotation of the differential caused by M2 - a total of 11 times (i.e. F+ΔF = 11Hz.). The differential is thus seen to act as an algebraic adder. The advantage of this method is that since the frequency difference ΔF is directly introduced, errors in speed appear as a percentage of ΔF so that even when (ΔF/F) is very small, ΔF may still be controlled with precision.

The outputs of alternators A1 and A2 can be connected to two gangs of the subject's control potentiometer (Fig. 4). If required,

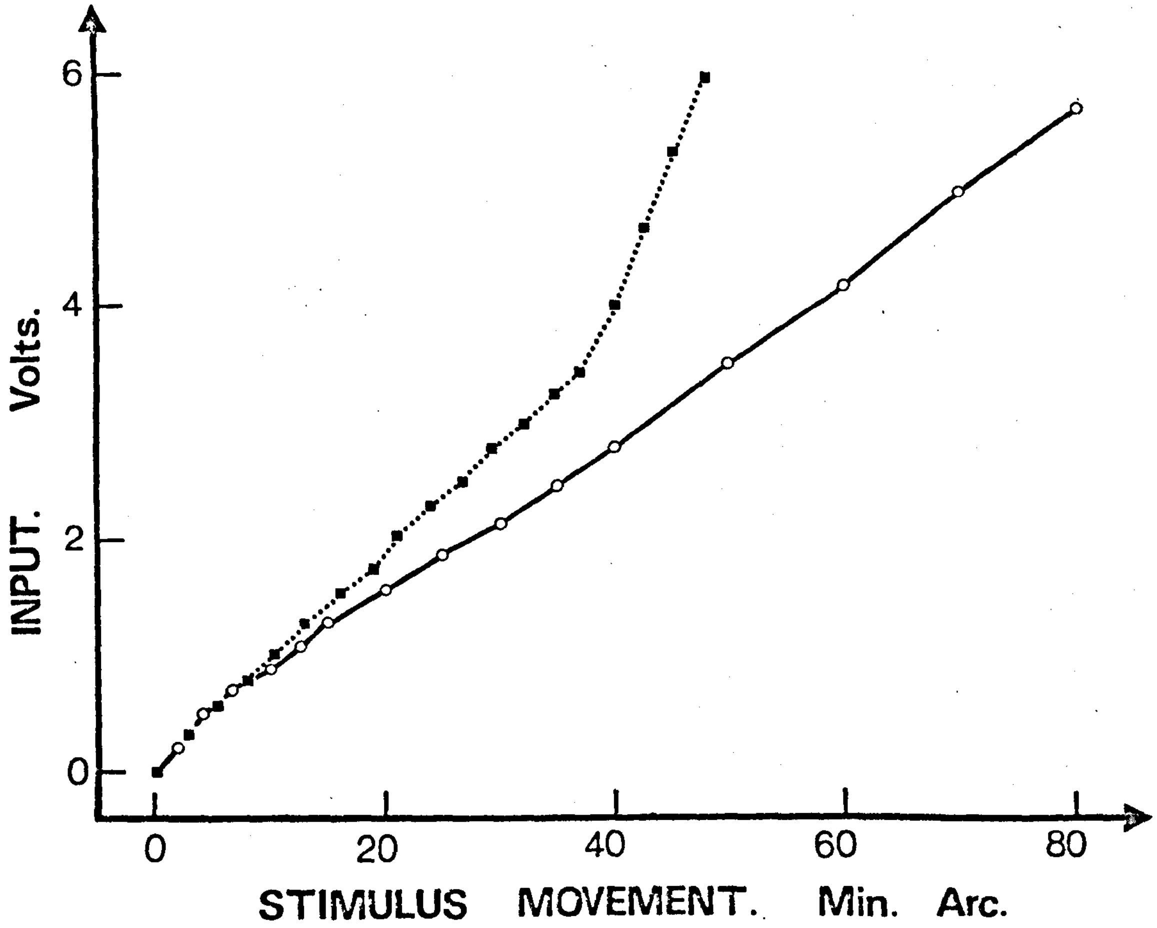
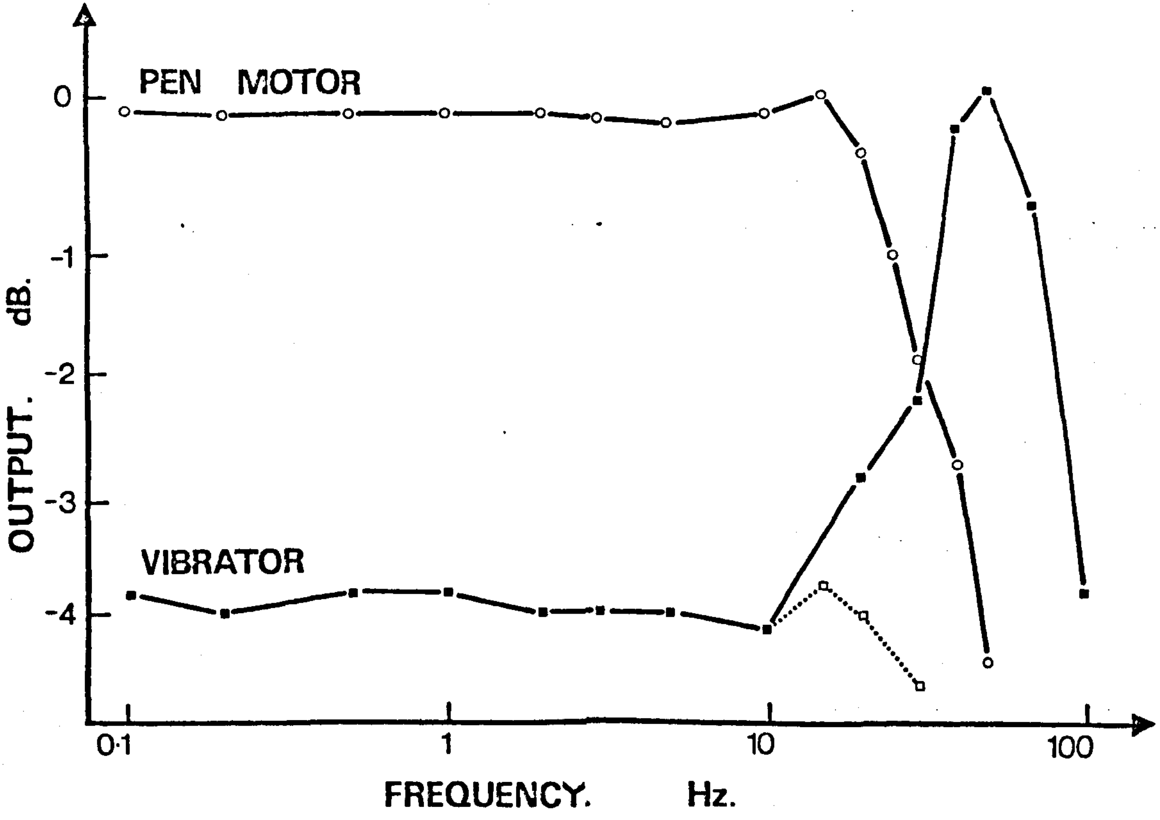


Figure 6. Calibration. Stimulus movement versus input voltage to a vibration generator (filled squares) or a pen motor (open circles). Both axes are linear.

<u>Figure 7</u>. Calibration. Frequency response curves for a vibration generator (filled squares) and a pen motor (open circles). The response of a vibration generator when a 100Hz. low- pass filter is inserted before the power amplifier is also shown (open squares). Ordinates are linear, abscissae are logarithmic.


PEN MOTOR
VIBRATOR
OUTPUT. dB.
0
-1
-2
-3
-4
FREQUENCY. Hz.
0·1
1
10
100

these sinewave outputs can be converted to squarewaves by means of two sinewave to squarewave converters (S). The sinewave to squarewave converters are 741 OPA operational amplifiers connected without feedback, and they act as amplifiers with voltage gains of approximately 100dB..

2:1:6. Calibrations.

Fig. 6 shows the change in stimulus position caused by a steady D.C. voltage applied to a vibrator (filled squares) or to a pen motor (open circles). The change in stimulus position was measured by means of a photocell (see Fig. 4), and the D.C. voltage was measured by a Model 8 Avometer. It is clear that the change in stimulus position was a linear function of the input voltage up to about 40 min. arc for the vibrator, and up to at least 80 min. arc for the pen motor. This was true for all the vibrators and pen motors used.

Fig. 7 shows the sinusoidal frequency response curves for a vibrator (filled squares) and a pen motor (open circles). The output was the peak to peak change in stimulus position measured by means of a photocell. For all curves the 0dB. level corresponds to 20 min. arc peak to peak change in stimulus position.

The results for the pen motor apply to its use in Apparatus 2 (see Section 2:1:2). It can be seen that the frequency response was flat (to within about ± 0.5dB.) to about 10Hz. and then dropped off steeply. Insertion of the 100Hz. low-pass filter before the power amplifier had no effect on this response.

The results for the vibrator apply to its use in both Apparatus 1 and Apparatus 3 (the graph in fact shows the results under Apparatus 3 conditions). Without the 100Hz. low-pass filter inserted before the power amplifier, the frequency response was flat (to within ± 0.5dB.) up to about 10Hz.; between 10Hz. and 100Hz.

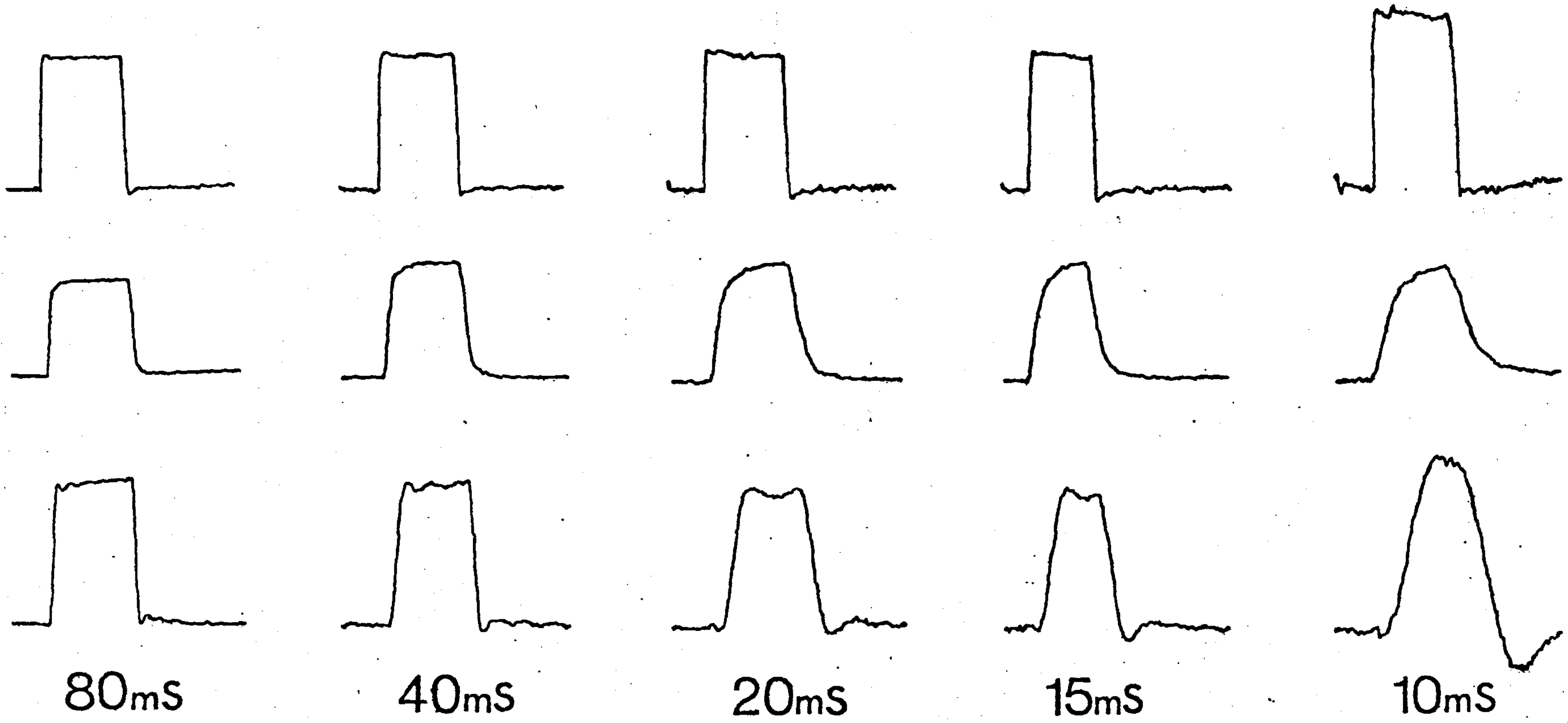


Figure 8. Calibration. Transient response of a vibration generator. Upper - signal generator output; middle - power amplifier output; lower - stimulus movement (as measured by a photocell). Each plot is the sum of 100 pulses averaged on a Data Retrieval Computer.

there was a +4dB. peak (caused by mechanical resonance); above 100Hz. the response dropped off very steeply (not shown). Insertion of the 100Hz. low-pass filter before the power amplifier removed the peak, making the frequency response flat (to within ± 0.5dB.) up to 30Hz. (open squares) and -6dB. at 100Hz. (not shown).

Fig. 8 shows the transient response of a vibrator as used in Apparatus 3, with a 100Hz. low-pass filter inserted before the power amplifier. The top row of curves show the output of the Wavetek signal generator. The middle row of curves show the output from the power amplifier (i.e. the input to the vibrator). The bottom row of curves show the movement of the stimulus measured by means of a photocell (see Fig. 4). The curves show that rectangular pulses down to 15 milliseconds duration were quite reasonably reproduced by the vibrator. The 20 millisecond pulse waveform shows the response to be expected from a 25Hz. squarewave, and it was concluded that squarewave stimulation up to this frequency could be performed with this apparatus.

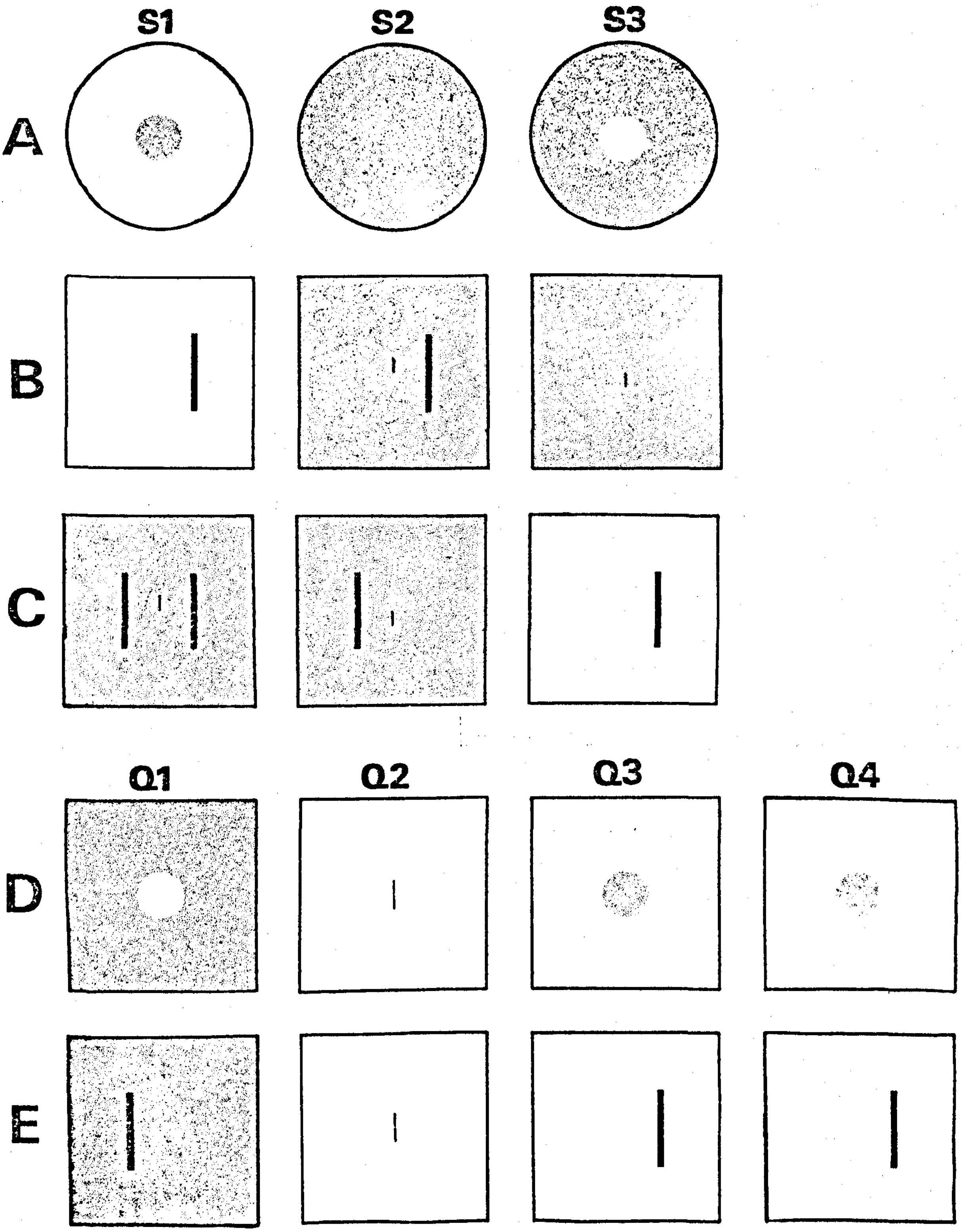


Figure 9. Stimulus transparencies. (a) Stimulus 1, used in apparatus 1; (b) Stimulus 2, used in apparatus 1; (c) Stimulus 3, used in apparatus 2; (d) Stimulus 4, used in apparatus 3; (e) Stimulus 5, used in apparatus 3. S1,S2,S3,Q1,Q2,Q3,Q4 - stimulus transparency labels referring to Figs. 1 - 3.

2:2. Stimuli.

All the stimuli were black and white transparencies, photographically produced on "Kodalith Ortho Film Type 3", an extremely high contrast negative film. A negligible amount of light was transmitted through the black parts of the stimulus transparencies. Less than 10% of the light was absorbed by the transparent parts of the stimulus transparencies. The luminance of the transparent parts of the stimulus transparencies was 110cd/m^2.

2:2:1. Stimulus 1 - Random Dot; Circular Surround.

The three stimulus transparencies which, when fused, made up Stimulus 1 are shown in Fig. 9A. Stimulus 1 was only used with Apparatus 1.

Stimulus transparency S1 was a 6.5cm. diameter transparent circle in the centre of which there was a 3.3cm. diameter circular area of irregularly-scattered black dots.

Stimulus transparency S2 was a 6.5cm. diameter circular area of irregularly-scattered black dots. The dots in the central 3.3cm. area were identical to the dots of transparency S1.

Stimulus transparency S3 was a 6.5cm. diameter circular area of irregularly-scattered black dots. The central 3.2cm. area was devoid of dots. The dots surrounding the transparent central area were identical to the dots in the corresponding area of transparency S2.

Stimulus transparency S2 was viewed by the right eye alone, and transparencies S1 and S3 were viewed by the left eye alone.

In all three transparencies the dots were of approximately 0.02cm. diameter and made up some 1% of the total area.

Since the transparencies were located 75cm. from the subject, 1cm. on the transparencies corresponded to a visual angle of 0.76 degrees of arc. The transparencies thus subtended some 5° with the central area some 2.5° in diameter.

2:2:2. Stimulus 2 - Single Moving Bar.

The three stimulus transparencies which, when fused, made up Stimulus 2 are shown in Fig. 9B. Stimulus 2 was only used with Apparatus 1.

Stimulus transparency S1 was a 6.5cm. square transparent area. There was a black bar 2.6cm. high and 0.15cm. wide situated so that the centre of the bar was 1.3cm. to the right of the centre of the square.

Stimulus transparency S2 was a 6.5cm. square area of irregularly-scattered black dots. There was a black bar 2.6cm. high and 0.15cm. wide situated so that the centre of the bar was 1.3cm. to the right of the centre of the square. There was a black nonius line 0.3cm. high and 0.02cm. wide situated so that the bottom of the nonius line was at the centre of the square.

Stimulus transparency S3 was a 6.5cm. square area of irregularly-scattered black dots. These dots were identical to the dots of transparency S2. There was a black nonius line 0.3cm. high and 0.02cm. wide situated so that the top of the nonius line was at the centre of the square.

Stimulus transparency S2 was viewed by the right eye alone, and transparencies S1 and S3 were viewed by the left eye alone.

In transparencies S2 and S3 the dots were of approximately 0.02cm. diameter and made up some 1% of the total area.

Since the transparencies were located 75cm. from the subject, 1cm. on the transparencies corresponded to a visual angle of 0.76 degrees of arc. The transparencies thus subtended some 5° with the black bars being 2° by $7'$ and the nonius lines being $15'$ by $1'$. The black bars were 1° to the right of the nonius lines.

2:2:3. Stimulus 3 - Single Moving Bar with Comparison Bar.

The three stimulus transparencies which, when fused, made up Stimulus 3 are shown in Fig. 9C. Stimulus 3 was only used with Apparatus 2.

Stimulus transparency S1 was a 5.5cm. square area of irregularly-scattered black dots. There were two black bars 2.2cm. high and 0.13cm. wide situated so that the centres of the bars were 1.1cm. to the left and right of the centre of the square. There was a black nonius line 0.3cm. high and 0.02cm. wide situated so that the bottom of the nonius line was at the centre of the square.

Stimulus transparency S2 was a 5.5cm. square area of irregularly-scattered black dots. These dots were identical to the dots of transparency S1. There was a black bar 2.2cm. high and 0.13cm. wide situated so that the centre of the bar was 1.1cm. to the left of the centre of the square. There was a black nonius line 0.3cm. high and 0.02cm. wide situated so that the top of the nonius line was at the centre of the square.

Stimulus transparency S3 was a 5.5cm. square transparent area. There was a black bar 2.2cm. high and 0.13cm. wide situated so that the centre of the bar was 1.1cm. to the right of the centre of the square.

Stimulus transparency S1 was viewed by the left eye alone, and transparencies S2 and S3 were viewed by the right eye alone.

In transparencies S1 and S2 the dots were of approximately 0.02cm. diameter and made up some 1% of the total area.

Since the transparencies were located 63cm. from the subject, 1cm. on the transparencies corresponded to a visual angle of 0.91 degrees of arc. The transparencies thus subtended some 5° with the black bars being 2° by 7' and the nonius lines being 15' by 1'. The black bars were 1° to the left and right of the nonius lines.

2:2:4. Stimulus 4 - Random Dot; Square Surround.

The four stimulus transparencies which, when fused, made up Stimulus 4 are shown in Fig. 9D. Stimulus 4 was only used with Apparatus 3.

Stimulus transparency Q1 was a 5.5cm. square area of irregularly-scattered black dots, in the centre of which there was a 2.1cm. diameter circular area devoid of dots.

Stimulus transparency Q2 was a 5.5cm. square transparent area. Two black nonius lines 0.3cm. high and 0.02cm. wide were situated, one immediately above the other, at the centre of the square.

Stimulus transparencies Q3 and Q4 were identical and consisted of a 5.5cm. square transparent area in the centre of which was a 2.3cm. diameter circular area of irregularly-scattered black dots.

Stimulus transparencies Q1 and Q2 were viewed by both eyes. Transparency Q3 was viewed by the left eye alone and transparency Q4 was viewed by the right eye alone.

In transparencies Q1, Q3 and Q4 the dots were of approximately 0.02cm. diameter and made up some 10% of the total area.

Since the transparencies were located 63cm. from the subject, 1cm. on the transparencies corresponded to a visual angle of 0.91 degrees of arc. The transparencies thus subtended some 5° with the central area some 2° in diameter. The nonius lines were each 15' by 1'.

2:2:5. Stimulus 5 - Two Moving Black Bars.

The four stimulus transparencies which, when fused, made up Stimulus 5 are shown in Fig. 9E. Stimulus 5 was only used with Apparatus 3.

Stimulus transparency Q1 was a 5.5cm. square area of irregularly-scattered black dots. There was a black bar 2.2cm. high and 0.13cm. wide situated so that the centre of the bar was 1.1cm. to the left of the centre of the square.

Stimulus transparency Q2 was a 5.5cm. square transparent area. Two black nonius lines 0.3cm. high and 0.02cm. wide were situated, one immediately above the other, at the centre of the square.

Stimulus transparencies Q3 and Q4 were identical, and consisted of a 5.5cm. square transparent area. There was a black bar 2.2cm. high and 0.13cm. wide situated so that the centre of the bar was 1.1cm. to the right of the centre of the square.

Stimulus transparencies Q1 and Q2 were viewed by both eyes. Transparency Q3 was viewed by the left eye alone and transparency Q4 was viewed by the right eye alone.

In transpar~~a~~ency Q1 the dots were of approximately 0.02cm. diameter and made up some 10% of the total area.

Since the transpar~~a~~encies were located 63cm. from the subject, 1cm. on the transpar~~a~~encies corresponded to a visual angle of 0.91 degrees of arc. The transpar~~a~~encies thus subtended some 5° with the black bars being 2° by 7′ and the noni~~b~~us lines being 15′ by 1′. The black bars appeared 1° to the left and right of the noni~~b~~us lines.

2:2:6. Stimulus 6 - Two Moving White Bars.

Stimulus 6, which is not illustrated, consisted of four transpar~~a~~encies which were the negatives of the four transpar~~a~~encies of Stimulus 5. Thus, the bars, the noni~~b~~us lines and the dots were white (transpar~~a~~ent) instead of black.

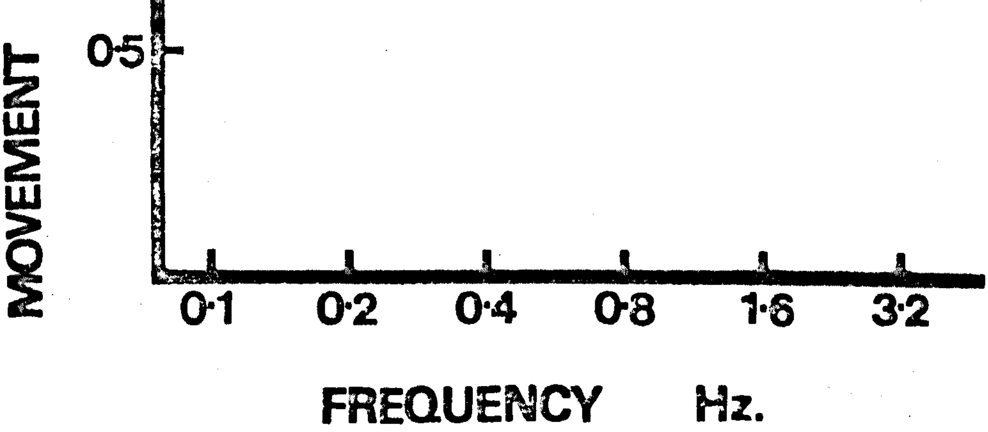
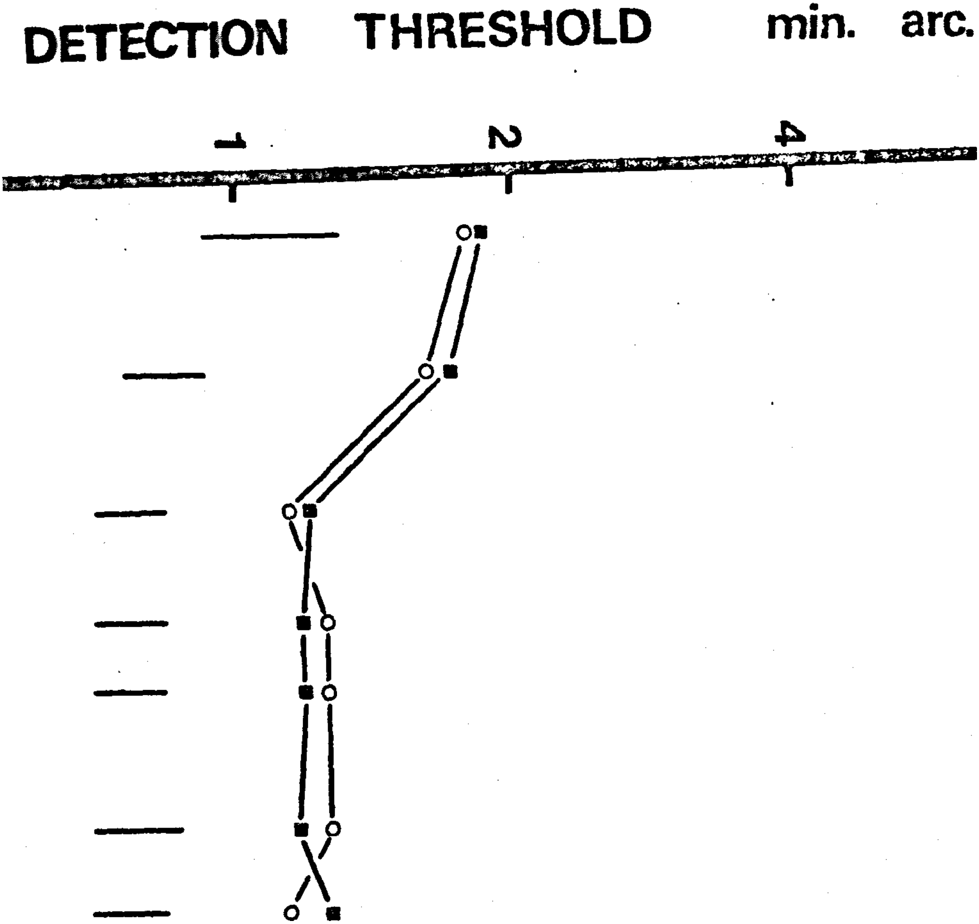


Figure 10. Comparison between two experimental methods. Movement detection threshold (mins. arc) versus frequency (Hz.) for the method of adjustments (filled squares, each point is the average of 10 settings) and the two forced-choice method (open circles, each point is the average of 5 trials). The vertical lines represent ± 1 standard deviation of the method of adjustments. The subject was J.B.. Both axes are logarithmic.


DETECTION THRESHOLD min. arc.
1
2
4

2:3. Methods.

2:3:1. Comparison of Methods.

Two different psychophysical methods were used to gather data for the results reported in this thesis. These methods were the method of adjustments and the two-alternative forced-choice method. In the method of adjustments the subject altered a control which varied the amplitude of stimulus oscillation until either he could just detect motion of the stimulus irrespective of whether the motion was from side to side or to and fro in depth (threshold experiments) or he considered that the stimulus moved to the same depth as a comparison stimulus (matched depth experiments). In the two forced-choice method the subject passively watched the stimulus and was asked either whether he saw the stimulus move (threshold experiments) or whether he considered that the stimulus moved to a point in front of or behind a comparison stimulus (matched depth experiments)

Fig. 10 shows the result of a comparison between the two methods. It is a plot of movement detection threshold <u>versus</u> frequency of sinusoidal oscillation with zero static disparity. The subject was J.B.. The conditions of the experiment were the same as for Fig. 13 in Section 3:1:3.

The filled squares show the mean of 10 settings using the method of adjustments. The open circles show the mean of 5 settings using the two forced-choice method. The vertical lines represent ±1 standard deviation of the method of adjustments results and are displaced downwards for the sake of clarity.

It is clear that the two methods give similar results.

In all experiments of Chapters 3 and 4 where a comparison between the two methods was made, similar results were observed. In the adaptation experiments of Chapter 5, a difference between the two methods was observed. This is discussed in Section 5:2.

Since all the subjects preferred the method of adjustments, the two forced-choice method was only used to confirm the results found by using the method of adjustments.

2:3:2. Method 1 - Threshold.

The subject used both eyes to view a fixation plane defined by a random dot pattern. The purpose of the dots was to assist the subject to maintain a steady convergence. For most experiments, two nonius lines were present; one was seen by the left eye alone, the other was seen by the right eye alone. When the two eyes were correctly converged on the fixation plane the two nonius lines appeared as a single vertical line. If convergence altered, the two nonius lines separated.

The central circular area of random dots (Stimulus 1) or the right hand black bar (Stimulus 2 and Stimulus 3) could be set at a constant retinal disparity (static disparity) so that it (the target) appeared to stand out in depth either in front of, on, or behind the fixation plane. The retinal disparity of the target was then oscillated about this mean static disparity causing the target to appear to oscillate to and fro in depth about a constant mean position.

In the experiments of Section 3:1:2 a different stimulus arrangement was used (Stimulus 5). Here the subject viewed four separate stimulus patterns in binocular fusion. Each eye viewed three of the patterns. The subjective appearance of the binocularly-fused pattern was a 5° by 5° plane of randomly-scattered black dots each of which subtended a visual angle of 1′. Two vertical black nonius lines were located in the centre of this plane to assist fixation (see above). Vertical black bars that subtended 2° by 7′ were located 1° to the left and right of the nonius lines. The distance in depth between the fixation plane and either bar could be preset by adjusting the mean disparity of the bar. This was done before each experiment. The right hand bar could be oscillated in depth by oscillating stimulus transparencies Q3 and Q4 (Fig. 9E) in antiphase (stereoscopic stimulation). This bar could also be oscillated from side to side by oscillating stimulus transparencies Q3 and Q4 in phase (binocular movement stimulation). The amplitudes of oscillation of Q3 and Q4 were equal. The only difference between stereoscopic and binocular movement stimulation was in the relative timing (phase) of the left and right retinal image movements. Monocular movement stimulation could be produced by occluding either eye.

It should be noted that, in fact, all parts of the actual stimulus, at all times, remained at a constant distance from the subject, since the illusion of movement in depth was produced entirely by altering retinal disparity.

In the binocular movement control experiments of Sections 3:1:1 and 3:1:4 it was convenient to generate the sideways moving stimulus in a different way than in the other experiments. In these experiments the moving target, viewed by both eyes, was physically oscillated from side to side by a vibrator. This target could be positioned (+) 5 min. arc in front of the fixation plane, (-) 5 min. arc behind the fixation plane, or very close to the fixation plane (less than 1 min. arc away). The other stimulus transparencies were occluded.

It should be emphasised that the stimuli seen by the right eye, in all the experiments, appeared identical. Only the left eye's stimuli differed.

A complete description of actual and apparent stimulus movements which occurred when using this method is given in Appendix 1.

The subject was instructed to alter the amplitude of the target's oscillations until he could just detect movement in depth. This setting was then repeated over a range of stimulus oscillation frequencies such that at least 5 settings were made at each oscillation frequency. By altering the calibration of the subject's control potentiometer, the experimenter was able to ensure that the position of the potentiometer gave no clue to the stimulus oscillation amplitude.

The target was then reset to a different static disparity and the experiment was repeated.

Both sinewave and squarewave stimulus oscillations were used.

All the subjects were given practise in the required psychophysical judgements before recordings were made. The subjects were allowed frequent rests during an experimental session.

2:3:3. Method 2 - Matched Depth.

This method was the same as Method 1 except that matched depth settings were made by the subject.

Only Stimulus 3 was used with this method.

The left hand black bar was always stationary. It could be adjusted so as to appear to stand out in depth either in front of, or behind the fixation plane, at some constant depth of up to 20 min. arc. The right hand black bar was then centred on the fixation plane and oscillated to and fro in depth.

The subject was instructed to alter the amplitude of oscillation of the right hand bar until he judged that the depth traversed by the oscillating bar in front of (or behind) the fixation plane equalled the depth of the static left hand bar in front of (or behind) the fixation plane. This setting was then repeated over the same range of stimulus conditions as described for Method 1.

2:3:4. Method 3 - Pulsed Movement.

The subject viewed four separate stimulus patterns in binocular fusion.(Stimulus 6). Each eye viewed three of the patterns. The subjective appearance of the binocularly-fused pattern was a 5° by 5° plane of randomly-scattered white dots, each of which subtended a visual angle of 1 min. arc. Two vertical, white, nonius lines were located in the centre of this plane to assist fixation (see Section 2:3:2). Vertical white bars that subtended 2° by 7′ were located 1° to the left and right of the nonius lines. The apparent distance in depth between the fixation plane and either bar could be preset by adjusting the mean disparity of the bar. This was done before each experiment. The left hand bar always remained stationary. During an experiment the right hand bar moved as follows.

After a variable interval (ranging from ½ second to 5 seconds) the bar appeared to move suddenly (risetime 1 millisecond) towards or away from the subject. After a preset interval (7 milliseconds to 1 second) the bar returned to its original position. The cycle was then repeated. In the sideways movement control experiments the right hand bar moved from side to side instead of towards or away from the subject, otherwise the cycle was similar.

It should be noted that, in fact, all parts of the actual stimulus, at all times, remained at a constant distance from the subject, since the illusion of movement in depth was produced entirely by altering retinal disparity.

A complete description of actual and apparent stimulus movements which occurred when using this method is given in Appendix 1.

The subject used a potentiometer to control the distance through which the right hand bar moved. The experimenter randomly varied the calibration of this potentiometer during the experiments so that the position of the potentiometer gave no clue as to the distance through which the bar moved.

In the threshold experiments the subject adjusted the potentiometer until he could just see the right hand bar move.

In the matched depth experiments the subject adjusted the potentiometer until he judged that the position to which the right hand bar appeared to move was at the same distance as the left hand bar from the fixation plane.

All the subjects were given practise in the required psychophysical judgements before recordings were made. The subjects were allowed frequent rests during an experimental session.

2:3:5. Method 4 - ΔF.

The subject viewed four separate stimulus patterns in binocular fusion (Stimulus 4). Each eye viewed three of the patterns. The subjective appearance of the binocularly-fused pattern was a 5° by 5° plane of randomly-scattered black dots. Two, vertical, black, nonius lines were located in the centre of this plane to assist fixation (see Section 2:3:2). The central 2° diameter circular area was made up of two identical areas of random dots (the targets), one seen by each eye. Both left and right targets could be moved from side to side independently of each other.

A complete description of actual and apparent stimulus movements is given in Appendix 4 for sinewave oscillations, and in Appendix 5 for squarewave oscillations.

For sinewave oscillations, the apparent movement of the stimulus can be summarized by saying that the fused target appeared to move from side to side at a frequency of FHz., the movement in depth waxing and waning at a frequency of ΔFHz.. The subject could easily discriminate between the two types of movement and was able to judge depth thresholds without contamination from sideways movement (see Section 4:1). In fact, considerable sideways motion of the fused target was often apparent at the threshold of depth perception. With squarewave stimulation, the fused target appeared to move irregularly, backwards and forwards in depth, between three different positions.

The subject used a potentiometer to control the oscillation amplitude of the targets' movements. The experimenter randomly varied the calibration of this potentiometer during the experiments so that the position of the potentiometer gave no clue as to the targets' oscillation amplitudes.

The subject was instructed to alter the oscillation amplitude until he could just see movement in depth. The subject was instructed to ignore all sideways movements of the fused target.

Throughout any one experiment, ΔF was held constant and the threshold for movement in depth was measured as a function of F. Sinewave and squarewave oscillations were used in separate experiments.

All the subjects were given considerable practise in the required psychophysical judgements before recordings were made. The subjects were allowed frequent rests during an experimental session.

2:3:6. Method 5 - Recovery from Adaptation.

The subject viewed four separate stimulus patterns in binocular fusion (Stimulus 4). Each eye viewed three of the patterns. The subjective appearance of the binocularly-fused pattern was a 5° by 5° plane of randomly-scattered black dots. Two, vertical, black, nonius lines were located in the centre of this plane to assist fixation (see Section 2:3:2). The central 2° diameter circular area was made up of two identical areas of random dots (the targets), one seen by each eye. Both left and right targets could be moved from side to side independently of each other.

A complete description of actual and apparent stimulus movements is given in Appendix 2. The apparent movement of the stimulus can be summarized by saying that the effect of altering the relative amplitudes of oscillation of the left and right targets (i.e. the L/R ratio) was to change the direction of the line along which the target appeared to oscillate in three-dimensional space.

The L/R ratio was set by adjusting the relative amplitudes of the signals fed to the vibrators. The subject, by adjusting a control potentiometer, could vary the absolute amplitude of the retinal image movements without altering the L/R ratio. In order to record the timecourse of recovery after adaptation, the subject's control potentiometer was ganged to another potentiometer which gave a voltage proportional to the amplitude through which retinal disparity oscillated. This voltage was recorded on a chart recorder (see Section 2:1:4).

The subject gazed for 15 minutes at the adapting stimulus. The stimulus oscillated at 0.8Hz. with a fixed L/R ratio and was initially well above threshold. Immediately the adaptation stimulus ceased, the subject adjusted the control potentiometer until he could "just see" movement in depth. The subject then adjusted the control potentiometer until he could "just not see" movement in depth. The subject continued alternating "just seeing" with "just not seeing" measurements until he was asked to stop by the experimenter (after about 3 minutes). In this way a record was made of the subject's short-term recovery from adaptation.

The subject returned to the apparatus at intervals (from 2 minutes to 30 minutes), and repeated the "just seeing" and "just not seeing" measurements for periods of about 30 seconds. The average oscillation amplitude set by the subject in these 30 second readings was used as a measure of the sensitivity to movement in depth of the subject, after varying durations of recovery from adaptation. In this way, a record was made of the subject's long-term recovery from adaptation.

Only one adaptation/recovery sequence was made by any one subject on any one day.

All the subjects were given practise in the procedure to be followed, before recordings were made.

2:3:7. Method 6 - Adaptation.

This method was the same as Method 5 up to the point at which adaptation ceased.

Immediately after adaptation ~~ceased~~, the L/R ratio was changed and the subject adjusted the control potentiometer until he could just see movement in depth. No more than 10 seconds were allowed for this adjustment for reasons discussed in Section 5:2. The L/R ratio was then changed back to the adapting L/R ratio * for a further 30 seconds adaptation. After this, the L/R ratio was changed to another value and a further threshold setting was made. This alternation of 10 seconds test L/R ratio, 30 seconds adaptation, was continued throughout the experiment which lasted some 45 minutes in all (15 minutes adaptation and 30 minutes testing). On request the subject was allowed more than one 10 second period per threshold setting.

Only one adapting L/R ratio was used with any one subject on any one day.

Unadapted thresholds were measured, over the range of L/R ratios, in a separate experiment,on a different day to adapted thresholds.

---

* The stimulus oscillation amplitude was constant for all periods of adaptation.

The experimenter randomly varied the calibration of the subject's control potentiometer during the experiments, so that the position of the potentiometer gave no clue as to the stimulus oscillation amplitude.

The experiments were repeated using the two forced-choice method. Here the subjects were allowed 5 seconds viewing of the test stimulus (alternating with 30 second adaptation periods), and had to say whether they could see the stimulus move in depth. Otherwise, the experimental procedure was similar.

All the subjects were given considerable practise in the experimental procedure before recordings were made.

Experiments recording the effect of the phase difference between the left and right eyes' stimulus oscillations (Section 5:4) were performed in exactly the same manner as is described above except that phase difference was the experimental variable instead of L/R ratio.

2:4. Subjects.

In all, 6 subjects were used in the experiments reported in this thesis.

Subject K.B. (the author), male, aged 24 years at the conclusion of the experiments, had uncorrected vision of 6/6.

Subject D.R., male, aged 38 years at the conclusion of the experiments, had vision corrected to 6/6.

The binocular vision of both these subjects was tested at the Moorfields Eye Hospital. Both subjects had appreciable stereopsis. K.B. had 2D exophoria at 6m. and 12D at ⅓m. with rapid recovery, and was able to converge 25D for ½m. target before suppression. D.R. had 1° divergence R/L 1D with good recovery at ⅓m., no deviation at 6m. and was able to converge 18D at ½m. before losing fusion, and 20D with SU slides.

Subject J.B.,* female, aged 25 years at the conclusion of the experiments, had vision corrected by contact micro-corneal lenses to 6/6.

Subject M.Y., female, aged 24 years at the conclusion of the experiments, had uncorrected vision of 6/6.

Subject J.J., male, aged 24 years at the conclusion of the experiments, had vision corrected to 6/6.

Subject S.H., male, aged 23 years at the conclusion of the experiments, had uncorrected vision of 6/6.

The binocular vision of the above four subjects was not tested. However, none had any difficulty in maintaining fusion of the stimuli and in seeing the stimuli move in depth. *

---

* But see Section 3:4:2 for subject J.B!s results for uncrossed disparities.

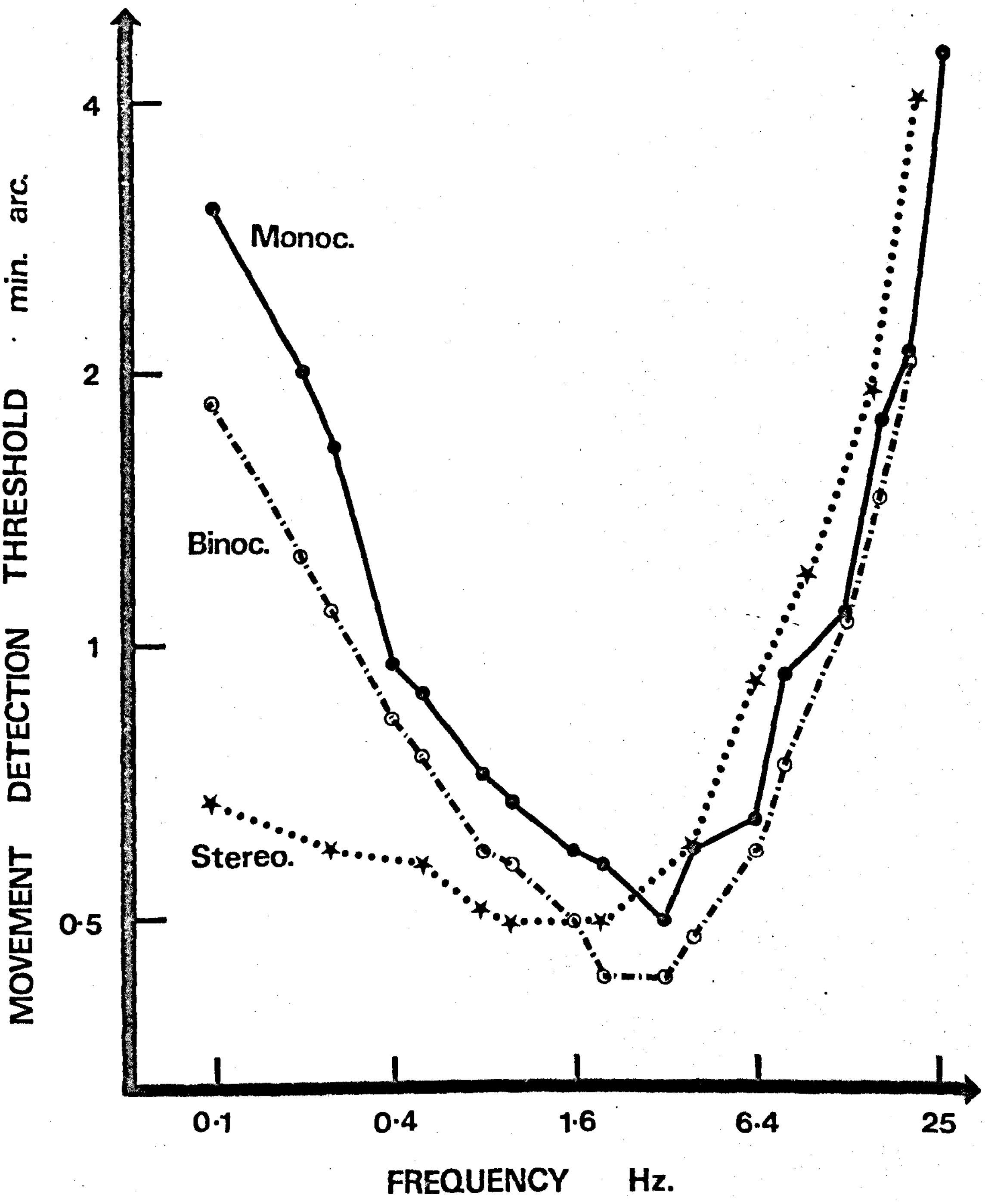


Figure 11. The effect of frequency upon movement detection threshold for sinewave stimulation. The continuous line shows monocular stimulation; the chain line shows binocular stimulation and the dotted line shows monocular-stereoscopic stimulation. The subject was K.B.. Both axes are logarithmic.

3/ SOME DYNAMIC FEATURES OF DEPTH PERCEPTION.

3:1. Sinewave Movement Threshold.

In this section, the statement of a "significant difference" implies that the probability that there is no significant difference is less than .05 using the Student's "t" test of significance. This test was used since there was no evidence that the distribution of the means was not normal (see Fisher, 1963).

The attenuation in dB/octave (where 20dB equals 10 times) of any curve is the slope of the regression line, fitted by the method of least squares, through the experimental points. These experimental points include either those whose abscissae are less than 0.6Hz. (low-frequency attenuation) or those whose abscissae are greater than 5.0Hz. (high-frequency attenuation). The turnover frequency (F_t) is the frequency where the regression line intersects the horizontal line through the threshold minimum.

3:1:1. The Effect of Frequency.

Fig. 11 illustrates the effect, upon the movement detection threshold, of varying the stimulation frequency under three viewing conditions for subject K.B.. There was a rapid threshold increase for the monocular-stereoscopic condition* (using Apparatus 1, Stimulus 1 and Method 1) as the stimulation frequency exceeded some 5Hz. (F_t equals 4.0Hz., attenuation equals 5.8dB/octave). There was also a slight, but significant, threshold increase for stimulation frequencies below 0.5Hz. (F_t equals 1.0Hz., attenuation equals 0.46dB/octave).

---

* See Appendix 1, p 188.

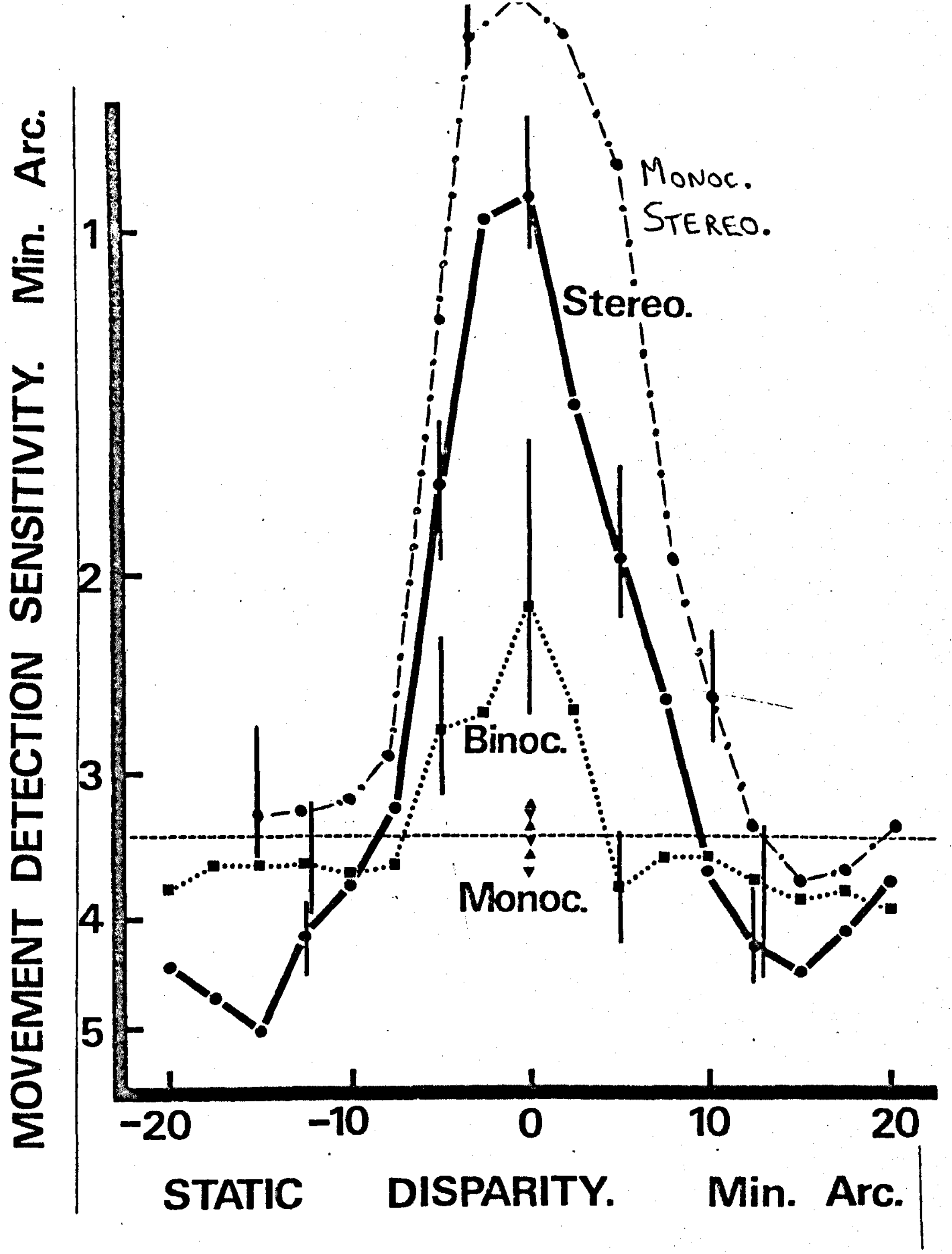


Figure 12. The effect of static disparity upon movement detection sensitivity ~~threshold~~ for sinewave stimulation. The plane of fixation is zero disparity; positive (crossed) disparities are in front of the fixation plane and negative (uncrossed) disparities are behind the fixation plane. The chain line shows monocular-stereoscopic stimulation; the continuous line shows stereoscopic stimulation; the dotted line shows binocular stimulation. For monocular stimulation, either the right (upright triangles) or left (inverted triangles) eye was occluded. The horizontal dashed line is drawn through the mean monocular threshold. The oscillation frequency was 0.1Hz.. Each point is the mean of 5 settings. The vertical bars show the total range of settings. Subject K.B.. Ordinates are logarithmic, abscissae are linear.

For the binocular movement condition (using Apparatus 1, Stimulus 1 and Method 1), the threshold increase at high frequencies (F_t equals 4.7Hz., attenuation equals 6.2dB/octave) was almost identical to the increase under monocular-stereoscopic conditions. However, for low stimulation frequencies, the threshold increased as the stimulation frequency decreased (F_t equals 1.1Hz., attenuation equals 3.5dB/octave).

Monocular movement stimulation (using Apparatus 1, Stimulus 1 and Method 1) also gave similar results at high frequencies. Threshold rapidly increased, however, as the stimulation frequency decreased (F_t equals 1.1Hz., attenuation equals 4.3dB/octave).

All three stimulation conditions were clearly equivalent for frequencies greater than about 5Hz.; binocular movement and monocular-stereoscopic conditions were clearly equivalent above about 1Hz.. All three subjects reported that, for frequencies in excess of 1Hz., suprathreshold stereoscopic stimuli hardly appeared to move in depth even when large sideways movements were visible. These findings suggest that stereoscopic movement threshold curves do not describe dynamic properties of depth perception at frequencies in excess of 1Hz..

No significant differences were observed when a bar pattern (Stimulus 2) replaced the random-dot pattern.

These findings were confirmed in two further subjects (D.R. and J.B.). In both these subjects the monocular-stereoscopic low-frequency attenuation was more pronounced than with subject K.B. (see Section 3:1:5 below).

3:1:2. The Effect of Static Disparity.

Fig. 12 illustrates the effect of varying the mean stimulus distance from the fixation plane (static disparity) upon the movement detection sensitivity under four viewing conditions for subject K.B.. Apparatus 3, Stimulus 5 and Method 1 were used. There was no change in movement sensitivity with static disparity for monocular stimulation (either the left or the right eye occluded). This was to be expected since altering the static disparity would merely move the image of the stimulus towards or away from the image of the fixation point on the retina. The small distance involved (±20 min. arc) would make a change in movement sensitivity unlikely.

Movement sensitivity was greatest at zero static disparity for binocular stimulation (zero phase shift between the oscillations in either eye), and decreased as static disparity was increased. Binocular movement sensitivity was significantly greater than monocular movement sensitivity for static disparities in the range +2.5 to -5 min. arc. There was no significant difference outside this range.

range.

Movement sensitivity was greatest at zero static disparity for stereoscopic stimulation (180° phase shift between the oscillations in either eye) , and rapidly decreased as static disparity was increased. Stereoscopic movement sensitivity was significantly greater than both monocular and binocular movement sensitivity for static disparities in the range +7.5 to -6.5 min. arc. Stereoscopic movement sensitivity was significantly less than monocular movement sensitivity for static disparities in the range -13 to -20 min. arc and at +15 min. arc. Stereoscopic movement sensitivity was significantly less than binocular movement sensitivity,only in the range -14 to -18 min. arc.

Movement sensitivity for monocular-stereoscopic stimulation (stationary stimulus in the left eye) was greatest at zero static disparity and decreased as static disparity was increased. Monocular-stereoscopic movement sensitivity was significantly greater than stereoscopic movement sensitivity over the ranges +7 to -5 min. arc and -11 to -15 min. arc; and was significantly greater than binocular and monocular movement sensitivities over the range +8 to -7 min. arc.

Sensitivity to movement in depth was significantly greater than sensitivity to sideways movement only within a narrow range (approximately ±7 min. arc) of static disparities from the fixation point. The movement sensitivities for all four stimulation conditions were equal at static disparities of ±10 min. arc. Stereoscopic movement sensitivity was slightly less than both monocular and binocular movement sensitivities for static disparities greater than 13 min. arc. This latter point was confirmed by subjective reports that, at -15 min. arc static disparity, a subthreshold stereoscopic stimulus movement could be detected if one eye was closed. Monocular-stereoscopic movement sensitivity was greater than binocular stereoscopic movement sensitivity, which in turn was greater than binocular sideways movement sensitivity, over approximately the same range (±7 min. arc) of static disparities.

Monocular-stereoscopic movement sensitivity was approximately twice (2.3 times) the stereoscopic movement sensitivity, which in turn was approximately twice (2.3 times) the binocular movement sensitivity, which in turn was approximately twice (1.6 times) the monocular movement sensitivity, in the fixation plane (zero static disparity).

All four curves are symmetrical about the fixation plane (to within 2.5 min. arc) which suggests that the subject had only a small fixation error.

These findings were confirmed in a second subject (J.B.), and the major finding, that there is a narrow region of high stereoscopic sensitivity around the fixation plane, was confirmed in a further two subjects (D.R. and J.J.).

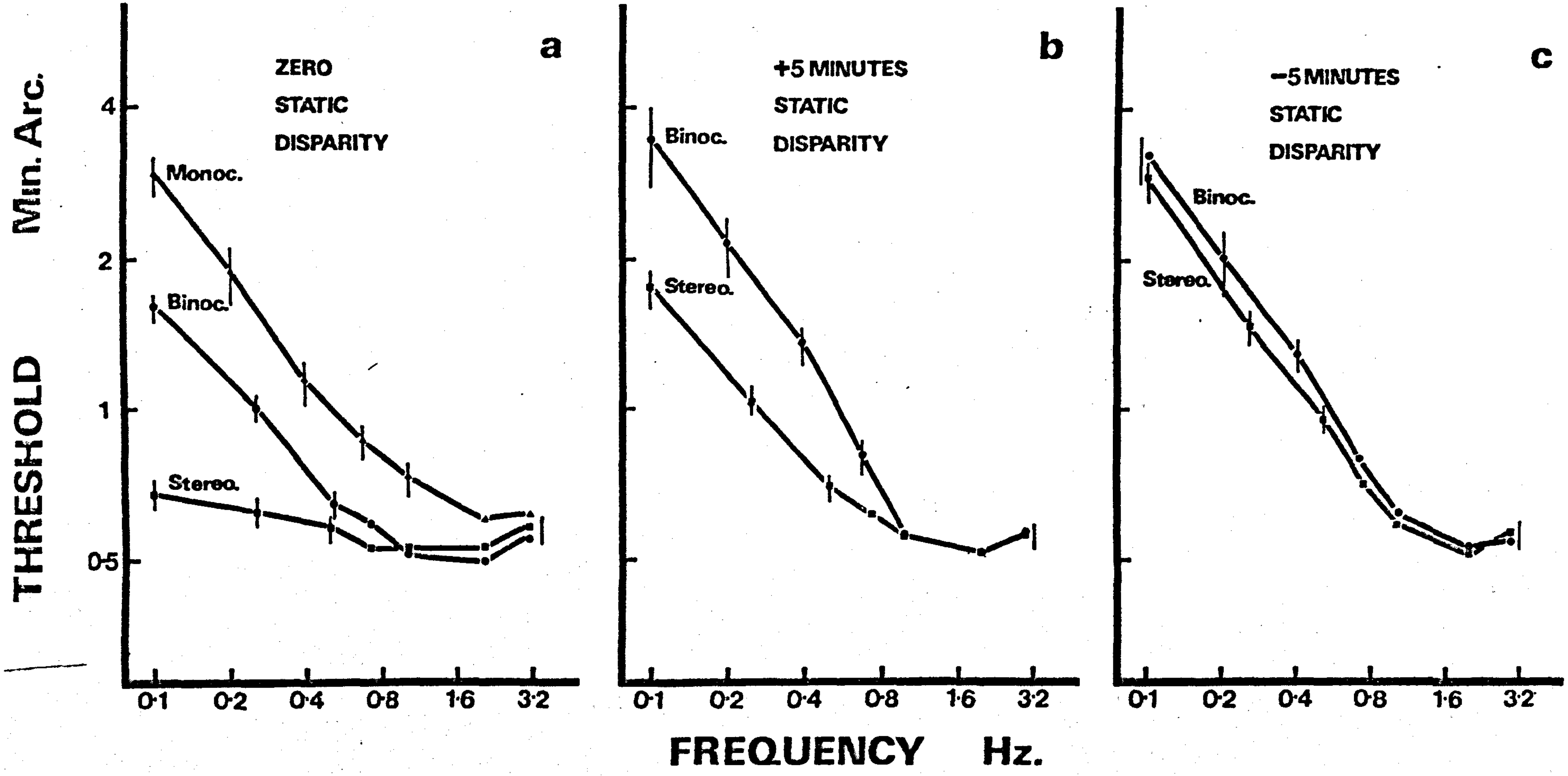


Figure 13. The effect of static disparity upon low-frequency movement detection thresholds. The curves shown are for monocular (triangles), binocular (circles) and monocular-stereoscopic (squares) stimulation conditions. A - zero static disparity; B - +5 min. arc static disparity (crossed); C - −5 min. arc static disparity (uncrossed). Vertical lines show ±1 standard deviation. Subject K.B.. Both axes are logarithmic.

3:1:3. The Effect of Static Disparity on Low-Frequency Thresholds.

Fig. 13 illustrates the effect of varying the stimulation frequency upon the movement detection threshold for three values of static disparity (0, +5 and -5 min. arc) for subject K.B.. The threshold increase at low frequencies, for monocular stimulation, (using Apparatus 1 , Stimulus 2 and Method 1) did not vary as the static disparity was altered (F_t equals 1.0Hz., attenuation equals 4.0dB/octave). The reason for this has already been given in Section 3:1:2.

The threshold increase at low frequencies, for binocular stimulation (using Apparatus 1, Stimulus 2 and Method 1) at zero static disparity (F_t equals 0.9Hz., attenuation equals 3.3dB/octave) was less rapid than the increase at +5 min. arc static disparity (F_t equals 1.6Hz., attenuation equals 4.0dB/octave). The increase at -5 min. arc (F_t equals 1.2Hz., attenuation equals 4.2dB/octave) did not significantly differ from the increase at +5 min. arc, and neither differed significantly from the increase for monocular stimulation (Fig. 13).

The threshold increase at low frequencies, for monocular-stereoscopic stimulation, (using Apparatus 1, Stimulus 2 and Method 1) was only slight at zero static disparity (F_t equals 1.3Hz., attenuation equals 0.56dB/octave). The increase was more rapid at +5 min. arc static disparity (F_t equals 0.9Hz., attenuation equals 3.4dB/octave) and still more rapid at -5 min.arc static disparity (F_t equals 1.0Hz., attenuation equals 4.1dB/octave). The increase at -5 min. arc did not differ significantly from the increase for monocular stimulation (compare Fig. 13a with Fig. 13c).

These findings suggest that the threshold for movement in depth became less contaminated with sideways movements of the

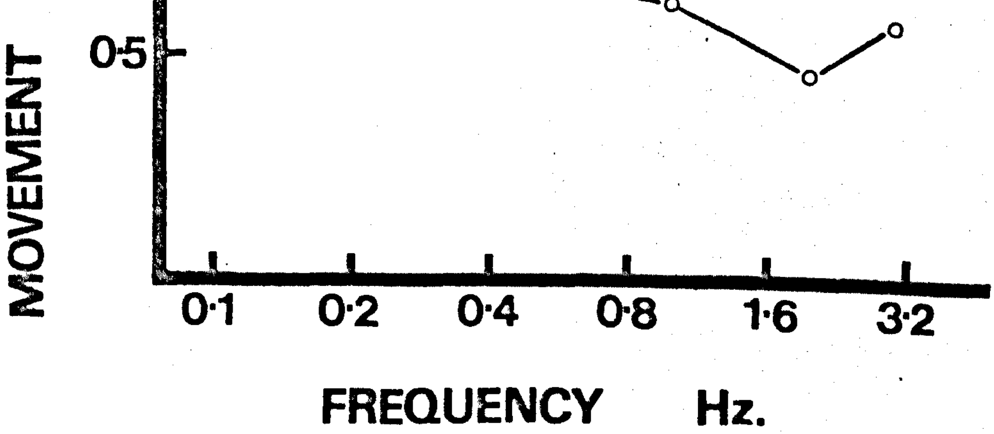
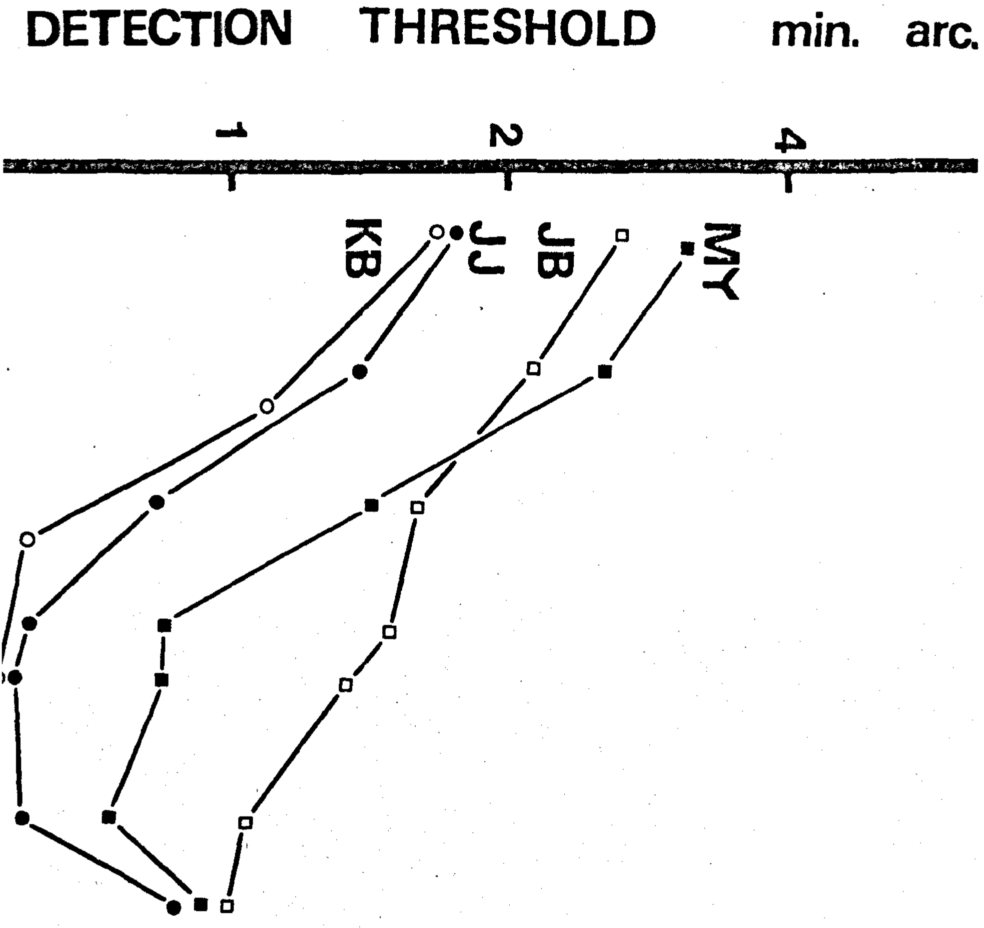


Figure 14. Control for inter-subject variability. The monocular-stereoscopic movement detection threshold versus sinewave stimulation frequency at +5 min. arc static disparity is shown for four subjects, K.B., J.J., J.B. and M.Y.. Each point is the mean of 10 settings. Both axes are logarithmic.


DETECTION THRESHOLD min. arc.
1
2
4
MY
JB
JJ
KB

retinal images, the lower the frequency of stimulation, and the smaller the static disparity. This adds further support to the findings of Sections 3:1:1 and 3:1:2. Fig. 13 also shows that the effects of lowering the stimulus frequency and increasing the static disparity combine to increase the threshold for stereoscopic stimulation.

The results shown in Fig. 13 for a stimulation frequency of 0.1Hz. may be directly compared with the equivalent results shown in Fig. 12, since the experiments were almost identical; the only change was the use of different stimulus patterns. The results shown in Fig. 13a and Fig. 11 may be compared for the same reason.

These findings were confirmed on three additional subjects (J.B., J.J. and M.Y.).

3:1:4. Controls.

The following control experiments were performed to determine the reliability of the experimental results. Quantitatively, there were large inter-subject differences even though, qualitatively, the results were similar. No averaging across subjects was therefore performed.

Fig. 14 gives an example of inter-subject variability and is a plot of monocular-stereoscopic movement detection threshold versus sinewave stimulation frequency. The stimulus had a static disparity of +5 min. arc and the results for four subjects are shown. The shapes of the curves were similar even though the absolute threshold values varied widely.

The results of a single subject tested on different occasions showed quantitative differences. These differences were usually small enough to be neglected, and data from different occasions were combined unless it is otherwise stated.

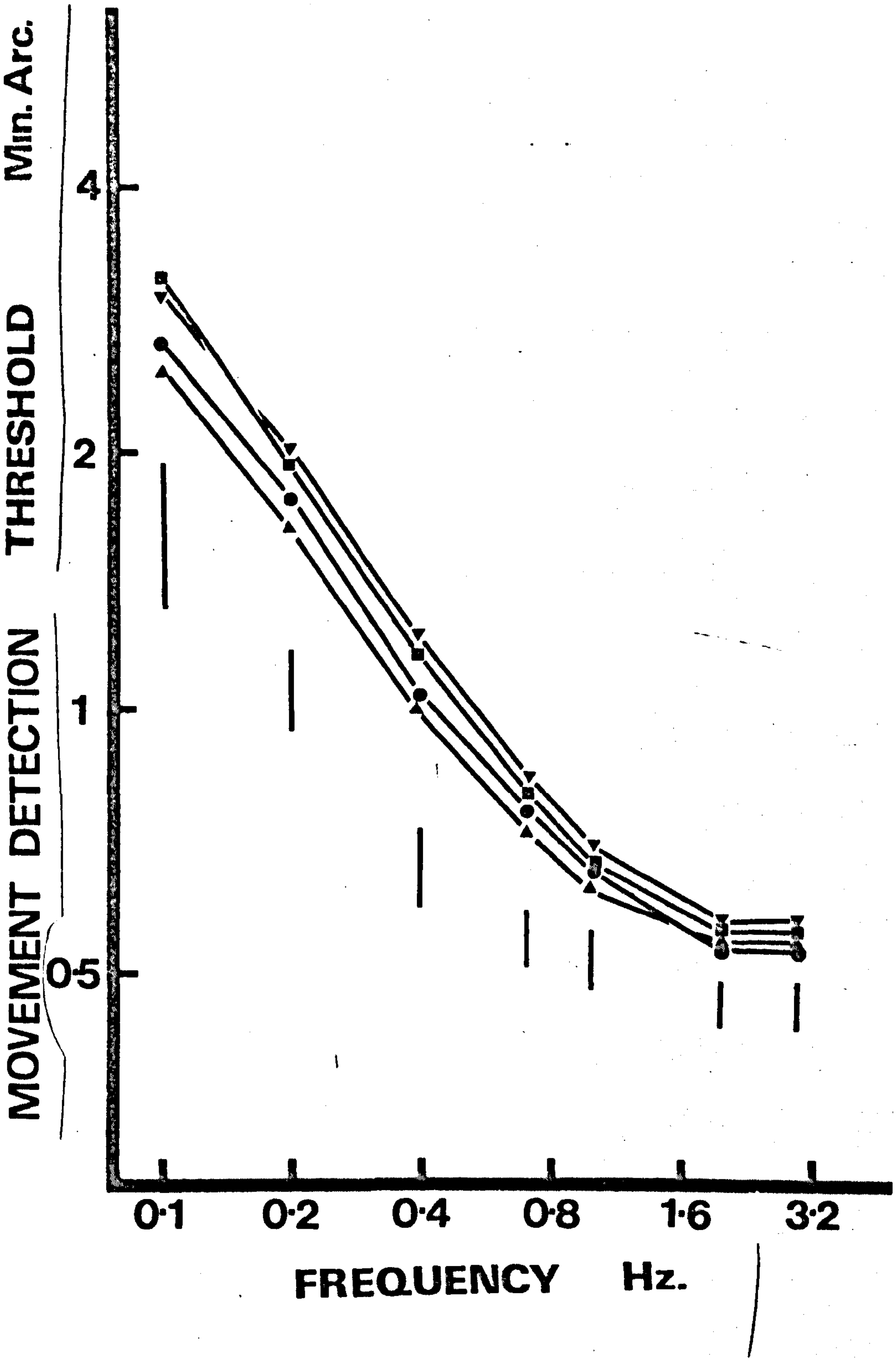


Figure 15. Control for intra-subject variability. The monocular movement detection threshold *versus* sinewave stimulation frequency at zero static disparity is shown for subject K.B.. The results of experiments performed on four different days are shown. The vertical bars represent ±1 standard deviation calculated from the results of a single experiment, and are vertically displaced for the sake of clarity. Each point is the mean of ten settings. Both axes are logarithmic.

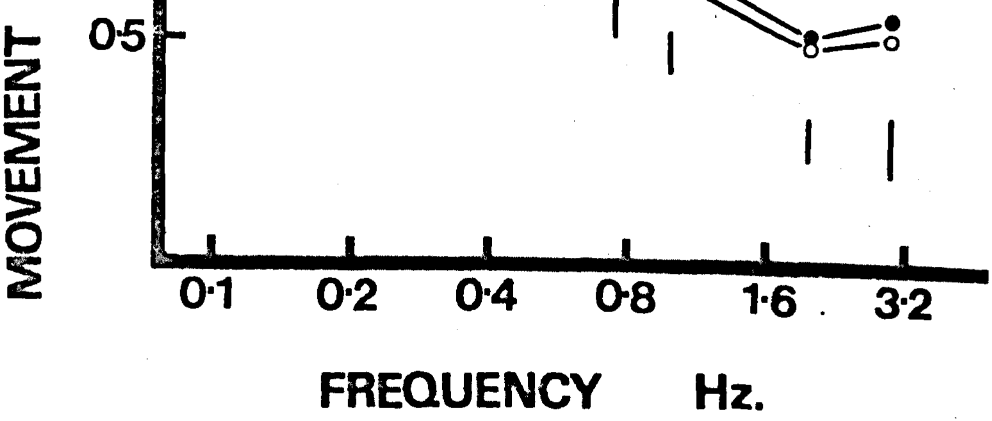
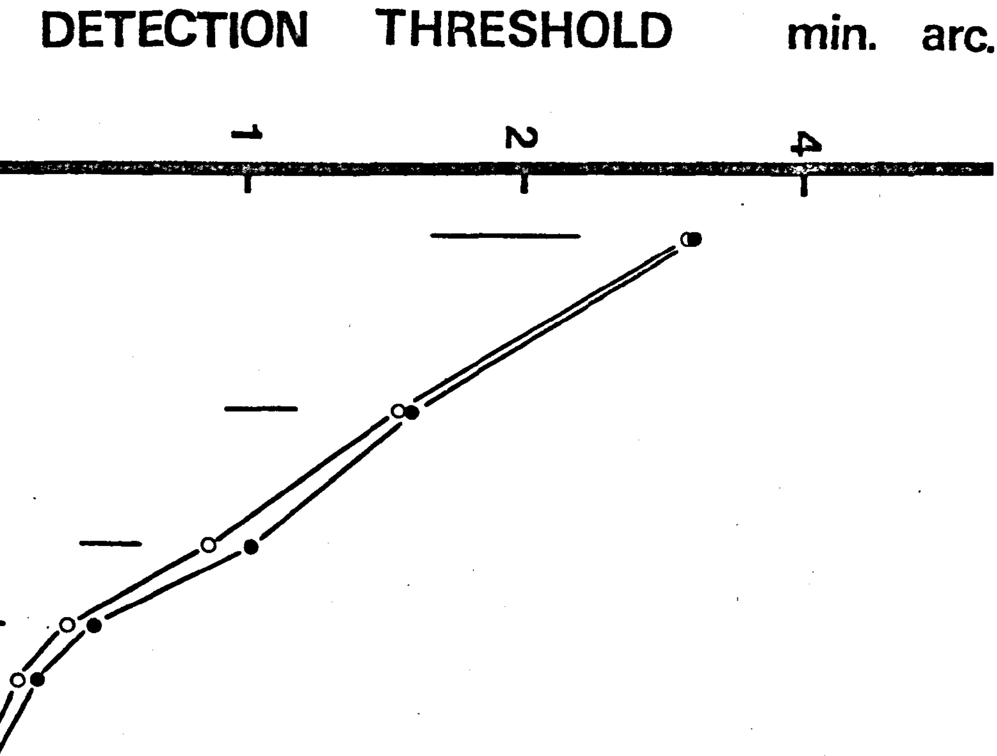


Figure 16. Control for sequence effects. The monocular-stereoscopic movement detection threshold *versus* sinewave stimulation frequency at -5 min. arc static disparity is shown for subject K.B.. The results for increasing frequency (open circles) and for decreasing frequency (filled circles) are shown. The vertical bars represent ±1 standard deviation calculated from the results for increasing frequency and are vertically displaced for the sake of clarity. Each point is the mean of 10 settings. Both axes are logarithmic.


DETECTION THRESHOLD min. arc.
1
2
4

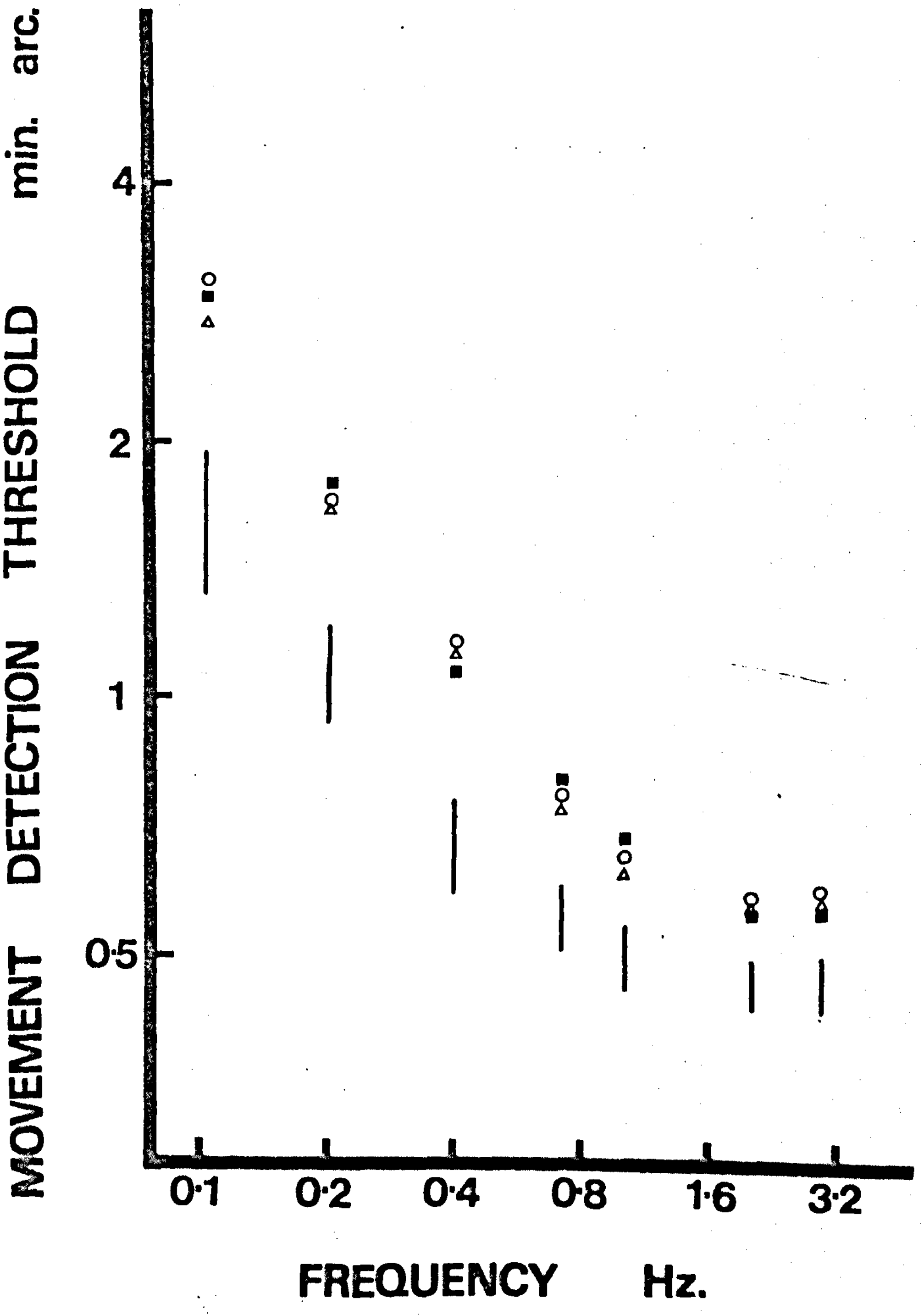


Figure 17. Monocular control experiments. The monocular movement detection threshold *versus* sinewave stimulation frequency at zero static disparity is shown for subject K.B.. The left eye either was occluded (squares); or viewed just the random-dot background seen by the right eye (triangles); or viewed the random-dot background seen by the right eye plus a horizontal bar (circles). The vertical bars represent ±1 standard deviation, calculated from the results for the occluded condition, and are displaced for the sake of clarity. Each point is the mean of 10 settings. Both axes are logarithmic.

Fig.15 gives examples of day-to-day intra-subject variability, and is a plot of monocular movement detection threshold <u>versus</u> sinewave stimulation frequency for subject K.B.. The results for four different experiments performed over a three-week period are shown. The vertical bars represent ±1 standard deviation calculated from the results of a single experiment, and are vertically displaced for the sake of clarity. The differences between the curves were insignificant.

The independent variable was usually varied systematically except where otherwise stated. Trials were always carried out in pairs; one increasing, the other decreasing the independent variable. The increasing and decreasing trials never differed significantly.

Fig. 16, which illustrates this lack of any order effect , is a plot of monocular-stereoscopic movement detection threshold <u>versus</u> sinewave stimulation frequency for subject K.B.. The vertical bars represent ±1 standard deviation calculated from the results for increasing frequency, and are vertically displaced for the sake of clarity. The differences between the curves were insignificant.

The monocular control experiments were carried out in one of three ways. Either the left eye was occluded (N.B. only the right eye's stimulus moved) or it viewed a pattern uncorrelated with the pattern viewed by the right eye. This uncorrelated pattern was either just the random-dot background viewed by the right eye, or the random-dot background viewed by the right eye plus a horizontal bar. When viewing these uncorrelated patterns, retinal rivalry occurred and the subject could only make threshold settings when his (right) eye could see the moving stimulus.

Fig. 17 is a plot of monocular movement detection threshold <u>versus</u> sinewave stimulation frequency for subject K.B.. It illustrates that the experimental results were the same for each of the three stimulus conditions. The vertical bars represent ±1 standard deviation calculated from the results for the occluded condition, and are vertically displaced for the sake of clarity.

3:1:5. Discussion.

In psychophysical experiments there are at least two cues that a subject can use to detect movements in depth since changes in disparity _must_ be accompanied by movements of one or both retinal images. The experimenter cannot be certain which cue (or cues) the subject was using in a depth threshold experiment. Therefore, the subject was instructed to adjust the control potentiometer until "the stimulus only just appeared to _move_", and to ignore "the direction of motion of the stimulus, whether it moved to and fro in depth or from side to side". It should be noted that, with stereoscopic stimulation, both cues to movement were present, whereas, with binocular (or monocular) stimulation, the only cue was retinal image movement. Consequently, the data presented above relate to the _detection_ of movement, and do not involve any _discrimination_ as to the type of movement. The possibility that subjects might have been able to discriminate between stimuli where disparity changed (stereoscopic stimulation) and stimuli where there was no change in disparity (binocular and monocular stimulation) at threshold is left open (see Section 4:1).

The following evidence supports the assumption that the subjects maintained steady convergence during each threshold setting. Subjects fixated nonius lines located at the centre of the stimulus. The upper line was seen by the left eye only, and the lower line by the right eye only. When the subject fixated in the plane of the stimulus the nonius lines were seen as one continuous line. However, when convergence deviated, the lines separated. A separation of half the width of a line could be detected easily. This corresponded to an error in convergence of 0.5 min. arc. Convergence could be held accurate to within this limit for 5 to 20 seconds, sufficient for a threshold setting to be made. This constancy of convergence was aided greatly by the fact that the moving part of the stimulus pattern was displaced 1 degree to the side of the fixation point. It had been found previously, that if the moving stimulus passed through the fixation point, then it was virtually impossible to prevent vergence eye movement tracking of the stimulus. Displacing the moving part of the stimulus 1 degree to the side of the fixation point, however, reduced vergence eye movements (and other eye movements) to less than ±0.5 min. arc.

Additional evidence suggesting that fixation was accurate, is given in Section 3:1:2. This evidence is that movement sensitivity was symmetrical with respect to zero static disparity to within ±2.5 min. arc. This suggested that any error in fixation was less than 2.5 min. arc, possibly much less.

The results shown in Fig.11 and Fig.13 suggested that above 1Hz. disparity cues had no effect on a subject's ability to detect movement. The results shown in Fig.12 and Fig.13 suggested that only for mean disparities less than ±5 min. arc was movement detection sensitivity enhanced by changes in retinal disparity. Under these conditions, movements in depth should be more easily visible than sideways movements.

For stimuli with mean disparities greater than ±10 min. arc, disparity cues reduced movement sensitivity. Therefore, under these conditions, movements in depth should be less easily visible than sideways movements. This was confirmed by occluding one eye, while the subject was viewing (barely) subthreshold stereoscopic stimulus motion, whereupon movement became visible.

These results suggest an explanation to Tyler's (1971) recent finding that sensitivity to stereoscopic depth movement was <u>less</u> than sensitivity to monocular movement. His fixation controls were poor; the use of only a single stationary fixation line would not enable large (greater than 5 min. arc) fixation errors to be detected. Errors of this order of magnitude could easily have been responsible for his results. ~~This~~ The latter use of only a single fixation line would not enable vergence tracking movements to be detected either.

" Tyler (personal communication) states that in later experiments he controlled for possible vergence tracking within Panum's fusional region by using two stimulus bars whose simultaneous oscillations in depth were such that they always moved in opposite directions. When the oscillation frequency was less than 1Hz. he no longer found that stereoscopic sensitivity was lower than monocular sensitivity." - (Regan and Beverley, 1973A)

It was shown in Section 3:1:1, however, that disparity cues only affected movement detection for frequencies less than 1Hz.. This suggests that Tyler's results were due to vergence eye movements.

The slope of the low-frequency attenuation curve for -5 min. arc static disparity,was greater than the slope for +5 min. arc static disparity,which in turn was greater than the slope for zero static disparity. The threshold dynamic characteristics of the neural mechanisms that process disparity cannot be obtained by simply subtracting the binocular from the stereoscopic data since this would assume an (unproven) assumption of linearity. This assumption has some support from Section 3:1:3, where it was shown that the effects of static disparity and frequency added, more-or-less linearly,to produce a decrement in the detectability of stereoscopic movement. This "linearity" held only over a fairly narrow range of frequencies (below 1Hz.) and static disparities

(-10 to +10 min. arc), however, and does not conclusively prove linearity. The most that one can say is that the effect of frequency upon depth perception is different for crossed, uncrossed and zero disparities. This finding is consistent with Richards' (1970; 1971) hypothesis of three pools of disparity detectors responding respectively to crossed, uncrossed and near-zero disparities.

None of the above conclusions is affected by the inter-subject variability discussed in Section 3:1:4.

The slope of the low-frequency attenuation for zero static disparity was not always as low as for subject K.B. (Fig. 11 and Fig. 13). For the subjects tested, the slopes varied between 0.46 dB/octave and 1·8 dB/octave. The reason for this difference is not known. It could have been due to the amount of practise the subjects had had, or, more likely, it could have been due simply to real inter-subject variability. Whatever the reason, the only effect this variability had, was to alter the frequency at which the difference between the stereoscopic and the binocular movement detection curves became significant.

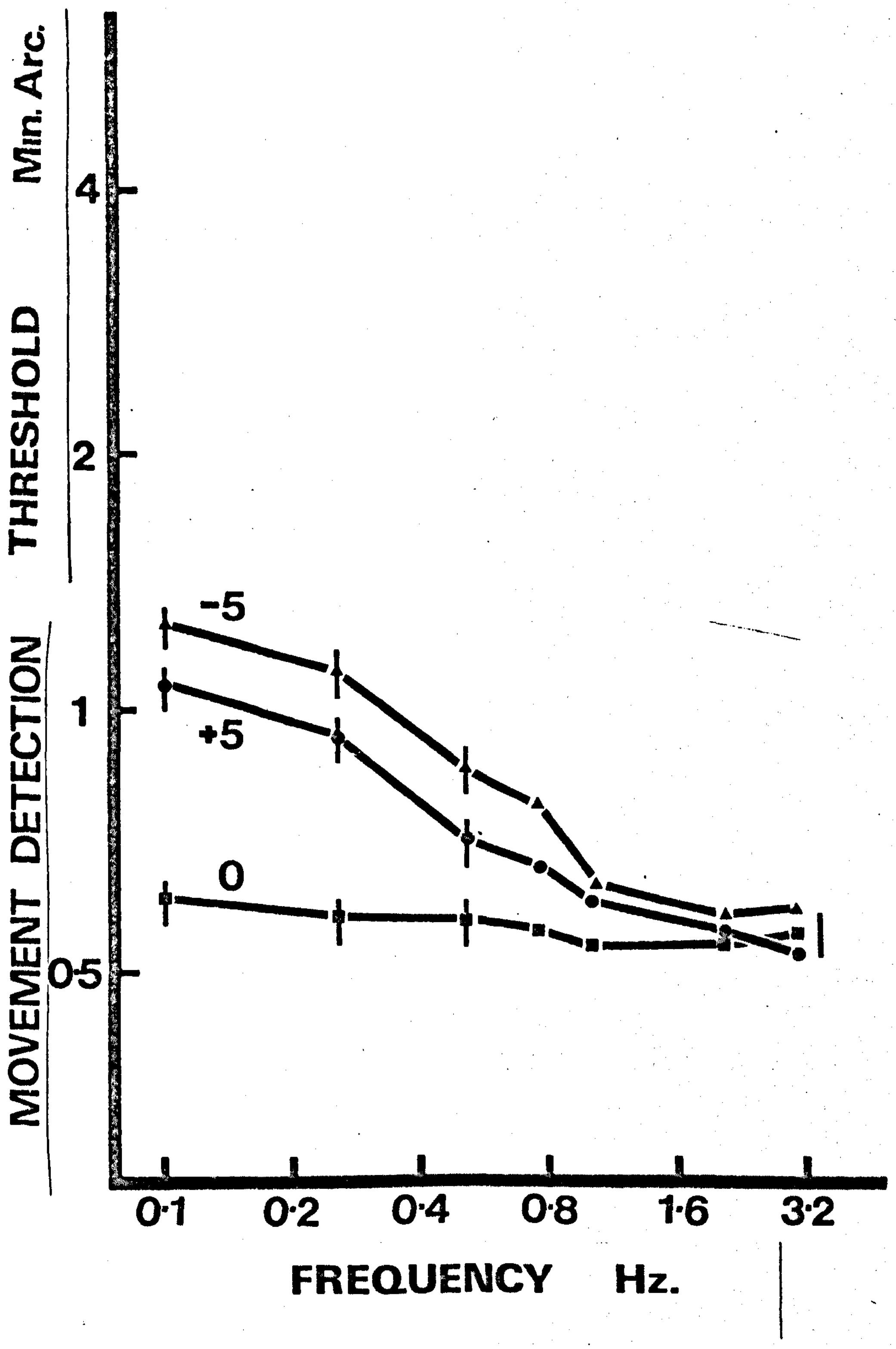


Figure 18. The effect of static disparity upon movement detection threshold for squarewave stimulation. The curves shown are for zero static disparity (squares), +5 min. arc static disparity (circles) and -5 min. arc static disparity (triangles). Vertical lines show ±1 standard deviation. Subject K.B.. Each point is the mean of 10 settings. Both axes are logarithmic.

3:2. Squarewave Movement Threshold.

In this section the statement of a "significant difference" means that the probability that there is no significant difference is less than .05 using the Student's "t" test of significance. This test was used since there was no evidence that the distribution of the means was not normal (see Fisher, 1963).

The attenuation in dB/octave (where 20dB equals 10 times) of any curve is the slope of the regression line, fitted by the method of least squares, through the experimental points whose abscissae are less than 0.6Hz.. The turnover frequency (F_t) is the frequency where the regression line intersects the horizontal line through the threshold minimum.

3:2:1. The Effect of Static Disparity on Low-Frequency Threshold.

Fig. 18 illustrates the effect of varying the stimulation frequency upon the movement detection threshold for three values of static disparity (0, +5 and -5 min. arc) for subject K.B.. There was no significant threshold increase at low frequencies for monocular-stereoscopic stimulation (using Apparatus 1, Stimulus 1 and Method 1) at zero static disparity. On the other hand, there was a marked threshold increase at +5 min. arc static disparity (F_t equals 1.9Hz., attenuation equals 1.4dB/octave) and also at -5 min. arc static disparity (F_t equals 3.2Hz., attenuation equals 1.4dB/octave) for low frequencies.

For frequencies above 2Hz. there was no significant difference between any of these curves. Neither was there any significant difference between the curves for sinewave and squarewave stimulation (not illustrated).

For low frequencies there was no significant difference between the threshold increases at +5 and -5 min. arc static disparity. Furthermore, there was no significant difference between the sinewave and squarewave curves for zero static disparity. However, for +5 and -5 min. arc static disparity the sinewave and squarewave curves differed markedly at low frequencies (compare Fig 13 a and b and Fig.18).

All four subjects reported that for frequencies in excess of 1Hz., stereoscopic stimuli which were only just above threshold, did not appear to move in depth although sideways movements were clearly visible. This result agreed with subjective reports for sinewave stimulation. However the subjective appearance of the stimulus changed dramatically when larger stimulus movements occurred (see Section 3:5:1).

Similar results were obtained when a bar pattern (Stimulus 2) replaced the random-dot pattern.

These results were confirmed in a second subject (M.Y.). However, for two further subjects (J.B. and J.J.) the +5, 0 and -5 min. arc static disparity curves were similar, as also were the sinewave and squarewave curves for zero static disparity (not illustrated, see Section 3:2:2 below).

3:2:2. Discussion.

For squarewave stimulation, as for sinewave stimulation, changes in retinal disparity had no effect upon movement detection sensitivity for frequencies in excess of 1Hz.. This adds additional support to the suggestion that threshold curves above 1Hz. did not describe a dynamic property of stereoscopic depth perception.

For frequencies below 1Hz., the low-frequency attenuation for squarewave stimulation was less than that for sinewave stimulation.

The results from Section 3:1:2 (Fig. 12) suggested that the movement sensitivity function was tuned with respect to static disparity. These two results suggest that for squarewave stimulation the tuning would be broader than for sinewave stimulation.

Two possible reasons for these effects are, firstly, that squarewaves can be thought of as being made up by superposition of several harmonically-related sinewaves (fundamental plus harmonics) and although the amplitudes of higher harmonics decrease progressively, even very low frequency squarewaves may have harmonics with appreciable amplitudes in the region of 1Hz.. The detection of low-frequency squarewave movement could thus be thought of as the detection of only those harmonics with frequencies near 1Hz.. A second and more likely reason lies in the abrupt nature of stimulus movements with squarewave stimulation. As frequency is decreased, the only change will be an increase in the time between movements. The movements themselves will remain the same, and hence their detectability should also (for zero static disparity). For extremely low frequencies, however, it will be impossible to maintain accurate fixation (the reason why the curves do not go below 0.1Hz.) so the detectability will probably change.

The suggested broadening of the movement sensitivity function ~~static disparity curves~~ could be the result of either of the above effects in conjunction with the sinewave movement sensitivity function (Fig. 12).

The similarity between the low-frequency attenuations for crossed and uncrossed disparities for squarewaves is consistent with Richards' (1972) results. The difference in the low-frequency attenuations for sinewave and squarewave stimulation is also consistent with Richards' (1972) results.

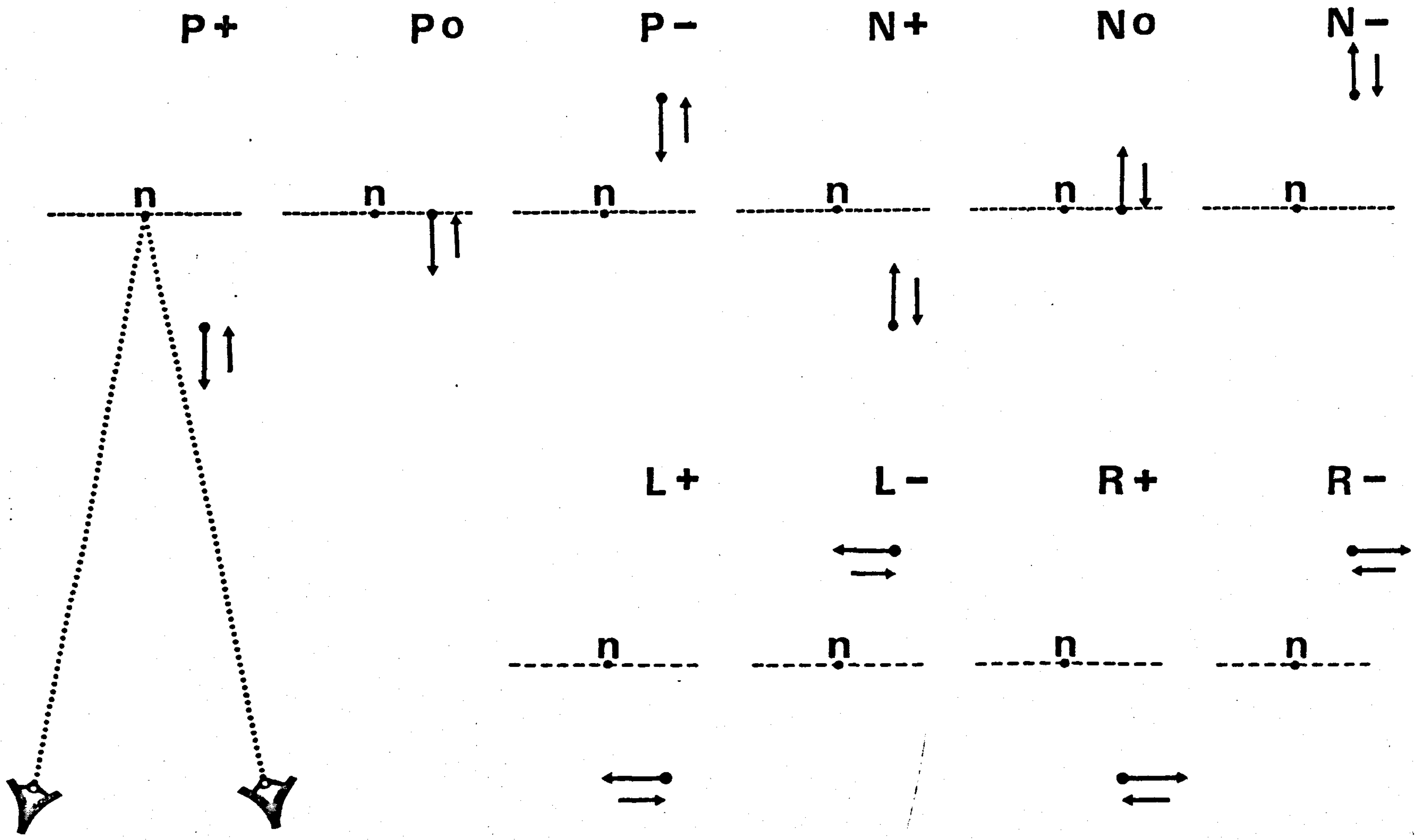
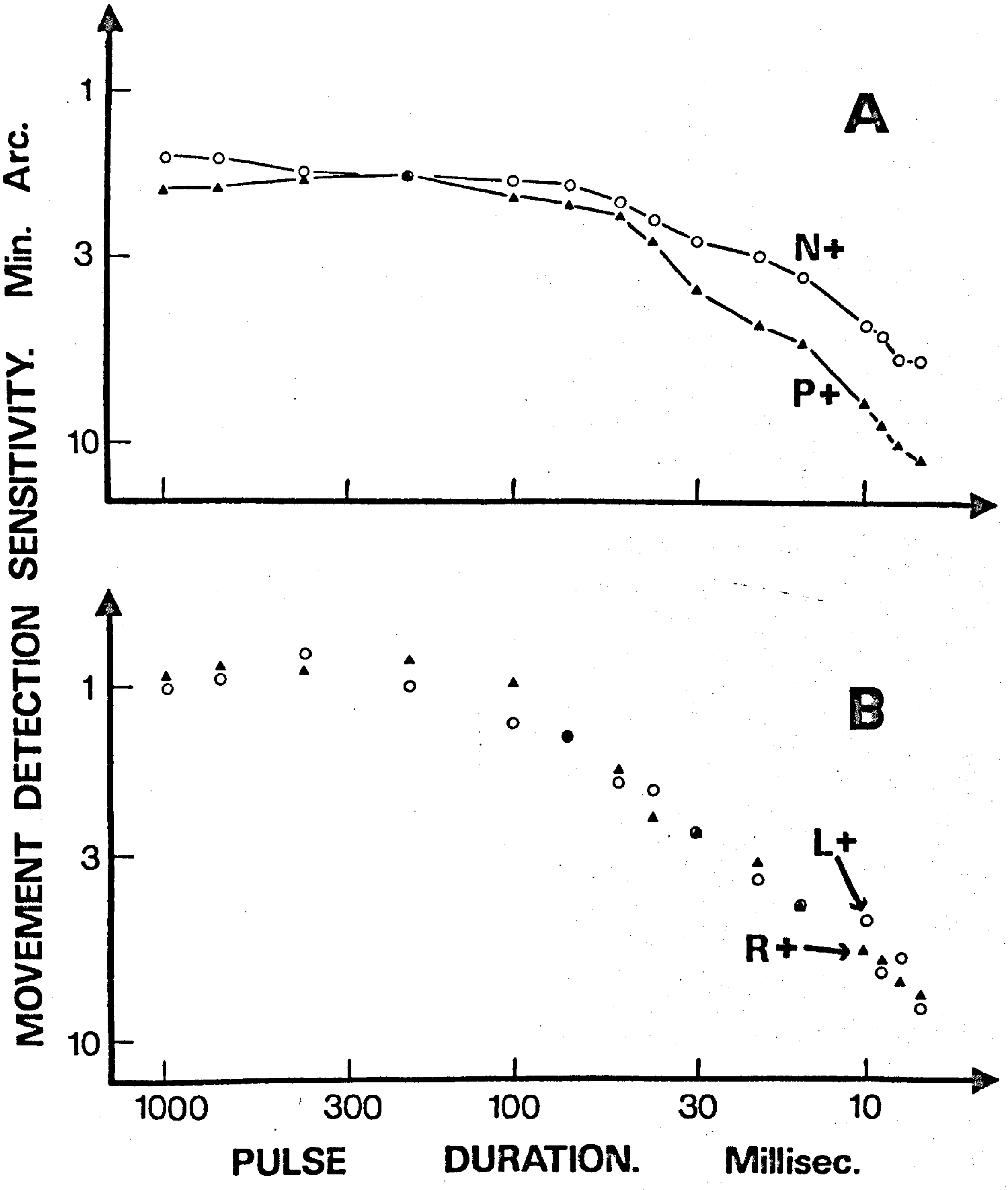


Figure 19. Schematic diagram illustrating the apparent motion of the stimulus. The left and right eyes (shown only once for simplicity) fixate the nonius lines (n) at the centre of the stimulus. The longer arrow illustrates the first half of the stimulus movement. There are ten stimulation conditions (see text).



<u>Figure 20</u>. The effect of pulse duration and pulse direction upon movement detection sensitivity for brief changes of disparity. Movement detection sensitivity <u>versus</u> pulse duration is shown for <u>A</u> disparity pulses and <u>B</u> sideways movement pulses. In all four stimulation conditions (N+ (circles in <u>A</u>), P+ (triangles in <u>A</u>), L+ (circles in <u>B</u>) and R+ (triangles in <u>B</u>)) the initial static disparity was +8 min. arc (in front of the fixation plane). Each point is the mean of 3 settings. Subject D.R.. Both axes are logarithmic.

3:3. Pulsed Movement Threshold.

The stimulation conditions were as follows (see Fig. 19). The stimulus bar moved either towards (positive pulse "P") or away from (negative pulse "N") the subject, and then returned to its initial position. The initial position of the bar could either be behind (uncrossed static disparity "-"), on (zero static disparity "0") or in front of (crossed static disparity "+") the fixation plane. This gave six experimental conditions (P+, P0, P-, N+, N0 and N-).

In separate control experiments the bar moved either to the left (leftwards pulse "L") or to the right (rightwards pulse "R") and then returned to its initial position. The initial position of the bar could either be behind or in front of the fixation plane, giving four control conditions (L+, L-, R+ and R-). In these control experiments no changes in retinal disparity occurred, and hence the bar did not appear to move in depth.

In this Section, the attenuation in dB/octave of any curve is the slope of the regression line, fitted by the method of least squares through the experimental points whose abscissae are less than 50 millisec. (note that 20dB equals 10 times). The pulse duration turnover point (T_t) is the pulse duration where the regression line intersects the horizontal line through the sensitivity maximum.

3:3:1. The Effects of Pulse Duration and Pulse Direction.

Fig. 20a illustrates the effects of varying the pulse duration and the pulse direction upon the movement detection sensitivity for brief (pulsed) changes of disparity. Apparatus 3, Stimulus 6 and Method 3 were used, and the subject was D.R..

There was no change in movement detection sensitivity with pulse duration for pulse durations longer than about 100 millisecs.. The movement detection sensitivity decreased, however, as the pulse duration was decreased. This decrease in movement detection sensitivity differed, for positive-going pulses (P+ condition, T_t equals 68 millisecs., attenuation equals 4.8dB/octave) and negative-going pulses (N+ condition, T_t equals 70 millisecs., attenuation equals 3.2dB/octave).

The subject could either have used changes in retinal disparity, or movements of one or both retinal images, or both cues to detect stimulus motion (see Section 3:1:5). That the difference between the attenuations for positive-going pulses and negative-going pulses was related to changes in retinal disparity alone is shown by the control experiments of Fig. 20b. In these experiments no changes in retinal disparity occurred so the stimulus did not appear to move in depth. Fig. 20b shows that the effects of varying the pulse duration and pulse direction upon movement detection sensitivity for brief (pulsed) sideways movements. Apparatus 3 , Stimulus 6 and Method 3 were used, and the subject was D.R..

The general shape of the curves was similar to the shape of the curves for disparity pulses. However, the decrease in movement detection sensitivity for short pulse durations was similar for both leftwards (L+ condition, T_t equals 116 millisecs., attenuation equals 4.2dB/octave) and rightwards pulses (R+ condition, T_t equals 124 millisecs., attenuation equals 4.3dB/octave). This suggested that changes in retinal disparity alone were responsible for the difference in attenuation between positive- and negative-going pulses shown in Fig. 20a.

These findings were confirmed on one additional subject

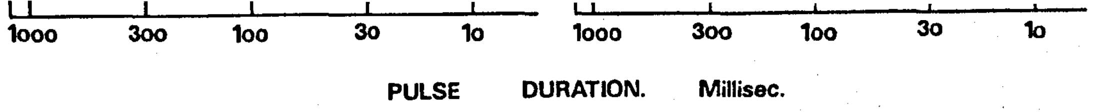
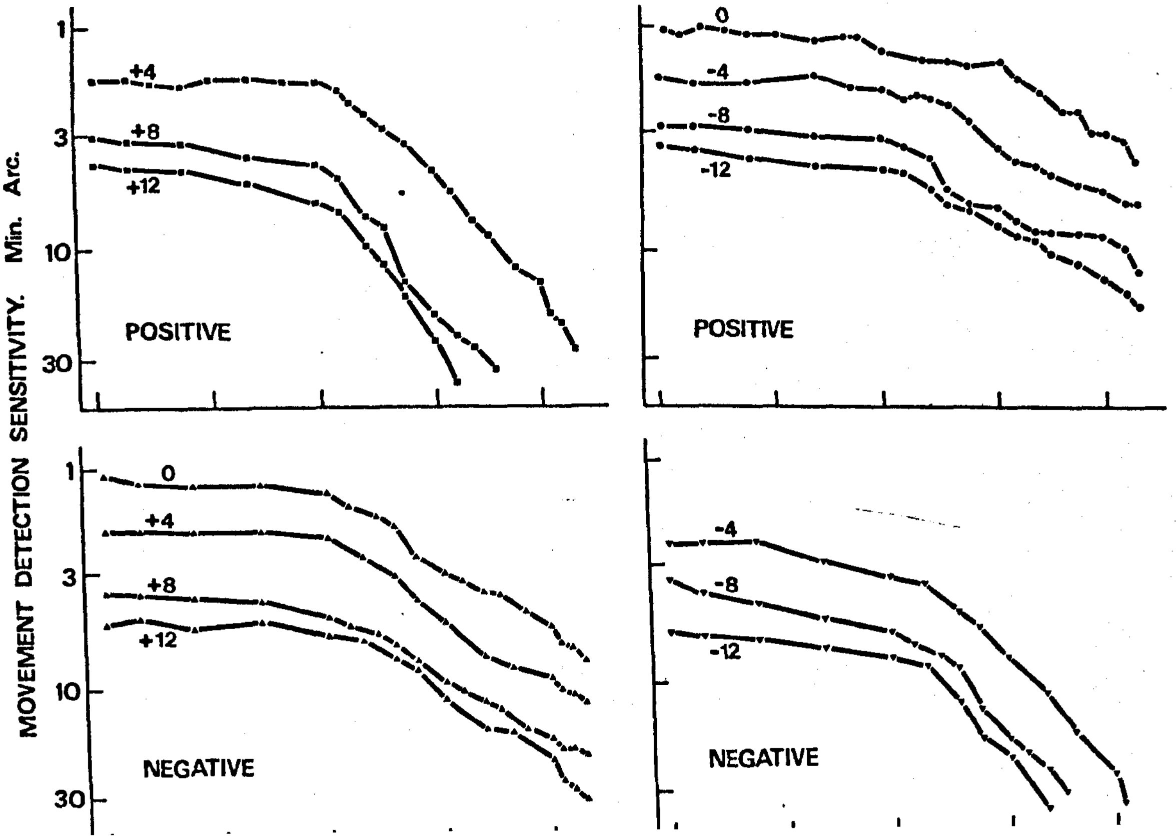


Figure 21. The effect of static disparity upon movement detection sensitivity for brief changes of disparity. The curves through the squares (upper left) are for positive pulses from a crossed static disparity (P+). The curves through the circles (upper right) are for positive pulses either from an uncrossed static disparity (P-) or from zero static disparity (P0). The curves through the triangles (lower left) are for negative pulses either from a crossed static disparity (N+) or from zero static disparity (N0). The curves through the inverted triangles (lower right) are for negative pulses from an uncrossed static disparity (N-). The numbers on the curves give the initial static disparity (mins. arc) of the stimulus bar. Each point is the mean of two settings. Subject K.B.. Both axes are logarithmic.


MOVEMENT DETECTION SENSITIVITY. Min. Arc.
1
3
10
30
+4
+8
+12
POSITIVE
0
-4
-8
-12
POSITIVE
1
3
10
30
0
+4
+8
+12
NEGATIVE
-4
-8
-12
NEGATIVE

(K.B.) (see Fig. 21).

3:3:2. The Effect of Static Disparity.

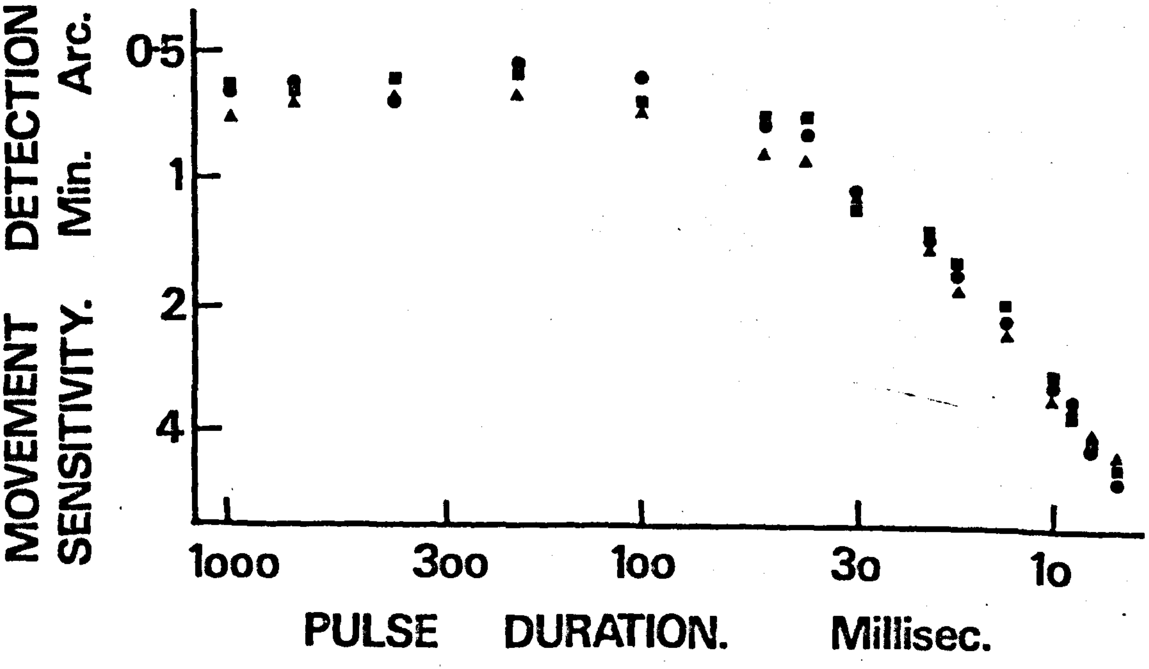
Fig. 21 shows the movement detection sensitivity of subject K.B. plotted *versus* the pulse duration for six experimental conditions (P+, P0, P-, N+, N0 and N-). The single P0 curve has been combined with the three P- curves and the single N0 curve with the three N+ curves. Apparatus 3, Stimulus 6 and Method 3 were used.

Fig. 21 shows that the three P+ curves were almost identical to the corresponding N- curves. In other words, similar psychophysical results were obtained for all pulses directed *away from* the fixation plane. All six curves were similar to a low-pass filter characteristic with a pulse duration turnover point at about 110 millisecs. (P+4 equals 85, P+8 equals 120, P+12 equals 110, N-4 equals 110, N-8 equals 145 and N-12 equals 110 millisecs.). The final slope approximated 7.2dB/octave (P+4 equals 7.2, P+8 equals 7.2, P+12 equals 8.4, N-4 equals 6.6, N-8 equals 6.7 and N-12 equals 6.8 dB/octave).

Similarly, the P- curves were almost identical to the corresponding N+ curves. In other words, similar psychophysical results were obtained for all pulses directed *towards* the fixation plane. Again, all six curves showed a response similar to that of a low-pass filter with a pulse duration turnover point at about 120 millisecs. (P-4 equals 115, P-8 equals 135, P-12 equals 125, N+4 equals 115, N+8 equals 160 and N+12 equals 95 millisecs.). The final slope approximated 3.4dB/octave (P-4 equals 3.0, P-8 equals 2.8, P-12 equals3.2, N+4 equals 4.0, N+8 equals 3.4 and N+12 equals 4.2 dB/octave).

The final slopes for the P+ and N- curves differed markedly from the final slopes for the P- and N+ conditions. However, the

<u>Figure 22</u>. Control experiments for brief changes of disparity. Movement detection sensitivity is plotted *versus* pulse duration for three experimental conditions. The squares show sensitivity to rightwards pulses from a crossed static disparity (R+). The circles show sensitivity to leftwards pulses from a crossed static disparity (L+). The triangles show sensitivity to leftwards pulses from an uncrossed static disparity (L-). The static disparity was 8 min. arc. Each point is the mean of two settings. Subject K.B.. Both axes are logarithmic.


MOVEMENT DETECTION
SENSITIVITY. Min. Arc.
0·5
1
2
4
1000
300
100
30
10
PULSE DURATION. Millisec.

pulse duration turnover frequencies were not markedly different.

This suggests that the visual sensitivity was determined not by whether the pulse was directed towards or away from the eyes (see Section 3:3:1.), but by the direction of the pulse relative to the fixation plane.

The curves for zero static disparity (P0 and N0), however, gave results similar to the P- and N+ curves, not to the P+ and N- curves as would have been expected. The pulse duration turnover point was approximately 100 millisecs. (P0 equals 70, N0 equals 130 millisecs.) and the final slope approximated 4.0dB/octave (P0 equals 4.2, N0 equals 3.9dB/octave).

Control experiments were carried out to determine whether these results were due to changes in retinal disparity alone or whether sideways movements of the retinal images contributed to the results (see Section 3:1:5.). In these experiments, no changes in retinal disparity occurred so that the stimulus did not appear to move in depth.

Fig. 22 shows movement detection sensitivity plotted <u>versus</u> pulse duration for L+ (circles), L- (triangles) and R+ (squares). Apparatus 3, Stimulus 6 and Method 3 were used, and the subject was K.B.. For each condition, the static disparity was 8 min. arc. A curve drawn through the experimental points would be similar in shape to the curves for disparity pulses. The decrease in movement detection sensitivity for short pulses was similar for all three conditions (T_t equals 50 millisecs., attenuation equals 5·9 dB/octave). These results, therefore, suggest that changes in retinal disparity were responsible for the differences between the types of curve in Fig. 21.

These findings were confirmed on one additional subject (D.R.) whose slopes were 5.1dB/octave (away from the plane), 3.1dB/octave (towards the plane) and 4.3dB/octave (sideways movement).

3:3:3. Discussion.

In no experiment was any displacement of the nonius lines associated with a stimulus movement. Since a change in convergence of some 0.5 min. arc could be detected with the nonius lines, it is unlikely that the findings were due to vergence eye movements (see also Fig. 23).

The results shown in Fig. 20 - 22 suggest that for pulse durations shorter than 110 millisecs. there was a progressive decrease in movement detection sensitivity. Figs. 20 and 21 show that this attenuation differed for different pulse directions. Fig. 21 shows that this attenuation also differed for crossed and uncrossed static disparities. That these differences were related to changes in retinal disparity alone, is shown by the fact that there were no differences for sideways movement stimulation (see Fig. 20b and Fig. 22).

The anomalous zero static disparity curves can be explained in one of two different ways. There could have been some small instrumental error (less than 0.5 min. arc) and/or a small fixation error. This explanation seems unlikely because nonius lines were used to aid fixation. This restricted fixation errors to less than about 0.5 min. arc (see Section 3:1:5.). Assuming that these errors were random in nature and were normally distributed, there is a .25 probability that the anomalous results could have been due to this cause.

The second and more likely possibility is that this anomaly is real. There is independent evidence that disparities for targets close to the fixation plane are handled by a "pool" of disparity

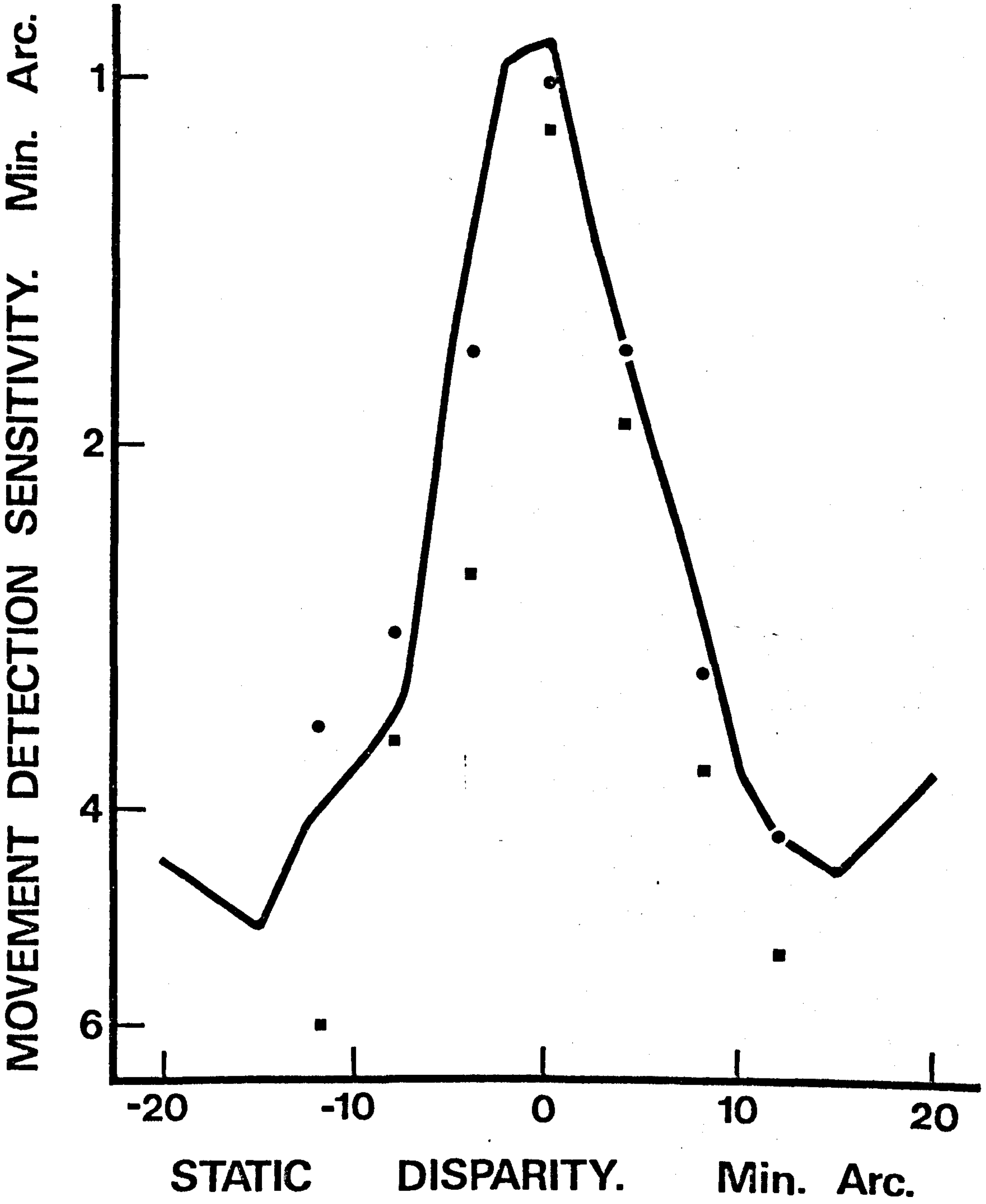


Figure 23. Comparison between 0.1Hz. sinewave oscillations of disparity and 1 second pulses of disparity. The continuous line is the curve for stereoscopic movement detection sensitivity *versus* static disparity replotted from Fig. 12. The circles show stereoscopic movement detection sensitivity for 1 second pulses derived from Fig. 21 for negative-going pulses. The squares show similar results for positive-going pulses of disparity. Subject K.B.. Ordinates are logarithmic, abscissae are linear.

detectors quite separate from the two pools for targets located in front of and behind the fixation plane (Richards, 1970, 1971; Regan and Beverley, 1973A; Section 3:1:5).

These findings suggest that information that a target's disparity has changed is handled differently when the target's movement is directed away from the fixation plane than when it is directed towards the plane (see Section 3:6:2).

All of the results for pulse durations of 1 second, which were derived from the curves of Fig. 21, are plotted versus static disparity in Fig. 23. Fig. 23 also shows the stereoscopic movement detection sensitivity versus static disparity curve for sinewave stimulation (Fig. 12). There was a good agreement between these results which suggests that, physiologically, there was little difference between the two stimulation conditions. The explanation of this similarity is almost certainly identical to the explanation suggested in Section 3:2:2 for squarewaves. It seems likely that there is no appreciable difference between a low-frequency squarewave (0.1 to 1Hz.) and an irregularly repetitive pulse of 1 second duration - certainly the subjects noticed no difference in the appearance of the "movements". This, therefore, adds additional support to the conclusion of Sections 3:1:5 and 3:2:2 that *movement detection sensitivity is tuned with respect to static disparity*.

The fact that movement detection sensitivity for 1 second pulses was maximal at zero static disparity (Fig. 23) adds additional evidence that fixation errors were small (Fig. 23 indicates that they were considerably less than 4 min. arc).

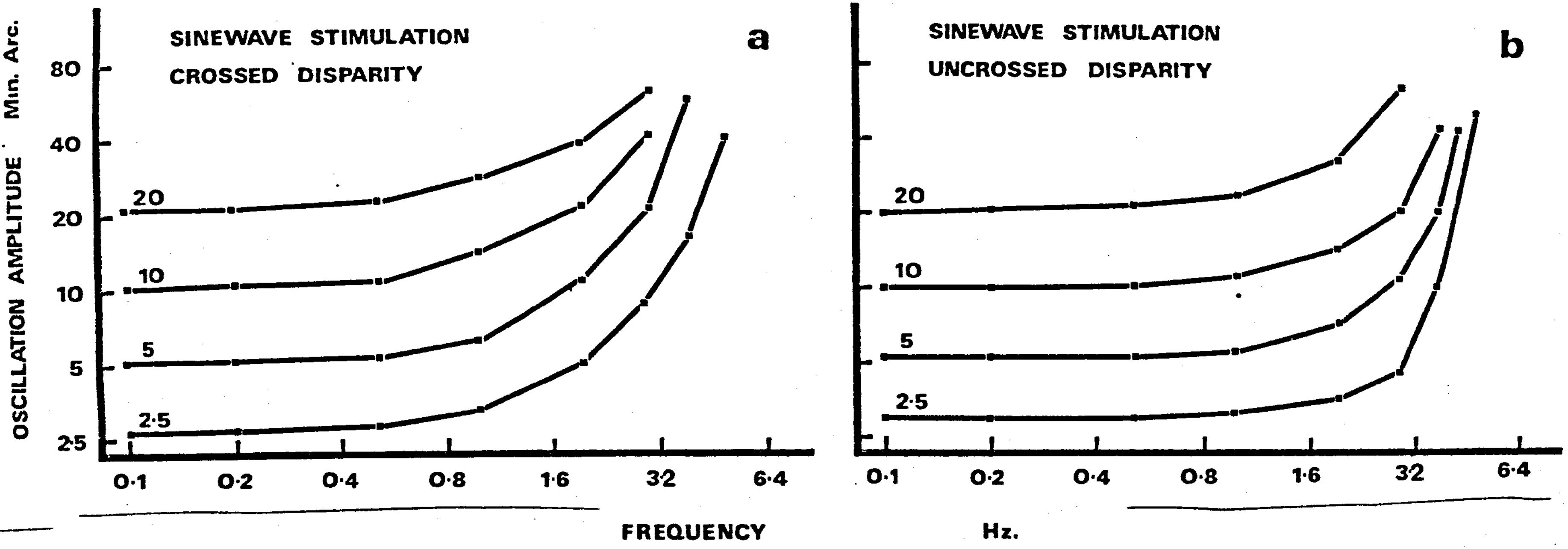


Figure 24. The effect of frequency upon the perceived oscillation amplitude (matched depth) for suprathreshold sinewave stimulation. A - crossed disparity. B - uncrossed disparity. The numbers on the curves give the static disparity (mins. arc) of the comparison bar to which the oscillation amplitude was matched. Each point is the mean of 5 settings. Subject K.B.. Both axes are logarithmic.

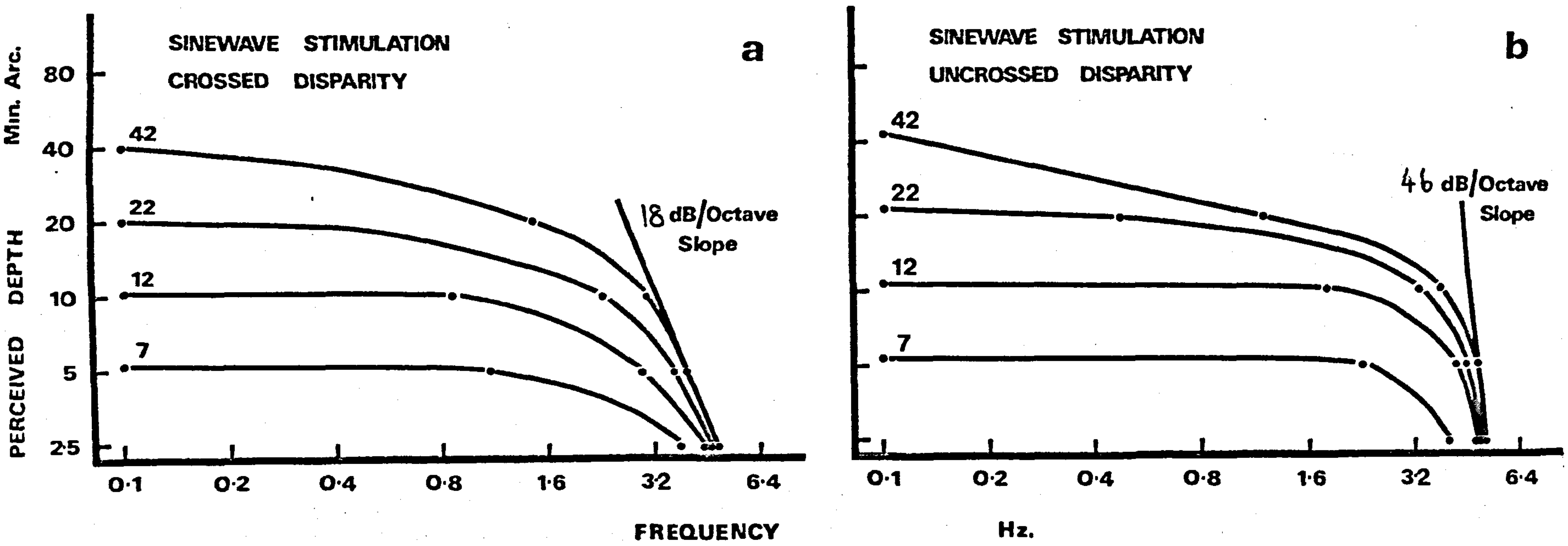


Figure 25. Matched depth *versus* stimulation frequency for sinewave stimulation for crossed and uncrossed disparities. The points are derived from Fig. 24 plus some additional results. The asymptotic slopes of the curves for crossed and uncrossed disparities are shown. The numbers on the curves refer to the matched oscillation amplitude of the moving bar (in mins. arc). *A* - crossed disparity. *B* - uncrossed disparity. Each point is the mean of 5 readings. Subject J.J.. Both axes are logarithmic.

3:4. Sinewave Matched Depth.

The limiting slope in dB/octave (where 20dB equals 10 times) of any curve is the slope of the line joining the two experimental points with the highest frequencies. The turnover frequency (F_t) is the frequency where this line intersects the horizontal line through the point where the frequency is lowest (0.1Hz.).

3:4:1. "Normal" Subjects.

Fig. 24 illustrates the effect of varying the stimulation frequency upon the perceived oscillation amplitude (matched depth) for sinewave stimulation. Apparatus 2, Stimulus 3 and Method 2 were used. The subject was K.B..

There was no increase in low-frequency oscillation amplitude, under matched depth conditions, for either crossed or uncrossed disparities (compare with Section 3:1).

There was a steep high-frequency increase, under matched depth conditions, for both crossed and uncrossed disparities, and for all matched depths in the range 2.5 to 20 min. arc. Under no conditions could a matched depth setting be made for frequencies in excess of 5Hz.. The turnover frequencies for crossed disparities were 2.8Hz. (at 2.5 min. arc), 1.7Hz. (at 5 min. arc), 1.5Hz. (at 10 min. arc) and 0.9Hz. (at 20 min. arc). For uncrossed disparities the turnover frequencies were 3.4Hz. (at 2.5 min. arc), 2.3Hz. (at 5 min. arc), 2.3Hz. (at 10 min. arc) and 1.6Hz. (at 20 min. arc). The slopes of the curves could not be accurately obtained because, at high frequencies, binocular fusion broke down due to the necessarily large oscillations of disparity.

In Fig. 25, data similar to that shown in Fig. 24 are replotted in such a way as to emphasise the difference between

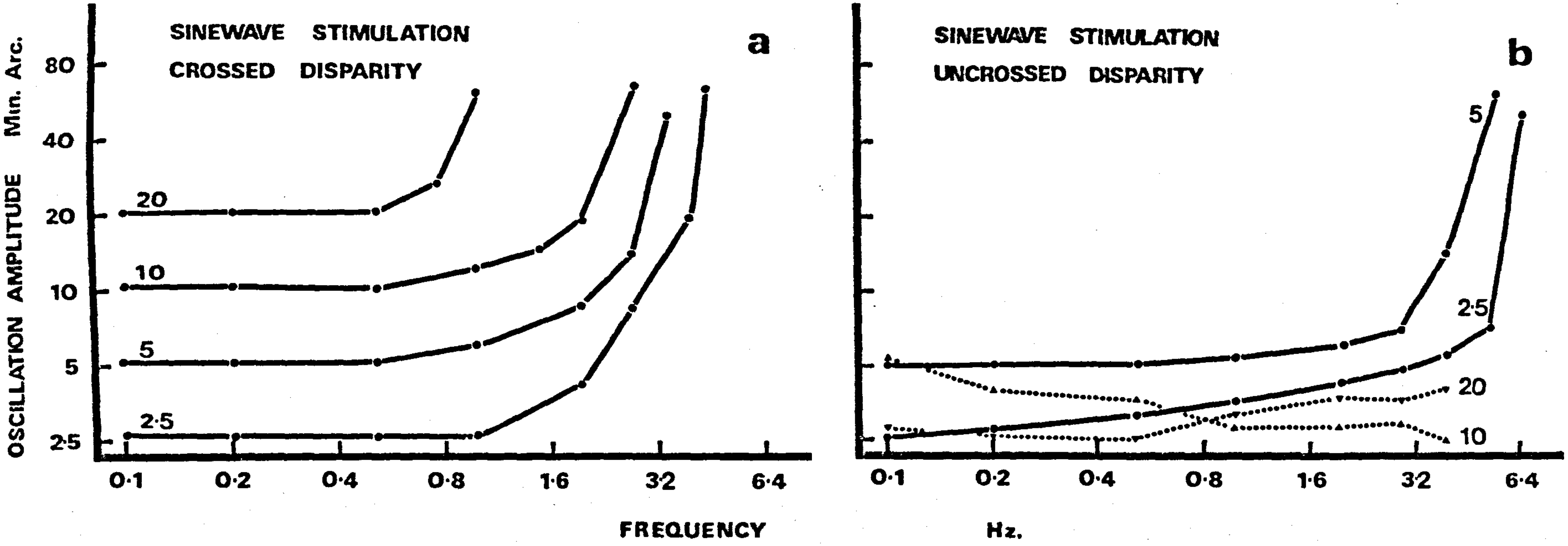


__Figure 26__. As Fig. 24 but for subject J.B..

crossed and uncrossed disparities. Each of the <u>curves</u> in plots such as Fig. 24 are transformed into a <u>horizontal set of points</u> in plots such as Fig. 25. Fig. 25 shows perceived depth plotted for different values of oscillation amplitude (as compared to Fig. 24 which shows the oscillation amplitude necessary for different values of matched depth to be perceived). The subject was J.J..

The perceived depth of a sinewave oscillation of constant amplitude decreased rapidly as frequency was increased for both crossed and uncrossed disparities. For all three subjects the decrease was more rapid for uncrossed than for crossed disparities. The limiting slopes for crossed disparities were 30 (K.B.), 18 (J.J.) and 20dB/octave (M.Y.); for uncrossed disparities they were 36 (K.B.), 46 (J.J.) and 38 (M.Y.). For one subject, the difference in the slopes for crossed and uncrossed disparities was as large as 2.5:1.

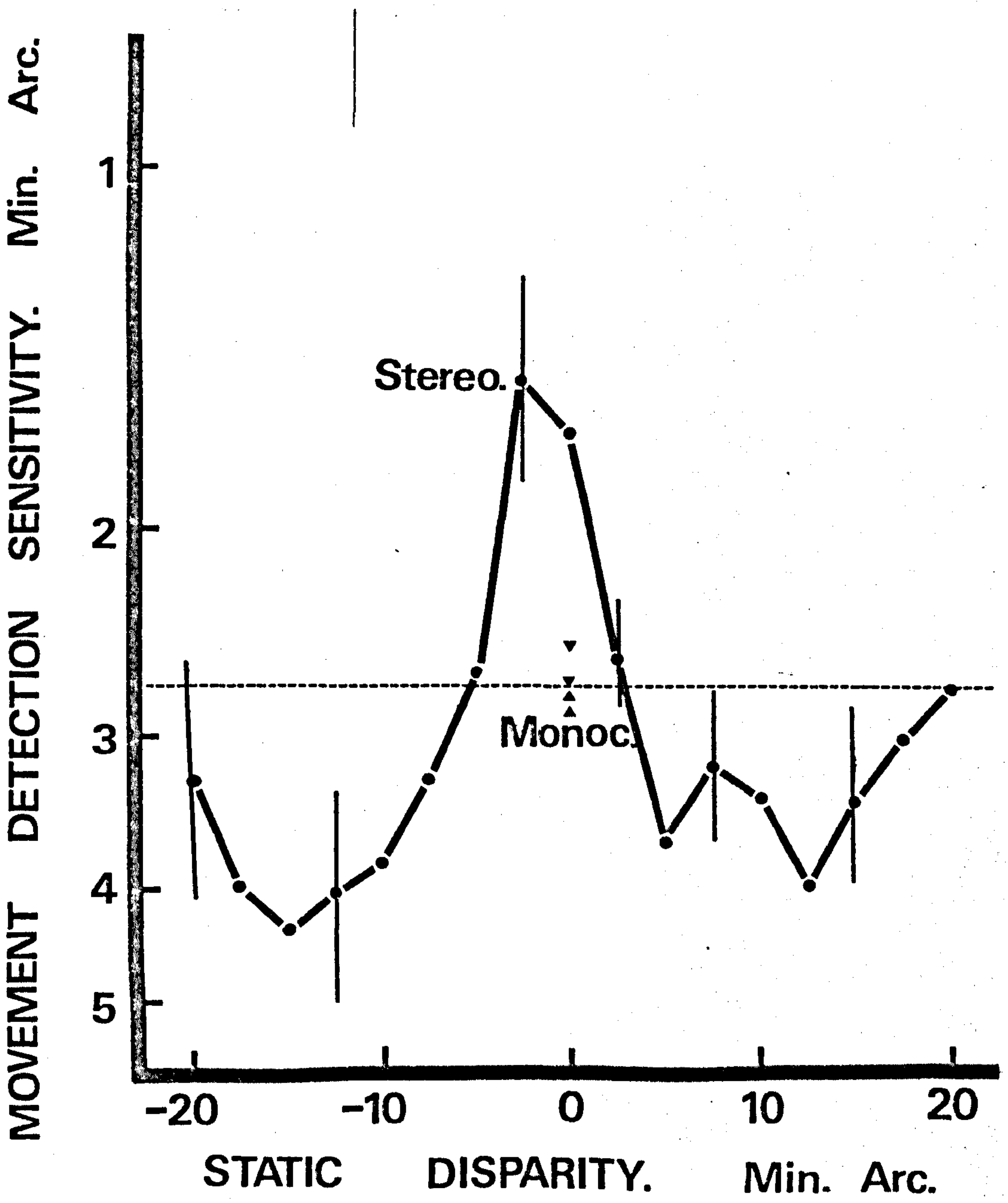
It was clear from these results that, unlike threshold experiments, matched depth experiments did not show a decrease in sensitivity at low frequencies.

Subjects did not see oscillations in depth when the stimulus frequency exceeded 5Hz. no matter how large the stimulus oscillation amplitude. Sensitivity to oscillations in depth decreased rapidly above about 2Hz.. This decrease in sensitivity was different for crossed and uncrossed disparities; in all subjects, the decrease was more rapid for uncrossed disparities.

Similar results were obtained for three subjects (K.B., J.J. and M.Y.). A fourth subject (J.B.) gave anomolous results (see Section 3:4:2).

<u>3:4:2. A "Stereoanomolous" Subject.</u>

Fig. 26 illustrates the effect of varying the stimulation



<u>Figure 27</u>. As Fig. 12 but for subject J.B.. The curves for monocular-stereoscopic stimulation and for binocular stimulation are omitted.

frequency upon the perceived oscillation amplitude (matched depth) for sinewave stimulation, for subject J.B.. Apparatus 2, Stimulus 3 and Method 2 were used.

Her results for crossed disparities (Fig. 26a) were similar to those for the other three subjects (Fig. 24a). However, for uncrossed disparities, only her curves for -2.5 and -5 min. arc were similar to those of other subjects. Her results for -10 and -20 min. arc were irregular, inconsistent and showed no systematic variation with frequency. The settings were as if the subject was merely "guessing" the matched depth setting. Her subjective report confirmed this. There was no appearance of depth for stimuli moving more than 5 min. arc behind the fixation plane.

An error in convergence would be the most likely explanation for this "anomalous" failure of subject J.B.'s depth perception for uncrossed disparities more than 5 min. arc behind the fixation plane, together with her "normal" depth perception for other disparities. In order to account for these results, an error in convergence greater than 15 min. arc (that is 20 min. arc minus 5 min. arc) would be required. This would seem to be ruled out by the results shown in Fig. 27.

Fig. 27 is a plot of movement detection sensitivity <u>versus</u> stimulus distance from the fixation plane (static disparity) for subject J.B.. Apparatus 3, Stimulus 5 and Method 1 were used. The symmetry of the stereoscopic curve about zero static disparity shows that any convergence error was unlikely to have exceeded 2.5 min. arc (see Sections 3:1:2 and 3:1:5, and Fig. 12).

This suggests that the "anomalous" results of subject J.B. were due to some error in the processing of uncrossed disparity information.

3:4:3. Discussion.

The results for suprathreshold sinewave stimulation differed from the results for threshold stimulation, at low frequencies. For suprathreshold stimulation, there was no low-frequency attenuation. This data is inconsistent with Richards' (1972) finding of low-frequency attenuation in sinewave matched depth experiments. However, his finding relates only to disparities exceeding 30 min. arc. In the experiments reported above, the largest disparity was 20 min. arc. For disparities less than 30 min. arc, Richards also finds no low-frequency attenuation.

The finding that sensitivity to oscillations in depth decreased rapidly above about 2Hz., adds support to the findings of Section 3:1 that, above 1Hz., disparity cues had no effect upon the detection of movement in depth.

The finding of a high-frequency difference in sensitivity for crossed and uncrossed disparities, adds support to the finding of Section 3:1 that the effect of frequency upon depth perception is different for crossed and uncrossed disparities. This finding is consistent with Richards' (1970, 1971) suggestion that crossed and uncrossed disparity detectors are organised into separate pools.

Richards (1970, 1971) has reported the existence of "amomalous" binocular depth perception, which he attributed to the functional abscence of one or more of the three hypothetical pools of disparity detectors. The "anomalous" results for subject J.B. could be explained along these lines as a selective loss of the uncrossed disparity detector pool.

The finding that J.B. showed neither suprathreshold nor threshold anomaly for uncrossed disparities up to 5 min. arc suggests "sparing" of disparity detectors close to the fixation plane. This would be consistent with Richards' (1970, 1971) suggestion that disparity detectors near the fixation plane form a separate pool.

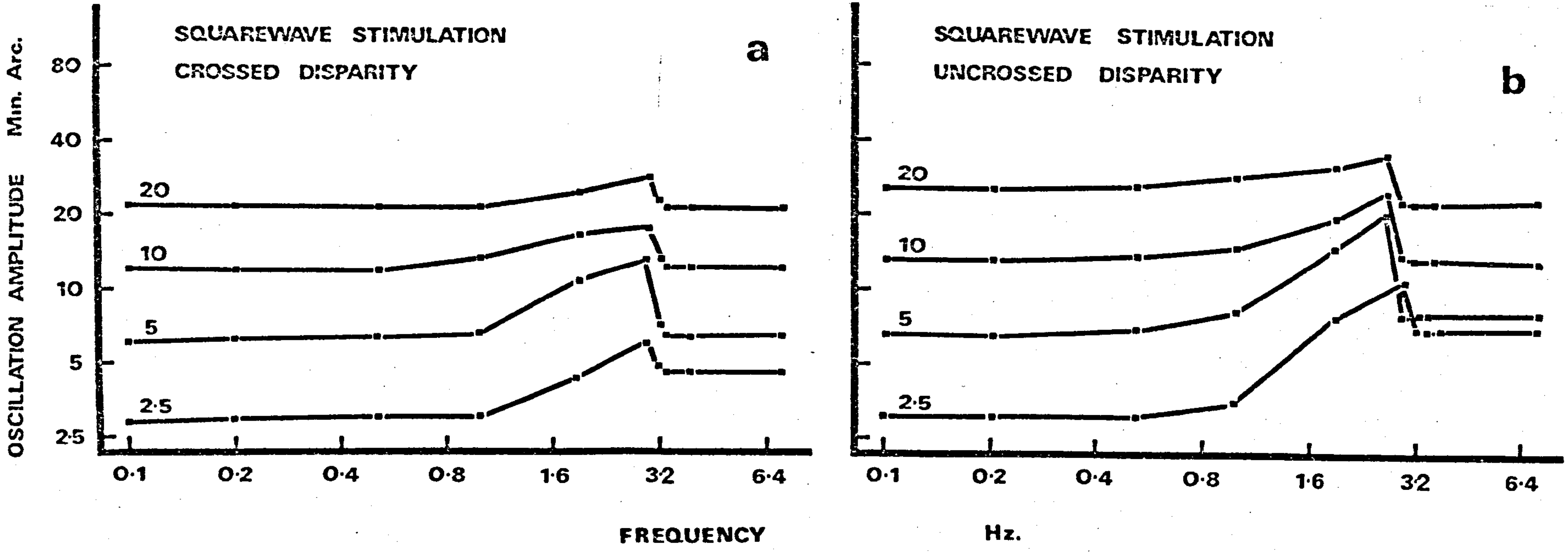


Figure 28. As Fig. 24 but for squarewave stimulation. Subject K.B..

3:5. Squarewave Matched Depth.

3:5:1. The Effect of Frequency.

Fig. 28 illustrates the effect of varying the stimulation frequency upon the perceived oscillation amplitude (matched depth) for squarewave stimulation. Apparatus 2, Stimulus 3 and Method 2 were used. The subject was K.B..

Like sinewave stimulation, there was no low-frequency increase in oscillation amplitude under matched depth conditions for either crossed or uncrossed disparities (see Section 3:4:1).

Unlike sinewave stimulation, there was no steep high-frequency increase under matched depth conditions for either crossed or uncrossed disparities (compare Fig. 24 with Fig. 28). There was, however, a slight increase up to about 3Hz. for both crossed and uncrossed disparities. Just above 3Hz. there was an abrupt increase in sensitivity to almost the low-frequency level. The perceived oscillation amplitude did not vary with frequency above this discontinuity.

The discontinuity became smoothed out in the curves of Fig. 28 for two reasons. Firstly, the frequency at which the discontinuity occurred was not constant (for example it varied over the range 2.8Hz. to 3.4Hz. for subject K.B. for 10 min. arc crossed disparity). Secondly, there was a hysteresis effect. Experimental trials in which frequency was gradually increased, gave consistently higher frequencies for the discontinuity than trials in which frequency was decreased. Although these variations were small, they were sufficient to smooth the discontinuities in the averaged results.

There was a perceptual change in the appearance of the stimulus which was <u>always</u> coincident with this discontinuity. For low frequencies, the stimulus bar was seen as a single bar abruptly moving from in front of the fixation plane to behind the fixation plane. Above the discontinuity, the stimulus appearance changed to that of two stationary bars, one in front of, the other behind the plane of fixation. Altering the oscillation amplitude, altered the distance of the bars from the fixation plane. Consequently, matched depth settings were easily made at these high stimulation frequencies. For all subjects and for all conditions, this change in appearance of the stimulus coincided with the discontinuity in matched depth sensitivity.

Each individual trial for squarewave stimulation closely followed the results for sinewave matched depth stimulation up to the discontinuity.

The mean frequency at which the discontinuity occurred was the same for all crossed disparities (3.1Hz. for subject K.B.), and also for all uncrossed disparities (2.6Hz. for subject K.B.). Although the frequencies at which the discontinuities occurred varied from subject to subject, the crossed-disparity discontinuity was always at a significantly higher frequency than the uncrossed-disparity discontinuity (Student's "t" test, probability greater than .99).

The matched depth amplitudes set above the discontinuity were slightly higher than the amplitudes set at very low frequencies. This was possibly due to a slight "blurring" of the stimulus (when doubled) due to the stimulus being in each position for only 50% of the time. (Julesz (1961,1965) has reported that depth sensations can be elicited by viewing two stationary patterns, one of which is sharp and the other optically blurred.)

Apparatus limitations permitted squarewave frequencies up to only 20Hz. to be generated. However, it seems likely that the doubling of the stimulus continues up to indefinitely-high frequencies.

These results were confirmed in a second subject (M.Y.). Results for crossed disparities for a third subject (J.B.) were also similar.

3:5:2. Discussion.

The results for suprathreshold squarewave stimulation differed from the results for threshold squarewave stimulation at low frequencies (see also the results for sinewave stimulation). For suprathreshold stimulation there was no low-frequency attenuation. This data is consistent with Richards' (1972) finding of no low-frequency attenuation for squarewaves.

The results for squarewaves (Fig. 28) paralleled the results for sinewaves (Fig. 24) in matched depth experiments for frequencies up to about 3Hz..

The psychophysical discontinuity at about 3Hz. exactly paralleled a perceptual change in the appearance of the stimulus. The frequency at which this discontinuity occurred was different for crossed and uncrossed disparities. This finding is consistent with Richards' (1970,1971) hypothesis that crossed and uncrossed disparity detectors are organised into separate pools.

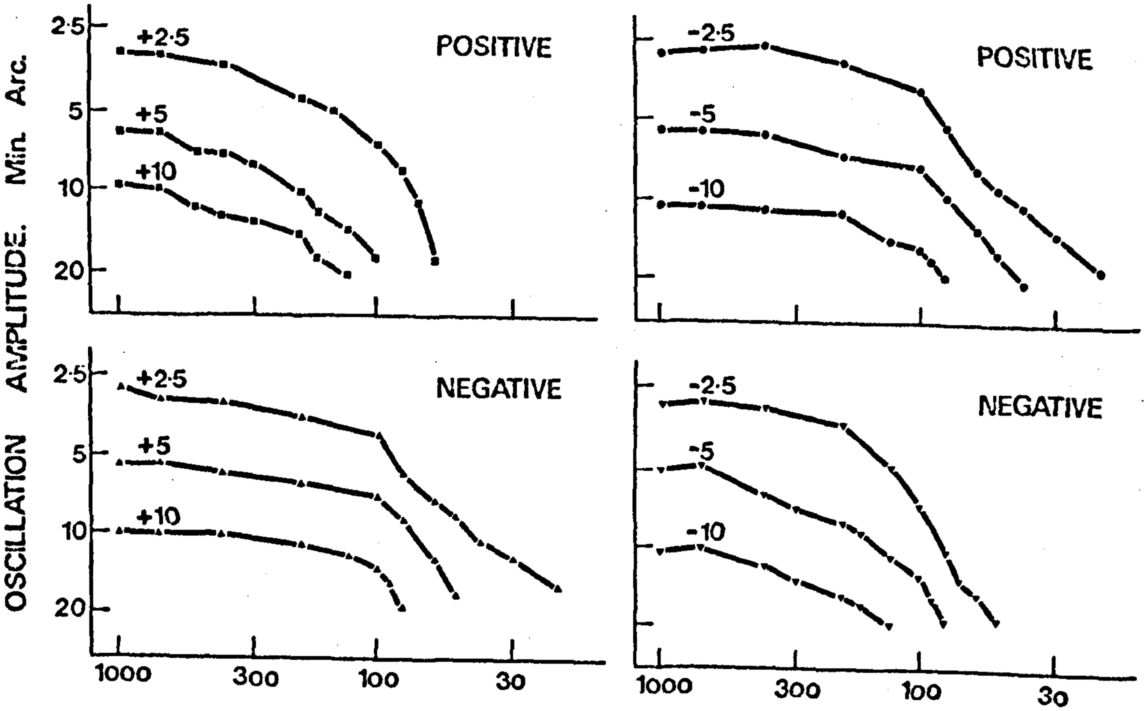
There is probably a causal relationship between the psychophysical discontinuity and the subjective change in the appearance of the stimulus. Below the discontinuity, movement of the stimulus generated an illusion of motion in depth. This can be likened to an analog in the depth dimension of the well known phi phenomenon. There are only two possible stimulus positions (see Appendix 1) at any given oscillation amplitude for squarewave stimulation (unlike sinewave stimulation where an infinite number of stimulus positions can occur). For low stimulation frequencies, the stimulus bar would appear to "jump" from one position to the other and back again (compare with the phi phenomenon), and thus would appear as a <u>single</u> (moving) bar. The discontinuity would be, therefore, the point at which this illusion of motion broke down (about 3Hz.). This is supported by the fact that the frequency at which the discontinuity occurred, varied slightly from one run to the next; also by the fact that hysteresis occurred around the point of discontinuity.

When the illusion of apparent motion broke down, <u>two</u> (stationary) bars were seen, "appearing" and"disappearing" in both of the two possible stimulus positions. In this "doubled" condition, both bars appeared blurred and of somewhat lower contrast than when only one bar was seen. The lower contrast would be due to the stimulus bar occupying each position for only half the time.

Side to side stimulus movements should also show a discontinuity when the phi phenomenon for sideways movement breaks down. This discontinuity was subjectively observed, but since it occurred at a much higher frequency (about 20Hz.) than for movement in depth, a quantitative investigation could not be carried out (due to apparatus limitations).

PULSE DURATION. Millisec.

Figure 29. Suprathreshold data. Pulse oscillation amplitude versus pulse duration under four experimental conditions. The curves through the squares (upper left) are for positive pulses from zero to a crossed static disparity (P+). The curves through the circles (upper right) are for positive pulses from an uncrossed to zero static disparity (P-). The curves through the triangles (lower left) are for negative pulses from a crossed to zero static disparity (N+). The curves through the inverted triangles (lower right) are for negative pulses from zero to an uncrossed static disparity (N-). The numbers on the curves give the static disparity (min. arc) of the comparison bar from which or to which the pulse amplitude was matched. Each point is the mean of two settings. Subject K.B..


OSCILLATION AMPLITUDE. Min. Arc.
2·5
5
10
20
+2·5
+5
+10
POSITIVE
-2·5
-5
-10
POSITIVE
+2·5
+5
+10
NEGATIVE
-2·5
-5
-10
NEGATIVE
1000
300
100
30

3:6. Matched Depth for Pulses.

In this section, the attenuation in dB/octave (where 20dB equals 10 times) of any curve is the slope of the regression line, fitted by eye, through the five experimental points with the shortest pulse durations. The pulse duration turnover point (T_t) is the pulse duration where the regression line intersects the horizontal line through the sensitivity minimum.

A description of the experimental conditions (P+, P-, N+ and N-) can be found at the beginning of Section 3:3.

3:6:1. Results.

Fig. 29 shows visual sensitivity for suprathreshold (matched depth) stimulation as a function of pulse duration for subject K.B.. Apparatus 3, Stimulus 6 and Method 3 were used. The pulse oscillation amplitudes necessary for the bar to appear to move through a preset disparity are plotted *versus* pulse duration for four experimental conditions (P+, P-, N+ and N-). For P+ and N-, the right hand bar was initially at zero static disparity and moved away from the fixation plane. For P- and N+, the right hand bar was initially at some preset static disparity and moved to the plane of fixation.

Fig. 29 shows that, as for threshold stimulation (Fig.21), the three P+ curves were similar to the corresponding N- curves. All six curves were similar to a low-pass filter characteristic. The apparatus used did not allow excursions of disparity larger than 30 min. arc to be generated. Neither the turnover point nor the final slope of these curves could, therefore, be estimated, due to lack of sufficient data points.

Fig. 29 also shows that, as for threshold stimulation (Fig. 21), the three P- curves were similar to the corresponding N+ curves.

All six curves were similar to a low-pass filter characteristic with a pulse duration turnover point at about 120 millisecs. and a final slope approximating 6.4dB/octave.

It is clear that the curves for the P+ and N- conditions differed markedly from the curves for the P- and N+ conditions. In other words, all psychophysical results obtained for pulses directed away from the fixation plane differed in a similar way from all psychophysical results obtained for pulses directed towards the fixation plane (compare with Section 3:3:2).

3:6:2. Discussion.

There was an increase in matched depth oscillation amplitude for pulse durations shorter than about 120 millisecs. (Fig. 29). This increase differed for different pulse directions and for crossed and uncrossed disparities (compare with Section 3:3:3). This suggests that the matched depth sensitivity was determined, not by whether the pulse was directed towards or away from the eyes, but by the direction of the pulse relative to the fixation plane.

These results, together with the results for threshold stimulation, suggest that information that a target's disparity has changed, is handled differently when the target's movement is directed away from the fixation plane than when it is directed towards the plane.

This finding is consistent with Richards' hypothesis of separate pools for crossed and uncrossed disparity detectors (Richards, 1970,1971; Regan and Beverley, 1973A). However, these results suggest that each of these pools has at least two functionally distinct parts. One part would be selectively sensitive to movement directed away from the fixation plane, and the other part would be sensitive to movement directed towards the fixation plane.

If the first half of the pulse either attenuates or enhances the response to the second half of the pulse, and if the dynamic characteristics of the neural mechanisms that process disparity changes differ, for movements directed towards or away from the fixation plane, then the effect of pulse direction could be understood. Such directional asymmetry of binocular depth mechanisms would be consistent with independent psychophysical (Beverley and Regan, 1973A,1973B; Regan and Beverley, 1973C) and electrophysiological (Regan and Beverley, 1974A) evidence for disparity-sensitive mechanisms "tuned" to the direction of movement in depth. Furthermore, neurones whose properties suggest that they might signal the direction of motion in depth have recently been found in cat (Pettigrew, 1973) and monkey (Zeki, personal communication).

This splitting of disparity pools would not be apparent when using sinewave or squarewave stimulation (e.g. Richards, 1972; Regan and Beverley, 1973A; Sections 3:1,3:2, 3:4 and 3:5) since these stimuli have no left-to-right asymmetry.

3:7. Summary.

Section 3:1 shows that changes in retinal disparity had no effect upon movement detection sensitivity for sinewave stimulation at frequencies above 1Hz. (Fig. 11 and Fig. 13). Movement could not be seen at all for frequencies above 30Hz.. For sinewave stimulation at frequencies below 1Hz. changes in retinal disparity enhanced movement detection sensitivity, but only for stimuli whose mean disparities were less than 5 min. arc from the fixation plane (Fig. 12 and Fig. 13). For stimuli with mean disparities more than 10 min. arc from the fixation plane, disparity cues reduced movement sensitivity. This may explain Tyler's (1971) finding that stereoscopic movement sensitivity was less than monocular movement sensitivity. This finding means that precise control of fixation is of central importance in any experiment on stereopsis.

For frequencies below 1Hz., the effect of frequency upon stereoscopic movement perception was different for crossed, uncrossed and zero disparities (Fig. 13). This is consistent with Richards' hypothesis that there are three pools of disparity detectors responding respectively to crossed, uncrossed and near-zero disparities.

Although there were large,quantitative,inter-subject differences in the above results (Fig. 14), qualitatively the results were similar. None of the variables tested caused significant intra-subject differences (Figs. 15 - 17).

Section 3:2 shows that the results for squarewave stimulation provide additional support to the conclusions based on sinewave stimulation. A difference between sinewave and squarewave stimulation was that low-frequency (less than 1Hz.) attenuation for squarewave stimulation was slightly less than that for sinewave stimulation (Fig.18).

Section 3:3 shows that for pulsed movements in depth there was a progressive decrease in movement detection sensitivity when pulse duration was reduced below 110 millisecs. (Figs. 20 - 22). This attenuation differed both for different pulse directions and for crossed and uncrossed static disparities. The differences were such that pulses directed respectively towards and away from the fixation plane gave different sensitivity curves (Fig. 21). Anomalous findings were obtained for pulses from zero static disparity. Control experiments confirmed that these results were due to changes in retinal disparity alone (Fig. 22).

The above findings are consistent with Richards' hypothesis that there are three pools of disparity detectors, if it is further assumed that the crossed and uncrossed pools have at least two, functionally distinct parts. One part being selectively sensitive to movement directed towards, and the other selectively sensitive to movement directed away from the fixation plane. This directional asymmetry is consistent with independent psychophysical, electrophysiological and neurophysiological evidence for disparity-sensitive mechanisms tuned to the direction of movement in depth.

Results for 1 sec. pulsed movement stimulation were consistent with results for 0.1Hz. sinewave movement stimulation (Fig. 23). This adds support to the suggestion that movement detection sensitivity is critically dependant on static disparity.

Section 3:4 shows that sensitivity to suprathreshold (matched depth) sinewave stimulation decreased rapidly above about 2Hz. (Fig. 24 and Fig. 25). This decrease was different for crossed and uncrossed disparities and again is consistent with Richards' hypothesis. Movement in depth could not be seen at all for sinewave frequencies above 5Hz..

Richards has reported the existence of "anomalous" binocular depth perception which he attributes to the functional absence of one or more disparity pools. One subject showed an abnormality in her suprathreshold results for uncrossed disparities greater than 5 min. arc (Fig. 26). Her results for other disparities were normal. There was no major error in her fixation (Fig. 27). Her results could thus be explained in terms of an absence of some of the uncrossed pool of disparity detectors.

Section 3:5 shows that sensitivity to suprathreshold (matched depth) squarewave stimulation was similar to sensitivity to sinewave stimulation, below about 3Hz. (Fig. 28). However, at about 3Hz. there was an abrupt increase in sensitivity for squarewave stimulation (discontinuity). Above this discontinuity, perceived oscillation amplitude did not vary with frequency up to the highest frequencies tested (20Hz.). The appearance of the stimulus also changed abruptly at the discontinuity. The appearance of a single bar moving to and fro in depth changed to an appearance of two stationary bars.

The illusion of a single bar moving in depth can be likened to an analog, in the depth dimension, of the phi phenomenon. The discontinuity corresponds to the point where this illusion breaks down. A prediction that side to side stimulus oscillations should also show a discontinuity when the phi phenomenon for sideways movements breaks down, was qualitatively confirmed.

The discontinuities for crossed and uncrossed disparities occurred at different frequencies, giving further evidence for Richards' pool theory.

Section 3:6 shows that the results for suprathreshold (matched depth) stimulation for pulses add further evidence to the results for threshold pulse stimulation (compare Fig. 21 with Fig. 29).

4/ THE DISSOCIATION OF SIDEWAYS MOVEMENTS FROM MOVEMENTS IN DEPTH.

Throughout this chapter, the following terminology will be used. F_l is the frequency of oscillation of the stimulus seen by the left eye. F_r is the frequency of oscillation of the stimulus seen by the right eye. ΔF is the frequency difference between the left and right eyes' stimulus oscillations and is independent of both F_l and F_r. Since F_l was always greater than F_r, $\Delta F = F_l - F_r$. ΔF is the frequency with which the amplitude of oscillations in depth wax and wane. Sideways oscillations of the fused stimulus occur at a frequency F which is the lower of the two frequencies seen by the left and right eyes. $F = F_l$ therefore.

For all experiments described in this chapter, Apparatus 3, Stimulus 4 and Method 4 were used.

4:1. Introduction.

A major problem in investigating the dynamics of stereoscopic depth perception is the fact that changes in disparity necessitate the movement of one or both retinal images. In threshold studies the problem is particularly difficult as it is difficult to be certain whether the subject is using stereoscopic cues, or cues related to the sideways movement of the stimulus on the two retinae, or both. It is possible to overcome this problem to some extent by using only suprathreshold depth judgements (e.g. Richards, 1972; Regan and

Beverley, 1973A; Sections 3:4, 3:5 and 3:6). However it is uncertain whether results from matched depth experiments can be extrapolated to threshold. What is required is a method for distinguishing between the effects of changes in retinal disparity, and the effects of sideways movements on the two retinae. One method of making this discrimination, so as to allow stereoscopic threshold to be measured independently of sideways movements, is described below.

Wheatstone (1838,1852) has shown that retinal disparity cues alone are sufficient to produce a sensation of depth. Two stimuli may therefore be presented, one to each eye, in such a manner that when fused, one area of the stimulus pattern appears at a different depth to the remainder. If the retinal disparity is rhythmically changed, one area (e.g. the centre) of such a stimulus can be made to appear to oscillate in depth (e.g. Regan and Spekreijse, 1970). However, the frequency of movement in depth is the same as the frequency of sideways movement on the two retinae, and it is thus difficult to distinguish between sideways and depth movements, particularly near threshold. This confusion of sideways movement and movement in depth occurs largely because the two movements produce qualitatively similar sensations near threshold. It is not necessary, however, that oscillations in depth and sideways oscillations should have the same frequency. If they have different frequencies the subject can use the difference in frequency as a cue to distinguish between sideways and depth oscillations near threshold. A single stimulus pattern can be made to oscillate in depth at a frequency which is different from the frequency of its side to side oscillation. One way of creating this illusion is as follows.

The stimulus pattern seen by the left eye is made to oscillate from side to side at one frequency (F_l), and the pattern seen by the right eye is made to oscillate from side to side at a slightly different frequency (F_r). Provided that fusion can be maintained, a stimulus is generated in which the frequencies of sideways oscillation on the two retinae (F_l and F_r) are different from the frequency at which the subject sees oscillations in depth ($\Delta F = F_l - F_r$). If the frequency difference ΔF is small compared with F_l (and F_r), the amplitude of the stimulus's apparent oscillations in depth waxes and wanes ΔF times per second. Neither F_l nor F_r need be related to ΔF, so that oscillations in depth can be dissociated from sideways oscillations at threshold by the difference in frequency. Furthermore, the frequency of oscillation in depth can be altered independently of the frequencies of sideways movement on the two retinae, thus the two threshold functions can be independently measured.

It should be emphasised that under all stimulation conditions both left and right eyes view unvarying sinewave (or squarewave) stimulus oscillations.

A complete description of actual and apparent stimulus movements is given in Appendix 4 for sinewave oscillations and in Appendix 5 for squarewave oscillations.

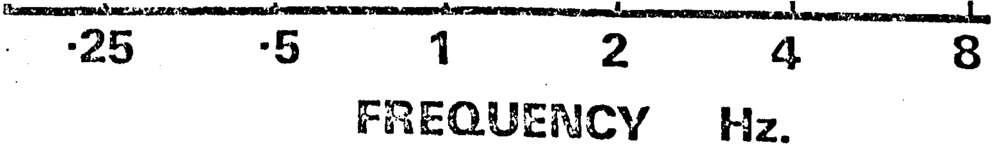
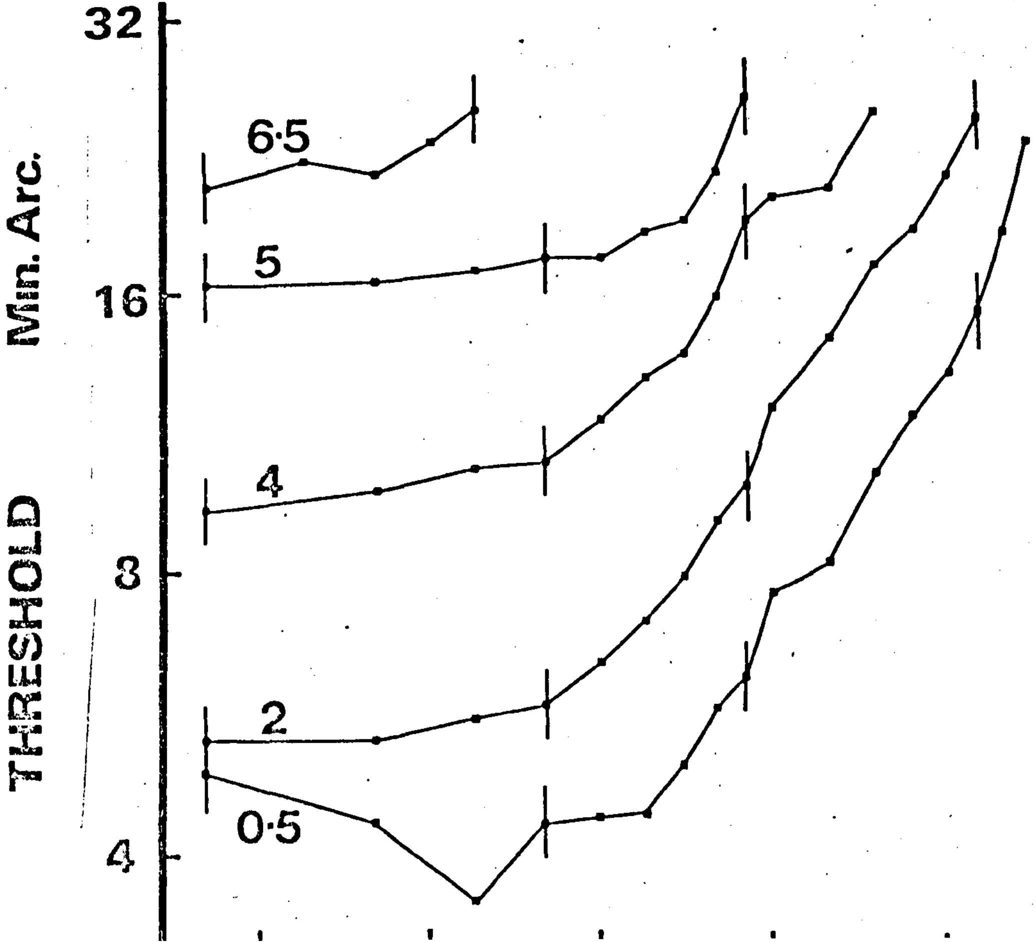


Figure 30. Visual sensitivity for movements in depth for squarewave oscillations of the stimulus targets. Thresholds for depth movements (mins. arc) are plotted versus the stimulus oscillation frequency ΔF (in Hz.) for F equals 0.5, 2, 4, 5 and 6.5Hz.. Subject K.B.. Both axes are logarithmic.


THRESHOLD
Min. Arc.
32
16
8
4
6·5
5
4
2
0·5

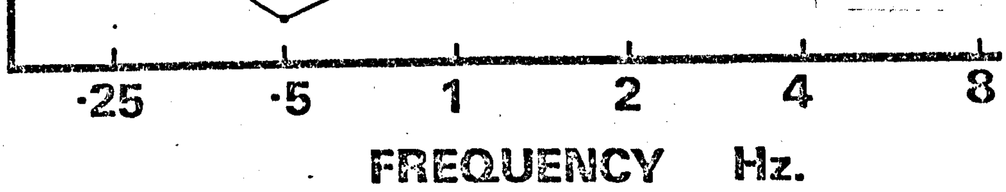
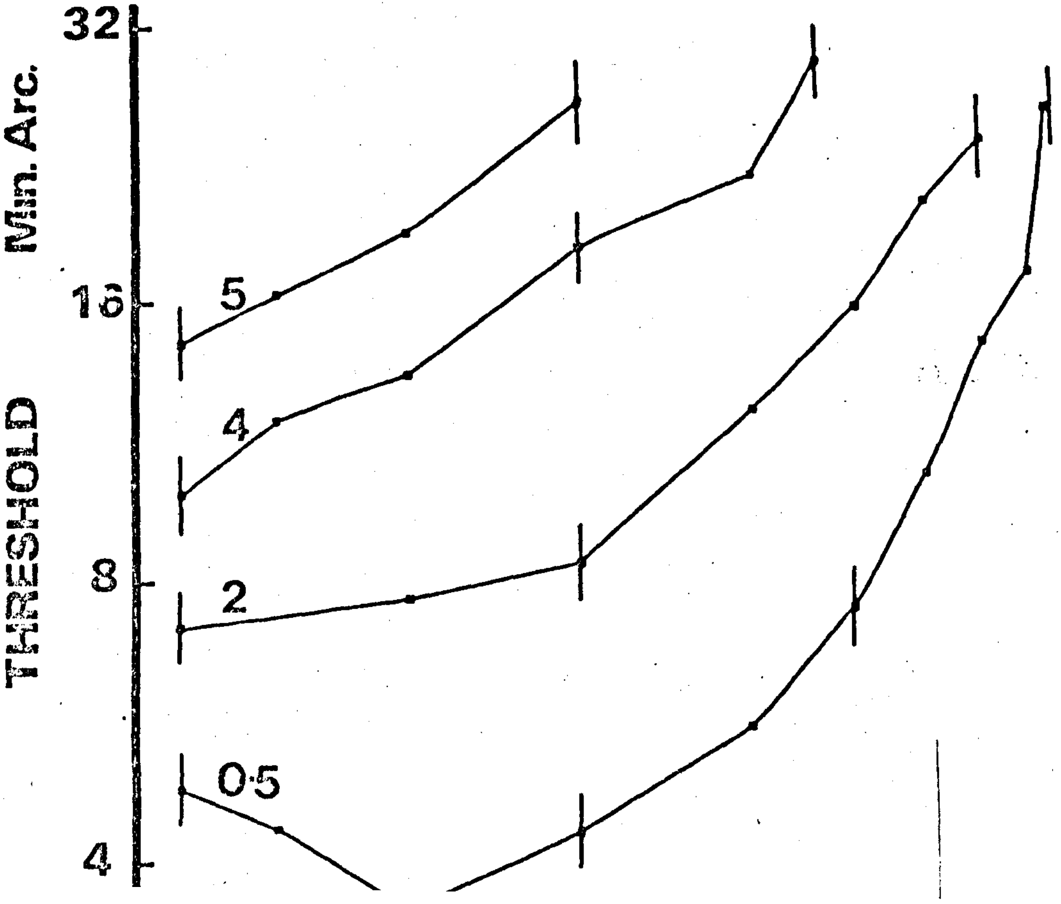


Figure 31. Visual sensitivity for movements in depth for squarewave oscillations of the stimulus targets. Thresholds for depth mavements (mins. arc) are plotted versus the stimulus oscillation frequency F (in Hz.) for ΔF equals 0.5, 2, 4 and 5Hz.. Subject K.B.. Both axes are logarithmic.



THRESHOLD Min. Arc.
32
16
8
4
5
4
2
0·5

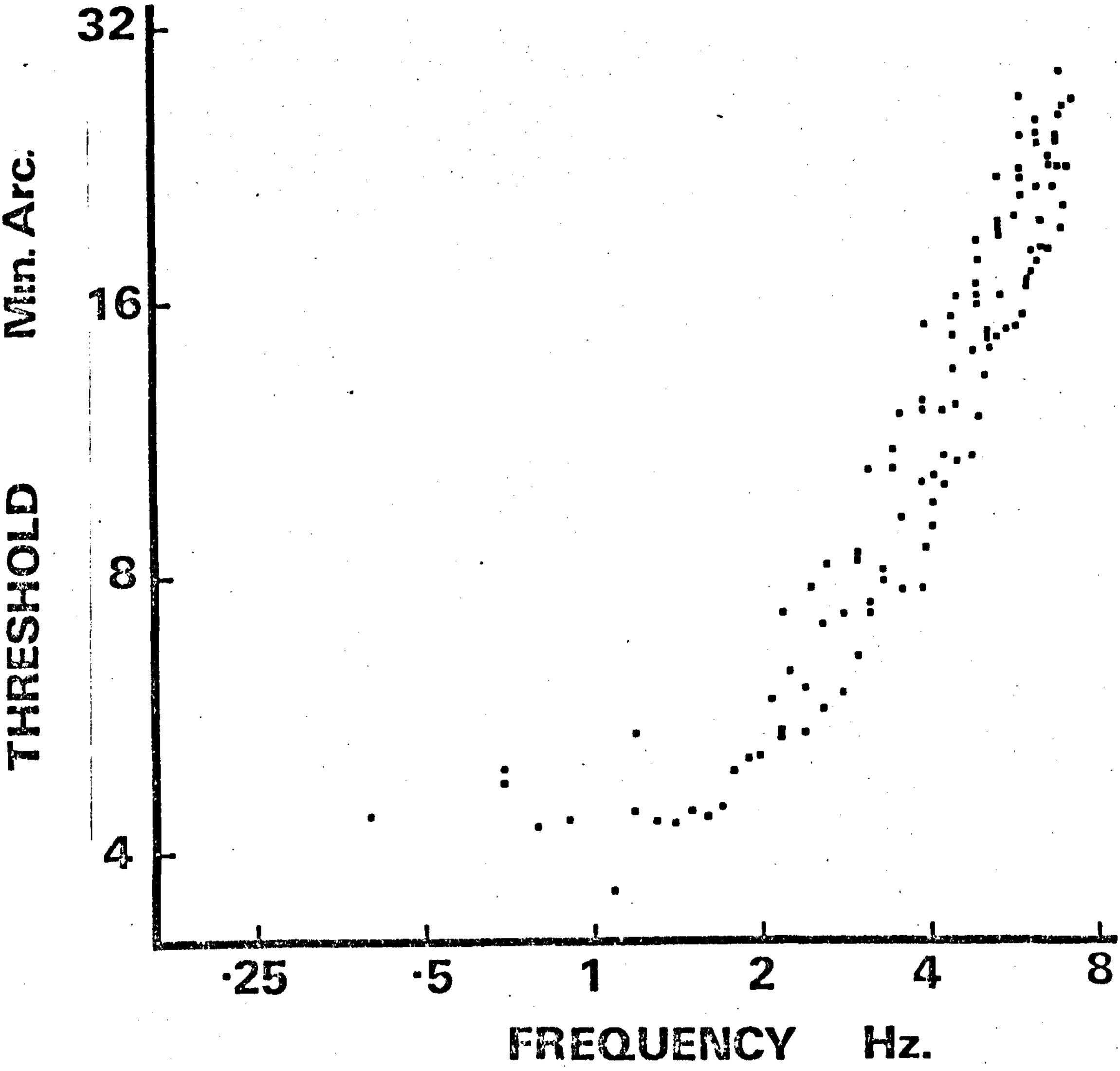


Figure 32. *Visual sensitivity for movements in depth for squarewave oscillations of the stimulus targets. The threshold measurements from Figs. 30 and 31 plus additional data are replotted versus (F + ΔF).*

4:2. Squarewave Stimulation.

4:2:1. Results.

Fig.30 shows the threshold for the perception of movement in depth (ordinate) plotted *versus* ΔF for five different values of F. The figure shows that, for constant F, psychophysical sensitivity for the perception of movement in depth fell sharply as ΔF was increased above roughly 1Hz.. Movement in depth could not be seen at all, no matter how large the change in disparity, when ΔF was increased beyond 6Hz.. Increasing the frequency F led to a decrease in this "cut-off" frequency. No movement in depth could be seen at all when F was 6.6Hz. for ΔF greater than 0.6Hz.. For F equals 0.5 Hz., there was a slight increase in depth threshold as ΔF was decreased below about 0.5Hz..

Similar results were obtained for a second subject D.R..

4:2:2. Discussion.

If the data from Fig. 30 are replotted *versus* F (the frequency of oscillation of the left eye's stimulus) instead of ΔF, the series of curves shown in Fig. 31 result. Comparing Fig. 30 with Fig. 31, a marked similarity was observed. One interpretation of this similarity is that physiologically there was little difference between the effects of F and ΔF, so that to a first approximation, the effects of F and ΔF could be described in terms of a single parameter.

If the data from Fig. 30 are again replotted, this time *versus* $F+\Delta F$ (the frequency of stimulation of the right eye) then all the points lie along a single curve (Fig. 32 - note additional data to that of Fig. 30 and Fig. 31 has been incorporated). This suggests that $F+\Delta F$ is the important stimulus parameter. The question now arises, what does the parameter $F+\Delta F$ represent? It is clear that the fact that $F+\Delta F$ was the frequency of stimulation of the right eye is irrelevant. The fact that $F+\Delta F$ was the highest frequency present, however, may be of somewhat more importance.

The form of the retinal disparity function with time is shown in Appendix 5. It is notable that only three discrete values of disparity are possible, and that the maximum "dwell time" at any one disparity is $1/(F+\Delta F)$ seconds. The importance of the parameter $F+\Delta F$ now becomes obvious. To a first approximation, the threshold for squarewave movement in depth can be described entirely in terms of a "dwell time" equal to $1/(F+\Delta F)$ seconds. As the maximum stimulus "dwell time" is increased, depth threshold falls. The slope is approximately 6dB/octave. This relationship fails at a "dwell time" of approximately 500 millisecs., which implies that somewhere in the stereoscopic visual system there are neural mechanisms which integrate disparity information over time.

This 500 millisec. integration time is considerably longer than the integration time for light intensity (60-100 millisecs., Bloch, 1885) and even longer than the integration time for wavelength changes (150-300 millisecs., Regan and Tyler, 1971) or visual tasks (200-350 millisecs., Kahneman and Norman, 1964).

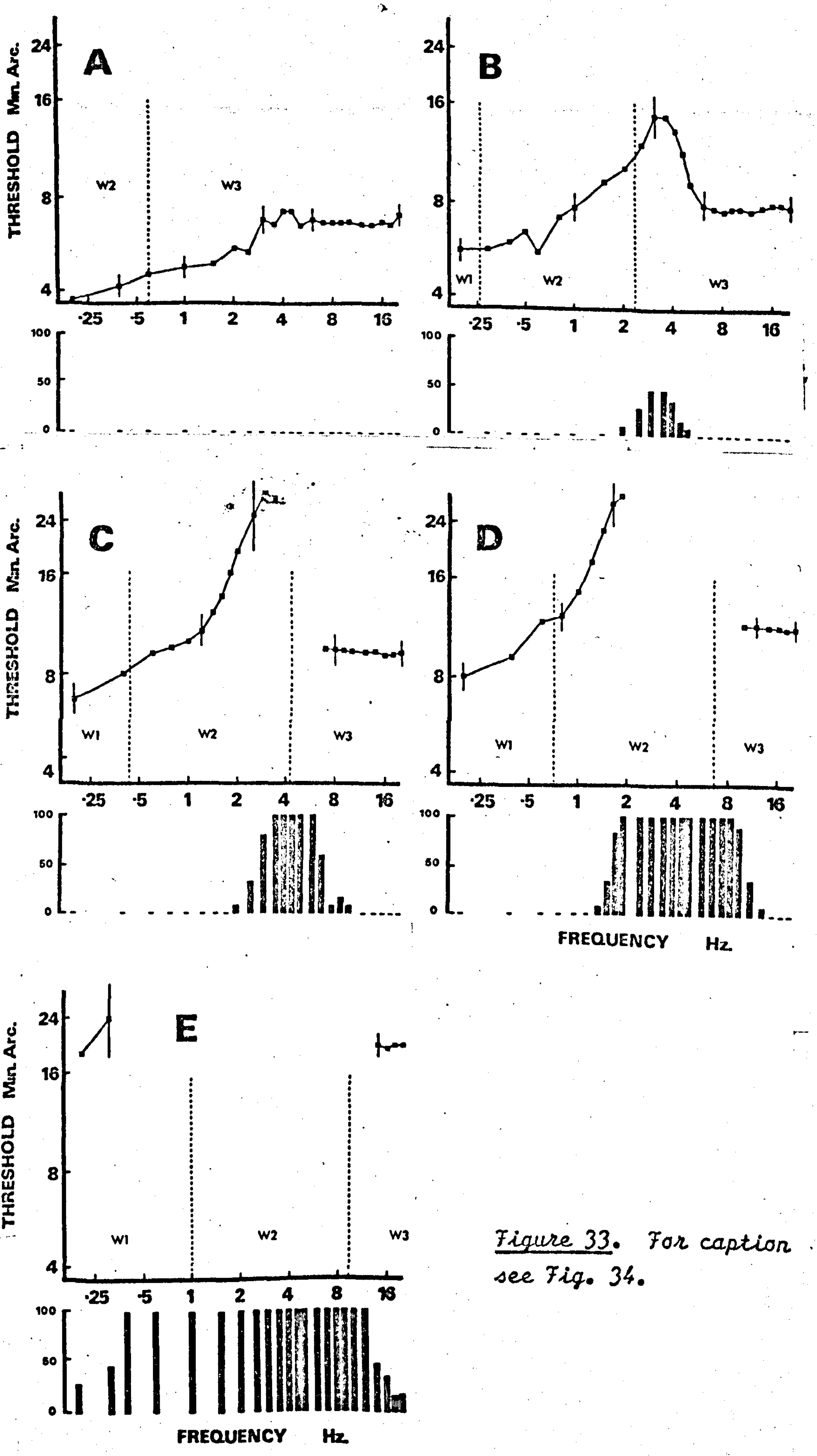


Figure 33. For caption see Fig. 34.

4:3. Sinewave Stimulation.

4:3:1. Results.

Fig. 33a (upper) is a plot of threshold for perception of movement in depth (ordinate) *versus* ΔF (abscissa), for a value of F of 0.2Hz.. The figure shows that psychophysical sensitivity for the perception of movement in depth (depth movement sensitivity) fell sharply as ΔF was increased to roughly 2Hz.. When ΔF was increased beyond 2Hz., the appearance of the stimulus altered surprisingly. If the right eye was closed, the left eye's stimulus appeared to be oscillating at FHz., however , if the left eye was closed, the right eye's stimulus appeared stationary, though blurred.

Instead of an oscillation in depth at frequency ΔFHz. (e.g. at 4Hz.), the binocularly-fused stimulus appeared to move slowly in depth at frequency FHz. (here 0.2Hz.). (Julesz (1961,1965) has reported that depth sensations can be elicited by viewing two stationary patterns, one of which is sharp and the other optically blurred.) The binocularly-fused stimulus appeared to move along a straight line directed towards the right eye. Within the limits of experimental error, depth movement sensitivity was now independent of frequency ΔF up to the highest frequency studied (20Hz.). This was termed "depth region 2".

Fig. 33a (lower) shows the percentage of readings for which depth could not be perceived (ordinate) plotted as a histogram *versus* ΔF. For $F=0.2$Hz., depth was seen in all cases.

Fig. 33b shows the results for $F=0.8$Hz.. Depth movement sensitivity decreased sharply as ΔF was increased to roughly 3Hz.. However, as ΔF was increased beyond 4Hz., depth movement sensitivity increased sharply. Beyond 6Hz., depth region 2 set in and depth movement sensitivity became independent of ΔF. Fig. 33b (lower) shows that for frequencies between 2Hz. and 6Hz., depth could not be perceived at all in some percentage of trials.

Fig. 33c shows the results for F=1.4Hz.. Depth movement sensitivity decreased sharply as ΔF was increased to roughly 3Hz.. For ΔF between 3Hz. and 7Hz., movements in depth were never seen, no matter how large the oscillation amplitude. Beyond 7Hz., depth could again be seen as depth region 2 set in. Between 7Hz. and 20Hz., depth movement sensitivity was independent of ΔF.

Fig. 33d shows the results for F=2.2Hz.. The region where depth was never visible had increased, and extended from 1.8Hz. to 10Hz.. The regions of normal stereoscopic depth perception and depth region 2 had decreased.

Fig. 33e shows the results for F=3.0Hz.. The region where depth was never visible had increased, and extended from 0.3Hz. to 14Hz.. The regions of normal stereoscopic depth perception and depth region 2 had further decreased.

For frequency F less than 3Hz., depth was usually visible for some values of ΔF. For frequency F greater than 3Hz., depth was never visible for frequencies of ΔF in the range 0.1 - 20Hz. (the limits of the apparatus).

It is clear that the curves shown in Fig. 33 have three distinct regions.

For low frequencies of ΔF (less than 2 - 3Hz.)*, depth movement sensitivity was strongly dependent on both F and ΔF. Depth movement sensitivity decreased when either F or ΔF was increased in frequency. Subjectively, the stimulus appeared to move in depth along a roughly elliptical path. Large depth excursions were visible, decreasing as either F or ΔF were increased in frequency. Considerable sideways movements of the stimulus could be seen in either eye. In this region depth was seen on practically 100% of trials.

For medium frequencies of ΔF (1 - 10Hz. dependent on F), sensitivity to changes in depth was low or inappreciable. The range of frequencies of ΔF over which depth could never be seen increased as F increased. Subjectively the depth impression was very poor and was only visible over a limited range of stimulus oscillation amplitudes. Frequently the impression of depth was completely absent. Considerable sideways movement of the stimulus could be seen in either eye. In this region depth was seen on practically 0% of trials.

For high frequencies of ΔF (greater than 5Hz. dependent on F), sensitivity to changes in depth was high and independent of ΔF. This region was termed the "depth region 2". Subjectively the stimulus appeared to oscillate sinusoidally in depth at FHz. along a straight line directed towards the right eye. The left eye's stimulus appeared to oscillate at FHz.. The right eye's stimulus appeared stationary but blurred. Increasing the stimulus oscillation amplitude until sideways movement became visible by the right eye caused the sensation of depth to break down. In this region depth was seen on practically 100% of trials.

Finally it is clear from Fig. 33 that X oscillations of retinal disparity per second produced no sensation that depth was changing X times per second unless X was less than 2 - 3Hz.. The exact frequency was different for different subjects, but if X exceeded this, the subject <u>could not see depth changes</u> however large the change in disparity.

4:3:2. Discussion.

All the depth movement sensitivity functions of Fig. 33 can be described in terms of three frequency regions. The most obvious explanation for the existence of these three frequency regions of the psychophysical curves would be if the stimulus disparity function

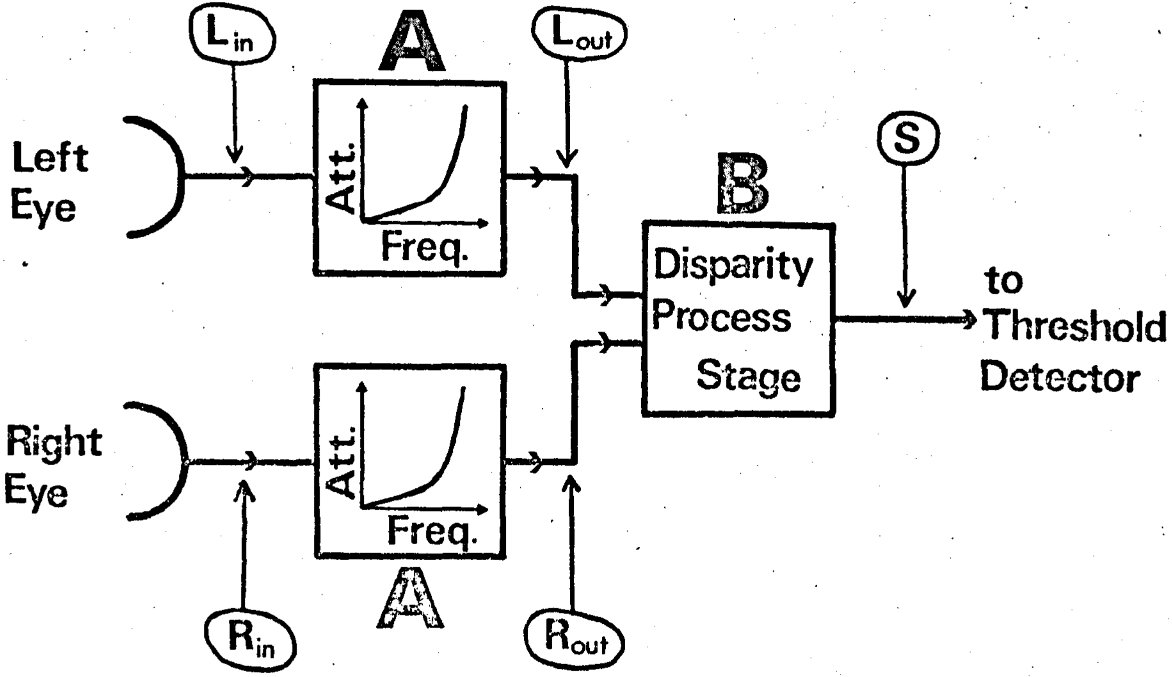
"Sine(F+ΔF) - Sine(F)" changed with time in one of three different ways. This is in fact the case (see Appendix 4), although there were no abrupt transitions from one waveform to the next. The frequencies at which the changeovers between the three stimulus waveforms occurred have been indicated by the vertical dotted lines in Fig. 33. (Note that although the criteria for the changeover frequencies adopted in Appendix 4 are, within limits, arbitary, they are not sufficiently so, as to affect the conclusions of this Section.) It is clear that these vertical dotted lines do not correlate with the boundaries of the three psychophysical regions (roughly where the percentage of no depth responses are 50%). This suggests that the psychophysical results are not due merely to changes in the appearance of the stimulus waveform, but must reflect changes in the visual processing of the stimulus.

One possible explanation for the perception of depth for high frequencies of ΔF (depth region 2) lies in the monocular behaviour of the stimulus. For high frequencies of motion oscillation ((F+ΔF) in the right eye), the stimulus appeared blurred but stationary. This would appear to be some form of "motion fusion", indicative of an integration process in the monocular pathway, sufficiently peripheral to be common to both motion and depth channels (Regan and Beverley, 1973A, 1973B; Section 3:1:1). For small oscillation amplitudes "motion fusion" occurred at frequencies as low as 5Hz.; it became more marked, however, at frequencies above 10Hz.. This indicates that the integration time constant was of the order of 16 millisecs. (The curves of Fig. 11 indicate a turnover frequency of 4.7Hz., and an integration time constant of 34 millisecs.). The stereoscopic stimulus for high frequencies of ΔF was, therefore, equivalent to a blurred stationary pattern in the right eye, and a slowly moving pattern of frequency F in the left eye. As is to be expected from Julesz's (1961, 1965) results, this stimulus is capable of producing a sensation of movement in depth; the frequency of movement being 7Hz.. If the stimulus oscillation amplitude were to be increased, then the "motion fusion" would break down and the depth sensation would be lost. This phenomena is thus limited to a restricted range of stimulus oscillation amplitudes.

One possible explanation of the threshold curves for low frequencies of ΔF (less than 2 - 3Hz.), lies in assuming an integration process to occur in the stereoscopic pathway. On this assumption the sensation of movement in depth would be expected to decrease as (the depth) frequency is increased (see Sections 4:4:1 and 4:4:2 for a quantitative analysis of this important point).

The depth sensitivity region for medium frequencies of ΔF, therefore, could be the region where the phenomenon of "motion fusion" did not occur, and where the range of normal depth perception was exceeded.

Thus, it can be seen that normal stereoscopic depth perception is limited to the situation where the stimulus oscillation frequency in both eyes is below 3Hz.. Even when one stimulus frequency exceeds about 1Hz., depth sensitivity is severely degraded. This supports Regan and Beverley's (1973A, 1973B) suggestion that stereoscopic depth thresholds for frequencies in excess of 1Hz. are in fact determined primarily by the sideways movements of the retinal images (see Chapter 3).



Left Eye
Right Eye
L_{in}
R_{in}
A
Att.
Freq.
A
Att.
Freq.
L_{out}
R_{out}
B
Disparity Process Stage
S
to Threshold Detector

Figure 34. Model. Stage A signals retinal image position and has the attenuation versus frequency characteristic shown. Stage B contains all signal processing after the signals from the two eyes unite. L_{in} and R_{in} are the peak-to-peak amplitudes of sinusoidal retinal image movements in the left and right eyes respectively. L_{out} and R_{out} are the peak-to-peak amplitudes of the sinusoidal outputs of the left and right Stage A elements respectively. S is the disparity output of Stage B which goes to the threshold detecting stage.

Figure 33. (preceeding Figure). Visual sensitivity to oscillations in depth for sinusoidal oscillations of the stimulus targets. Upper part of each graph is a plot of threshold for depth movement (mins. arc) versus the difference frequency ΔF (in Hz.) between the oscillation frequencies of the left and right eyes' stimulus targets. Each filled square is the mean of 10 settings; each unfilled square is the mean of less than 10 settings. Vertical bars represent $\pm$ 1 S.D.. Vertical dashed lines indicate the frequencies at which the changeovers between the three stimulus waveforms occurred (regions W1, W2 and W3). Lower part of each graph shows the percentage of trials in which depth movements could not be seen for any amplitude of disparity oscillations. Frequency of sideways oscillation of left eye's target was 0.2Hz. (A), 0.8Hz. (B), 1.4Hz. (C), 2.2Hz. (D) and 3.0Hz. (E). Subject K.B..

4:4. Models.

4:4:1. Failure of a "Simple" Model.

Section 4:3:2 suggested that the decrease in depth movement sensitivity for low frequencies of ΔF (less than 2 - 3Hz., see Fig. 33) could be explained by assuming an integration process to occur in the disparity processing pathway. In this Section an alternative hypothesis - that all integration takes place before the signals from the two eyes interact - is considered.

Fig. 34 shows a simple model which assumes that the depth threshold is determined solely by attenuation in the monocular pathway before the signals from the two eyes unite. Stage A, which signals retinal image position, contains the integrative element. Stage B, into which is condensed all signal processing after the signals from the two eyes unite, contains no integrative elements. L_{in} and R_{in} are the peak to peak amplitudes of sinusoidal retinal image movements in the left and right eyes respectively. L_{out} and R_{out} are the peak to peak amplitudes of the sinusoidal outputs of the left and right stage A elements respectively. S is the disparity output of stage B which goes to the threshold-detecting stage. It is assumed that threshold judgements are made at a particular value of S. It is further assumed that S is proportional to $L_{out} - R_{out}$ (i.e. that stage B is linear).

As ΔF tends towards 0Hz., $(F+\Delta F)$ tends towards FHz. and the apparent movement of the stimulus becomes a simple sinusoidal oscillation in depth with unchanging peak to peak amplitude. The threshold attenuation of this depth oscillation with frequency must represent the total attenuation affecting disparity processing. Since all the attenuation is assumed to occur at stage A, then the high-frequency attenuation of the curve representing depth movement threshold <u>versus</u> stimulus oscillation frequency $(F+\Delta F)$Hz., as ΔF

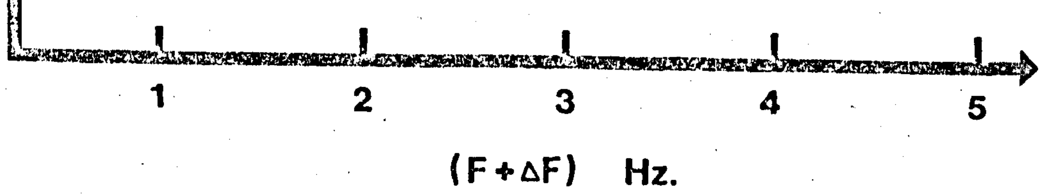
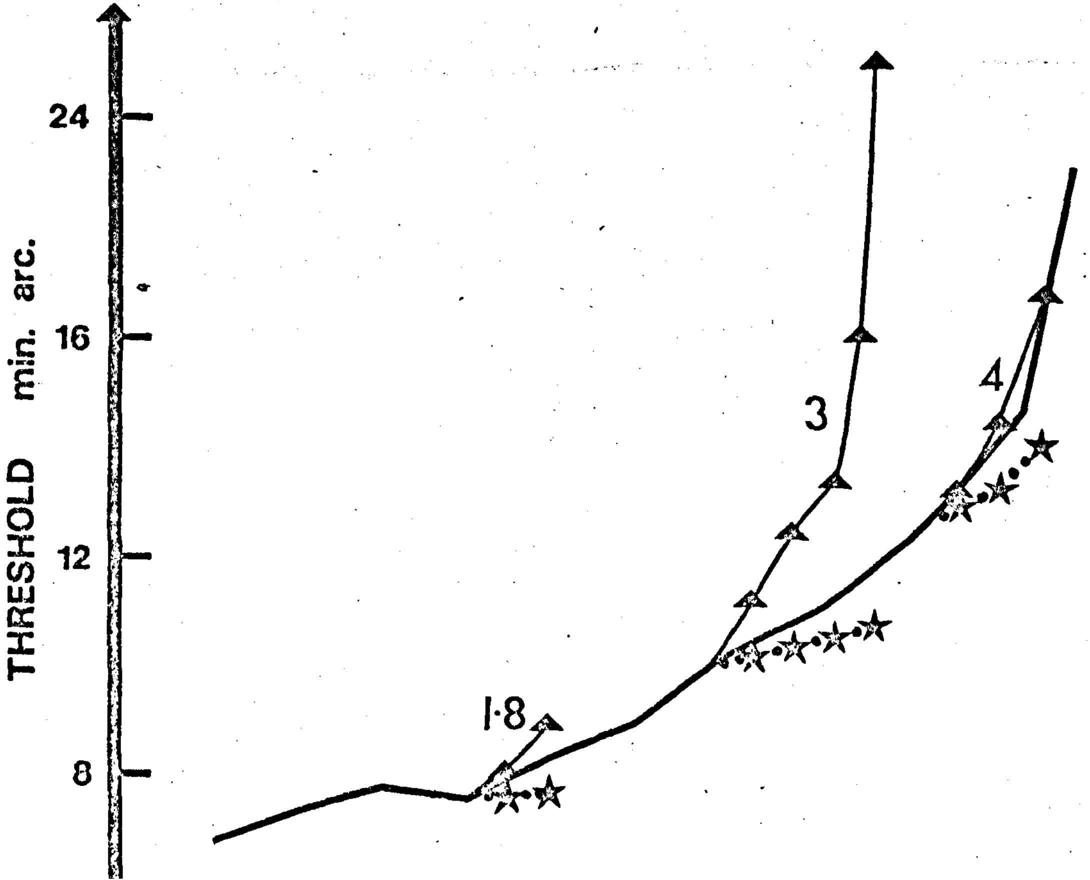


Figure 35. Theoretical prediction of the effect of ΔF upon depth threshold. The thick continuous line joins experimentally-measured values of depth threshold for different values of $(F + \Delta F)$ with ΔF very small (0.2Hz.). The continuous thin lines join experimentally-measured points and show the effect of increasing ΔF for fixed values of F equal to 1.8, 3 and 4Hz.. The dotted lines join predicted values of threshold shown as stars (see text).


THRESHOLD min. arc.
24
16
12
8
1·8
3
4

tends towards 0Hz. will be the linear sum of the high-frequency attenuations in the left and right monocular channels.

The heavy full line in Fig. 35 represents this attenuation curve (It is actually the curve for $\Delta F = 0.2$Hz. plotted <u>versus</u> $(F+\Delta F)$Hz.).

(It is probably equally justifiable to derive the stage A attenuation from the suprathreshold curves of Fig. 24 as matched depth tends towards 0 min. arc. This procedure gives results which do not differ significantly from the results presented below).

The high-frequency attenuations of the left and right stage A's are, therefore, half the attenuation represented by this curve, and are shown in Table 1. (Attenuation in stage A left, $(L_{in}-L_{out})/L_{in}$ = attenuation in stage A right, $(R_{in}-R_{out})/R_{in}$.)

Table 1

Frequency Hz.	Threshold min. arc	Total Attenuation %	Attenuation in Either Eye %
0.8	5.5	0	0
1.2	6.5	17	8
1.6	7.2	25	12
2.0	6.9	21	11
2.4	8.3	35	17
2.8	9.4	42	21
3.2	11.6	53	27
3.6	13.0	58	29
4.0	15.2	64	32
4.4	18.1	70	35
4.8	22.8	77	39

Where the frequencies of stimulation of the left and right eyes differ (ΔF greater than 0), the total attenuation due to stage A will be equal to the sum of the attenuations in the left and right channels. For example, if F = 2.8Hz. and ΔF = 0.8Hz. (that is, left eye's stimulus frequency is 2.8Hz., right eye's stimulus frequency is 3.6Hz.) then the total attenuation due to stage A will be 21% (left) + 29% (right) = 50%. The predicted depth threshold for F = 2.8Hz., ΔF = 0.8Hz., is, according to Table 1, between 9.4 and 11.6 min. arc (by interpolation 10.9 min. arc).

Points calculated in this manner are plotted in Fig. 35 as stars (dotted line) for three different frequencies for F. Corresponding experimentally-determined points are plotted as triangles (fine line). The number by each line is F.

It is clear that there is a large discrepancy between the predicted and experimental values. This suggests that the assumption - "there is no attenuation after the signals from the two eyes unite" - is wrong. Furthermore, the larger the frequency difference ΔF, the larger was the discrepancy between the predicted and the experimental values. The effect of ΔF upon depth movement threshold must, therefore, be explained, at least in part, by signal processing after the signals from the two eyes unite.

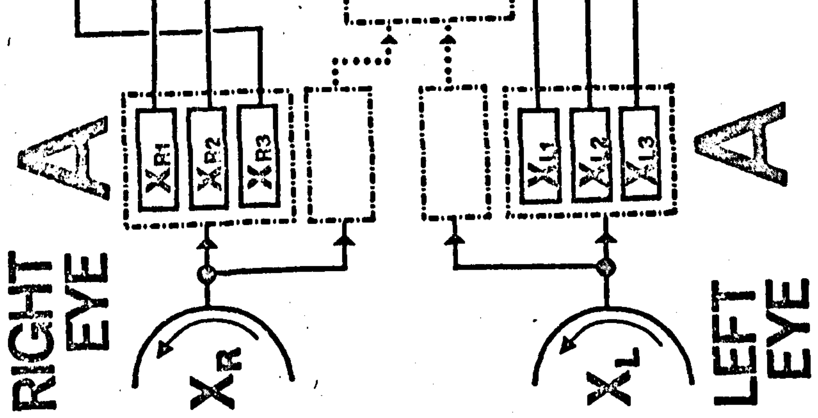
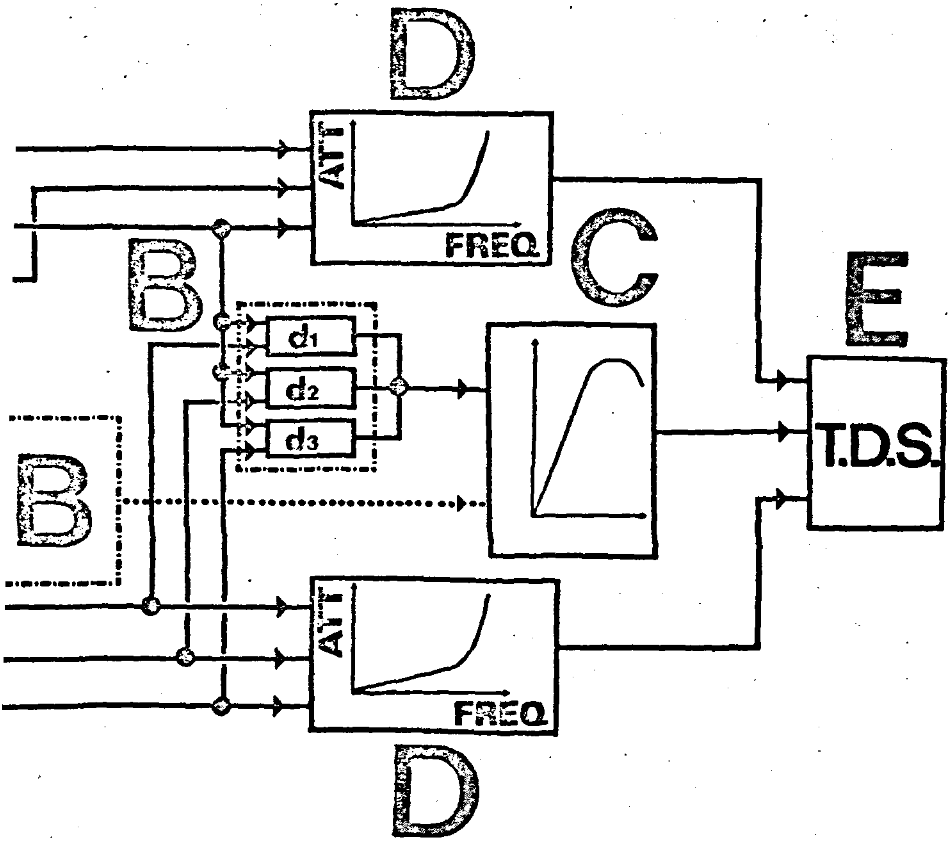


Figure 36. Model. Neural processing of retinal disparity information. Stage A - boxes bounded by chain lines signal retinal image position. Each box contains a population of elements (e.g. X_{r1}, X_{r2} etc.). Each element is sensitive over a restricted retinal region. Stage B - boxes bounded by chain 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 (centered on d1, d2 etc.). Stage C - sums the outputs of the disparity computing elements of Stage B. The input-output characteristic of Stage C is shown. Stage D - signals translational velocity of the retinal image and hence the sideways velocity of the stimulus target. Stage D has the attenuation versus frequency characteristic shown. Stage E - threshold detection stage.


D
ATT
FREQ
B
C
E
d1
d2
d3
T.D.S.
B
ATT
FREQ
D

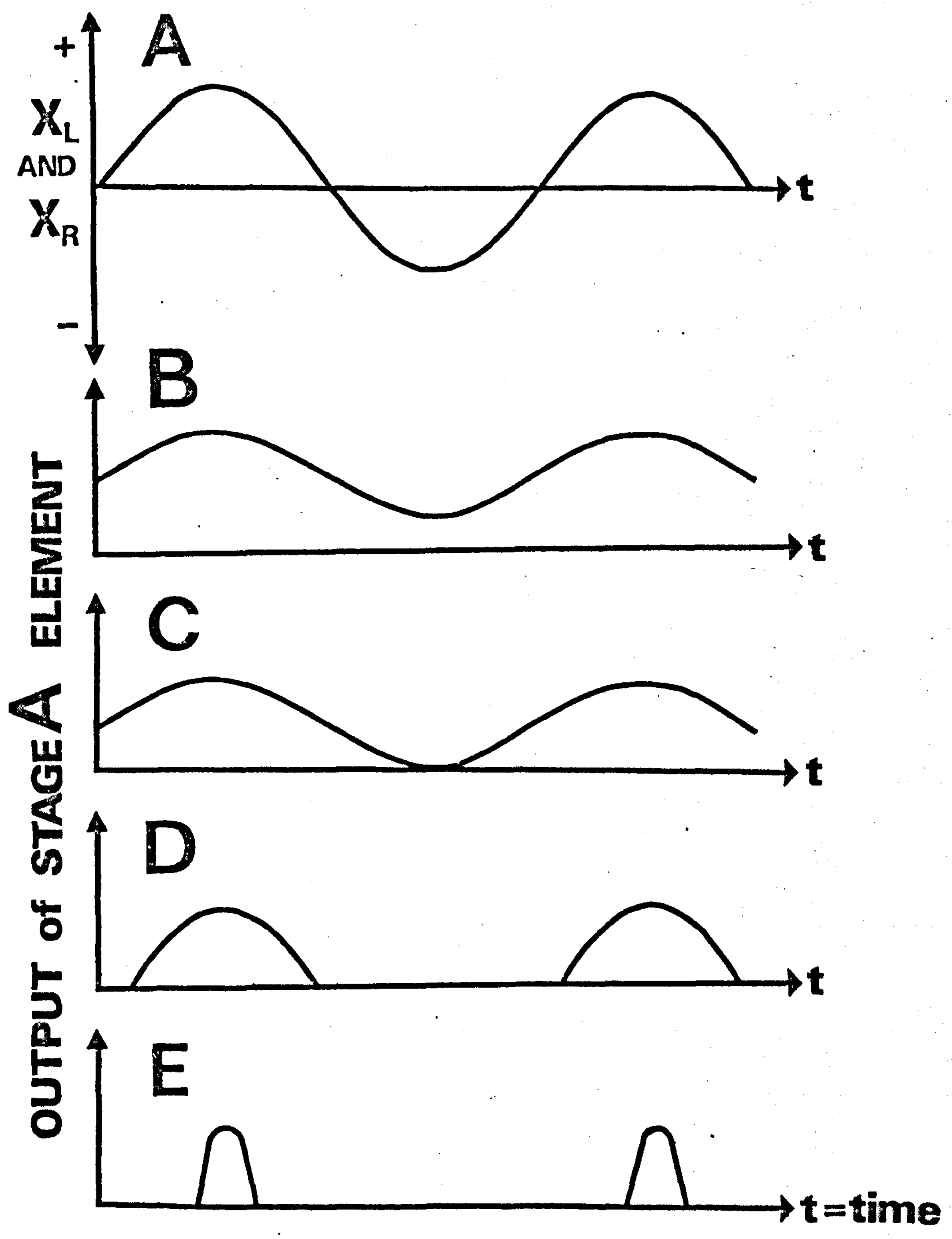


Figure 37. A - sideways displacements of targets viewed by left and right eyes. X_l and X_r are the positions of the retinal images in the left and right eyes. This stimulus causes Stage A elements to respond as shown in B, C, D and E. B is for a Stage A element whose retinal receptive field is large. C, D and E are for progressively smaller receptive fields.

4:4:2. Description of a Second Model.

The model shown in Fig. 36 can account for most of the findings of Chapters 3 and 4.

Stage A consists of contour position (contrast) detectors (X_{R1}, X_{L1}, X_{R2}, etc.) each of which gives an output whenever the position of the retinal image (X_L, X_R) lies within its receptive field. Some stage A elements respond preferentially to retinal image movements directed from left to right; other stage A elements respond preferentially to movements from right to left. The contrast detectors integrate retinal image movement with respect to time. This means that if the stimulating contour does not remain sufficiently long within the receptive field then the output of the contrast detector will be attenuated.

If the excursion of the retinal image remains within the receptive field of any stage A element, then the output of that element will be approximately sinusoidal and of the same frequency as the stimulus oscillation frequency (see Fig. 37A). The stage A elements which have the largest receptive fields will give the smallest sinusoidal response to stimulus oscillations (compare Figs. 37B, C, D and E). The outputs of the elements with the largest receptive fields will also be the first to fuse when the stimulus oscillation frequency is increased.

The results of Section 3:1:1 (Fig. 11) suggest that the integration time constant (τ_A) is approximately 30 milliseconds for stage A elements whose receptive field exceeds some 0.5 min. arc. This probably includes all stage A elements since the monocular receptive field size for the majority of binocularly-sensitive neurons (in cats) has been reported to be in excess of some 20 min. arc (Pettigrew, Nikara and Bishop, 1968).

The output of stage A elements with small response areas (Fig. 37E) will only be attenuated when the durations of the

Figure 38. The effect of temporal integration on the outputs of individual disparity computers. A - plot of relative response versus retinal disparity for a narrowly-tuned Stage B element. B - time-course of retinal disparity changes caused by a target which executes sinewave oscillations in depth. C - output of narrowly-tuned disparity computer shown in A. Disparity computer responds to increasing but not to decreasing disparity. D - as C, but disparity computer responds only to decreasing disparity. E, F, G and H are similar to A, B, C and D, but refer to a broadly-tuned Stage B element which responds over the whole range of stimulus disparities. C, D, G and H also show the effects of a short (dotted line) and a long (chain line) integration time constant.

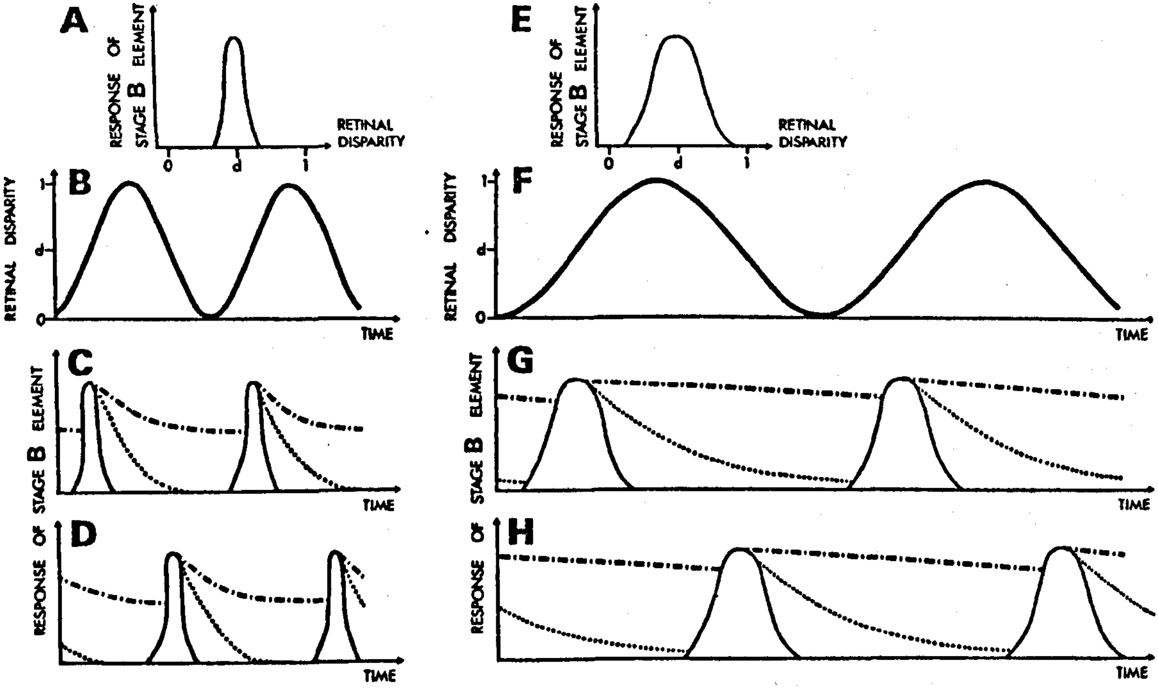

A
RESPONSE OF STAGE B ELEMENT
RETINAL DISPARITY
0
d
1
B
RETINAL DISPARITY
1
d
0
TIME
C
D
RESPONSE OF STAGE B ELEMENT
TIME
TIME
E
RESPONSE OF STAGE B ELEMENT
RETINAL DISPARITY
0
d
1
F
RETINAL DISPARITY
1
d
0
TIME
G
H
RESPONSE OF STAGE B ELEMENT
TIME
TIME

Fig. 37E pulses are comparable with 1/F (where F is the stimulus oscillation frequency). This will only occur at high stimulation frequencies, when depth movement sensitivity is already greatly reduced.

Stage B consists of a matrix of disparity computers (d1, d2, d3, etc.). Each element receives contour position information (X_L and X_R) from the left and right eyes and computes the retinal disparity for a small retinal area ($d = X_{Ln} - X_{Rm}$). Stage B elements only respond to a restricted range of retinal disparities. Each individual stage B element has an integration time constant (τ_B). The effect of τ_B upon the outputs of individual stage B elements is shown in Fig. 38.

Fig. 38A - D show a stage B element which only responds over a very narrow range of retinal disparities. Fig. 38E - H show a stage B element responsive to a broad range of retinal disparities. Fig. 38A and E represent the responses of two stage B elements plotted versus retinal disparity. Fig. 38B and F represent the sinewave oscillations of the retinal disparity of the stimulus. Fig. 38C shows the response of a narrowly-tuned stage B element which responds during only a small part of the stimulus cycle. If the stage B element has a short τ_B then its output will follow the dotted line; for a long τ_B its output will follow the chain line. For a given input, a longer τ_B will mean less variation in the output from the stage B elements, and therefore, lower sensitivity to movements in depth. Increasing the frequency of stimulation for a constant τ_B will also lower the sensitivity to movements in depth.

Stage B elements whose response is restricted to 1/10th. of the stimulus cycle will show the required decrease in depth movement sensitivity with frequency (Fig. 35 thick line) for a τ_B of 53 milliseconds (single-stage R-C filter). Stage B elements whose response is restricted to ½ of the stimulus cycle (Fig. 38G) will show a similar decrease in depth sensitivity for a τ_B of 30 milliseconds.

Disparity-selective single units have been described whose sensitivity had fallen by 10% when retinal disparity was altered by 1.5 min. arc (Pettigrew _et al_, 1968). This suggests that 3 min. arc will be a generous estimate of the minimum width of the sensitivity curve shown in Fig. 38A. The maximum retinal disparity excursion used in these experiments was 30 min. arc which means that the minimum width of the sensitivity curve is 1/10th. of a stimulus cycle. This in turn means that the longest τ_B for the most selective stage B element will be 53 milliseconds. For subject D.R. the longest τ_B will be 62 milliseconds.

Segregation of left-right and right-left retinal image movements is maintained beyond stage B.

Stage C sums the outputs of the disparity-computing elements of stage B. The outputs of the stage B elements are weighted, progressively higher weighting being given the larger the retinal disparity. The weighted sum of the outputs of stage B determines the amount of depth seen. If the weighted sum grows too large, however, the output of stage C falls to nearly zero (see Fig. 36 for input/output characteristic). This discontinuity coincides with the loss of binocular fusion for large disparities. The finding that depth sensations can be elicited by retinal disparities which cannot be fused (Ogle, 1953) requires that the output from stage C remains above zero for very large disparities.

Segregation of left-right and right-left retinal image movements is maintained beyond stage C.

Stage D computes the sideways velocity of the retinal images and hence the sideways velocity of the stimulus. The left-right and right-left outputs from the stage A elements are segregated up to stage D in order to account for the well known aftereffects of seen movement (see for example Barlow and Hill, 1963).

<u>Stage E</u> is the threshold detection stage.

<u>4:4:3. Findings Explained by the Second Model and Some Predictions.</u>

The decrease in sideways movement sensitivity at high frequencies (Fig. 11) can be explained by the temporal integration of stage A elements (time constant τ_A), together with the temporal integration of stage D elements (see Fig. 36). The decrease in sensitivity to sideways movements at low oscillation frequencies (Figs. 11, 13 and 18) can be explained by high pass filtering associated with stage D. The decrease in sensitivity to movements in depth for frequencies above about 1Hz. can be explained by the time constants (τ_B) of 30-60 milliseconds for stage B elements.

For suprathreshold squarewave stimulation at frequencies in excess of 3Hz., two stationary stimulus patterns located at different depths are seen instead of one moving stimulus pattern (Section 3:5:1). This subjective observation can be explained by the integration time constants (τ_B) of the stage B elements. The two sets of stage B elements representing the two possible retinal disparity values will give alternate outputs at low stimulation frequencies. For higher frequencies, however, τ_B will cause the outputs to overlap in time; eventually the overlap will be complete and there will be two constant outputs from stage B representing two separate objects. The finding that the "dwell time" for retinal disparity governs threshold for squarewave stimulation (Section 4:2:1) can be explained by time constants (τ_B) up to 500 milliseconds for stage B elements.

The existence of the high-frequency (depth mode 2) and medium-frequency regions for sinewave stimulation (Section 4:3:1) can be explained as follows. In the depth mode 2 region, temporal

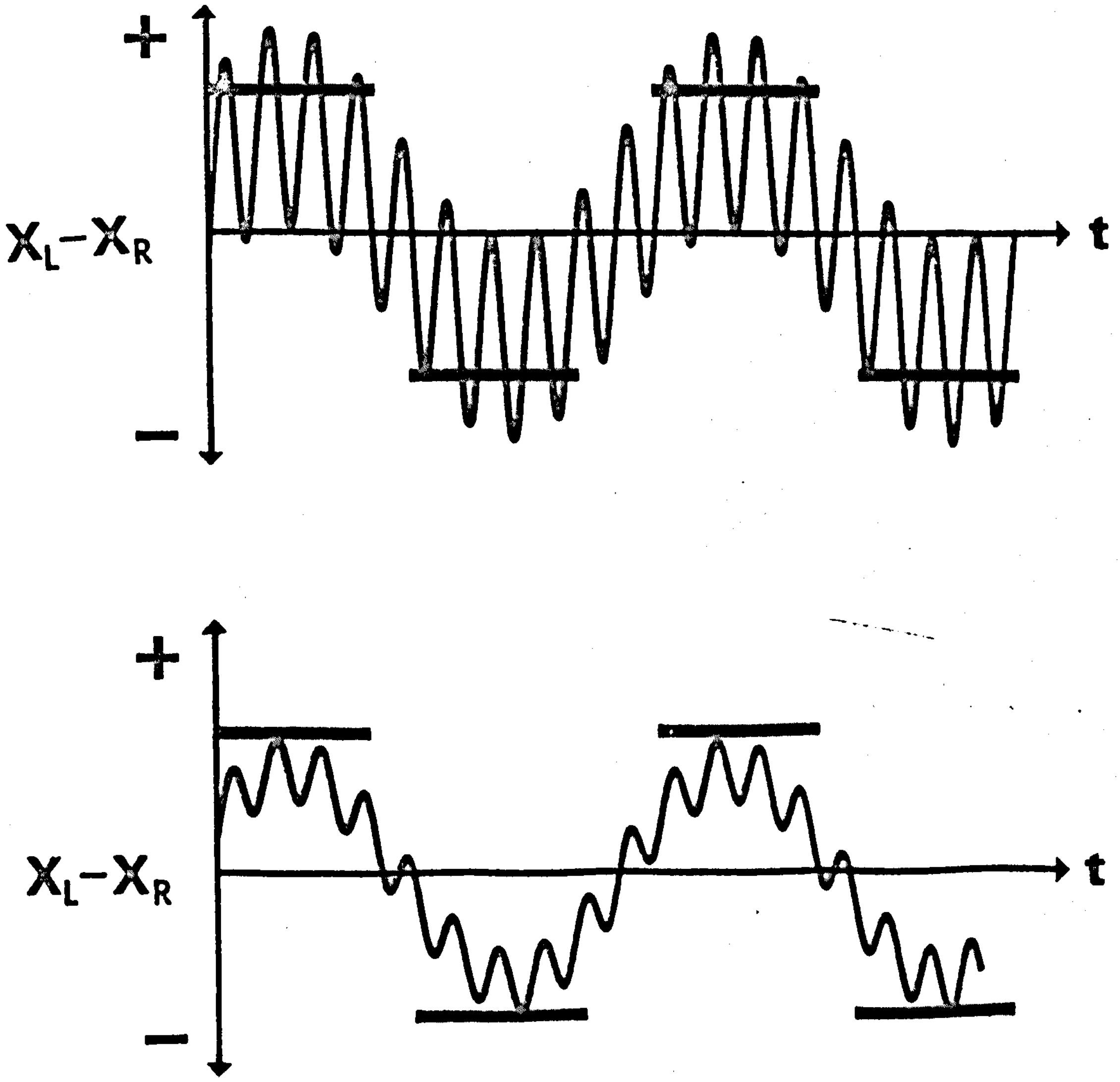


Figure 39. Upper – retinal disparity (X_l – X_r) output of Stage B disparity computers for $\Delta F > 3F$. The horizontal bars represent the values of retinal disparity beyond which overdriving occurs in Stage C. Lower – the effect of temporal integration (low-pass filtering) upon the waveform above.

integration in stage A causes the output of stage A to be much reduced. The output of the stage B disparity computers will then be similar to Fig. 39B. This disparity signal will pass through stage C to the threshold detection stage E. In the medium-frequency region, with $(F+\Delta F)$ less than about 8Hz., temporal integration in stage A is insufficient to prevent large excursions in the retinal disparity signal reaching stage C (Fig. 39A). These large excursions will overdrive stage C whose output will fall to almost zero at the retinal disparity peaks (see characteristic of stage C in Fig. 36). The horizontal bars in Fig. 39A represent this breakdown. If there is hysterisis in stage C then these brief breakdowns will degrade depth perception throughout the stimulus cycle. These brief breakdowns of depth perception were observed by both subjects and were associated with generally degraded depth perception (see Section 4:3:1).

Fig 35 has shown that the effect of increasing ΔF was to produce an unexpectedly large decrement in depth sensitivity. Section 4:3:3 has shown that the higher the frequency ΔF, the greater the difference between the predictions of the simple model and the experimental findings of Section 4:3:1. This means that the effect of ΔF cannot be entirely explained in terms of the time constants (τ_A) of stage A.

The effect of ΔF can be explained by the second model (Section 4:3:4) as follows.

If the left (X_L) and right (X_R) eyes' stimuli are both oscillating sinusoidally at frequency FHz., then the phase difference (θ) between the two sinewaves is constant. If X_L leads X_R by a phase difference θ then X_L reaches its maximum value $\theta/360F$ seconds earlier. If, however, X_L oscillates at FHz. and X_R oscillates at $(F+\Delta F)$Hz. then θ is continually changing, passing through 360 degrees in $1/\Delta F$ seconds (see Appendix 4).

If it is now assumed that the disparity computing elements of stage B are responsive to only a restricted range of phase angles then the "effective" peak to peak amplitude of the disparity signal will be decreased. If there are n phase-selective mechanisms, each with a tuning curve of 360/n degrees, then the disparity function spends a time of only $1/(n*\Delta F)$ seconds within the phase angle of each mechanism. When this time equals the integration time constant of the stage B elements (T_B) then the input to stage C will have fallen by half. With a maximum T_B of 62 milliseconds (Section 4:4:2) and a maximum ΔF of about 1Hz. (Section 4:3:1), n is approximately 3. This means that there must be at least 3, probably more, phase selective mechanisms to explain the effect of ΔF.

Fig. 57 in Appendix 4 shows that for some values of phase (θ less than 180°) the stimulus moves anticlockwise, and as a result both retinal images are moving right-to-left when retinal disparity is near its maximum crossed value. For other values of phase, the situation is reversed (ϕ greater than 180°). If one class of stage B elements is fed entirely from right-to-left stage A elements, and a second class of stage B elements is fed entirely from left-to-right stage A elements, then stage B would show phase selectivity. The well-known Waterfall aftereffect supports this supposition. Furthermore, the results for pulsed movement stimulation (Sections 3:3 and 3:6) suggest that there are separate classes of stage B elements for crossed and uncrossed disparities. These four phase-selective mechanisms would therefore explain the effect of ΔF upon depth movement sensitivity.

The segregation of the outputs of the left-right and right-left stage A elements up to stage C predicts a new type of stereoscopic movement adaptation effect similar to the well known aftereffect of sideways movement (Barlow and Hill, 1963). This prediction of adaptation to direction of movement in depth is discussed in Chapter 5.

One way of explaining the effect of ΔF upon depth movement sensitivity is to assume the existence of several phase-selective mechanisms tuned to different phase differences between the left and right eyes' stimulus oscillations. This prediction can be directly tested, and is discussed in Chapter 5.

4:5. Summary.

This chapter describes a method for discriminating sideways movements from movements in depth, at threshold. The method is to cause the oscillation frequency for sideways movements to differ from the oscillation frequency for movements in depth. A subject can make use of this difference in frequency to set depth thresholds independently of sideways retinal image movements. In fact, at the threshold for movement in depth, large sideways movements of the stimulus can be seen.

The left eye views a stimulus pattern which oscillates from side to side at F_l Hz.. The right eye views an identical pattern which oscillates from side to side at F_r Hz. (where $F_r = F_l + \Delta F$). Provided that ΔF is small compared with F_l (less than $\frac{1}{3}$ - see Appendix 4), and provided that fusion can be maintained, oscillations in depth can be seen with amplitude waxing and waning ΔF times a second. ΔF can be made independent of both F_l and F_r, hence the timecourse of sideways motion will differ from the timecourse of motion in depth, and the threshold functions for the two stimulus parameters can be independently measured.

Under all stimulation conditions, both left and right eyes view unvarying sinewave (or squarewave) stimulus oscillations.

For squarewave stimulation, there was a rapid decrease in sensitivity to movement in depth as both F (equals F_l) and ΔF were increased. No movement in depth could be seen at all when either F or ΔF was greater than 7Hz.. To a first approximation, these results can be described in terms of the single parameter ($F + \Delta F$). Where $1/(F + \Delta F)$ is the maximum "dwell time" of the stimulus pattern at any one disparity (see Appendix 5). As the dwell time is increased, depth sensitivity is increased (at 6dB/octave). This relationship fails at a dwell time of approximately 500 milliseconds.

The results for sinewave stimulation can be described in terms of three frequency regions.

a) Low frequencies. When ΔF was less than 3Hz., oscillations in depth could be seen. Depth sensitivity decreased as both F and ΔF were increased. At threshold, considerable sideways movements of the stimulus could be seen in both eyes. Movements in depth could be seen on practically 100% of trials.

b) Middle frequencies. When ΔF was in the range 1 to 10Hz. (dependent on F) sensitivity to oscillations in depth was low. At threshold, considerable sideways movements of the stimulus could be seen in both eyes. Movements in depth could be seen on practically 0% of trials.

c) High frequencies. When ΔF was above about 5Hz. (dependent on F) sensitivity to oscillations in depth was high and independent of ΔF. Oscillations in depth appeared at frequency F. Movements in depth could only be perceived over a restricted range of oscillation amplitudes. At threshold the right eye's stimulus appeared stationary although the left eye's stimulus appeared to oscillate from side to side. Movements in depth could be seen on approximately 100% of trials.

The stimulus disparity waveform could also be described in terms of three frequency regions. These three regions did not coincide, however, with the three psychophysical regions. This suggests that the three psychophysical regions reflect changes in the visual processing of the stimulus.

The existence of depth perception in the high-frequency region can be explained in terms of temporal integration before the signals from the two eyes unite, and at a point common to both disparity and sideways motion channels. The integration time constant would be about 30 milliseconds.

The middle-frequency region can be explained as the region beyond the point at which the low-frequency depth mechanism operates, and before the point at which "motion fusion" occurrs.

The low-frequency region is the region of "normal" stereoscopic depth perception, and is limited to the situation where both eyes' stimulus oscillation frequencies are below 3Hz.. The effect of ΔF upon depth movement sensitivity in this region cannot be explained by assuming that all integrative processes occur before the signals from the two eyes unite. Therefore, some form of temporal integration must occur at a site central to binocular convergence. The integration time constant would be of the order of 50 milliseconds.

A model which will account for most of the findings of Chapters 3 and 4 is proposed (Section 4:4:2). This model assumes the existence of 2 or more phase-selective mechanisms tuned to different phase differences between the left and right eyes' stimulus oscillations. This predicts that selective adaptation would occur to phase differences between the two eyes' stimulus oscillations. This prediction is tested in Chapter 5.

The model also predicts a new kind of stereoscopic movement adaptation effect selective to the direction of movement in space. For example, it should be possible to selectively adapt to one direction of motion in space and leave one's sensitivity to other directions of motion unaffected. This prediction is also tested in Chapter 5.

5/ SELECTIVE ADAPTATION TO THE DIRECTION OF MOTION IN SPACE.

5:1. Introduction.

It has been suggested that " the human visual system contains motion detectors that respond preferentially to a retinal image which is moving in a specific direction. The particular detectors that are excited by a moving stimulus provide a physiological representation of the direction of movement. The balance between the outputs of detectors with different "preferred" directions is upset when all detectors with the same "preferred" direction are selectively fatigued, and this imbalance (can) produce an illusion of movement." (Wohlgemuth, 1911).

More recently, Barlow and Hill (1963) have found motion-sensitive neurons in the rabbit's visual pathway which have differing responses to different directions of retinal image movement, and thus could be responsible for this aftereffect.

It is possible that there are directionally-selective mechanisms in the human visual system, other than those selectively responsive to the direction of sideways motion. In particular, there may be disparity-sensitive mechanisms selectively responsive to the direction of motion in depth. Binocularly-activated neurones which respond only when disparity is changing in a particular direction have recently been found in cat (Pettigrew, 1973). Zeki (personal communication to D. Regan) has found similar neurones in rabbit which only respond to a change in disparity. Regan and Beverley (1973E) have recently reported an electrophysiological experiment which gave evidence for such mechanisms in man.

In Section 3:6:2 psychophysical evidence was reported for the existance of such mechanisms in man.

Further evidence for such directionally-selective disparity mechanisms can be deduced from the experiments reported in Chapter 4. It was shown in Section 4:3:1 that an unexpectedly large decrement in depth sensitivity occurred when there was a small frequency difference between the oscillations seen by the left and right eyes. It was shown in Section 4:4:3 that this finding can be accounted for by postulating the existance of several classes of disparity detectors selectively sensitive to the phase differences between the left and right eyes' stimulus oscillations. If this assumption is correct, it might be possible to selectively fatigue one (or more) of the phase-selective mechanisms by adapting to a stimulus with a specific phase difference between the left and right eyes' stimulus oscillations. The results of adapting to such a stimulus are reported in Section 5:4.

The model discussed in Section 4:4:3 assumes that the left-right and right-left outputs from the contour position detectors (stage A) are segregated up to the summation stage ~~summer~~ (stage C). If this is so, then a type of stereoscopic movement adaptation effect similar to the well known aftereffect of sideways movement (see above) should occur. For example, it should be possible to selectively adapt to one direction of motion in space and leave one's sensitivity to other directions of motion unaffected.

It is possible to generate a stimulus which appears to oscillate along a specific direction of motion in space by using Apparatus 3 and Stimulus 4, and by varying the relative amplitude of stimulus oscillation seen by the left and right eyes. The results of adapting to such a stimulus are reported in Section 5:3.

A complete description of actual and apparent stimulus movements is given in Appendix 3 for adaptation to phase differences between the two eyes stimulus oscillations, and in Appendix 2 for adaptation to amplitude differences between the two eyes' stimulus oscillations.

In all the experiments described in this chapter, both left and right eyes viewed unvarying sinewave stimulus oscillations. This means that the leftwards and rightwards motions were exactly balanced for each eye.

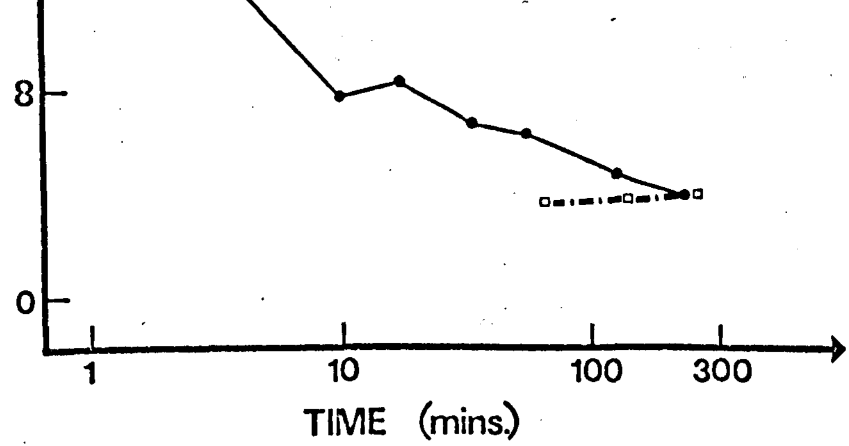
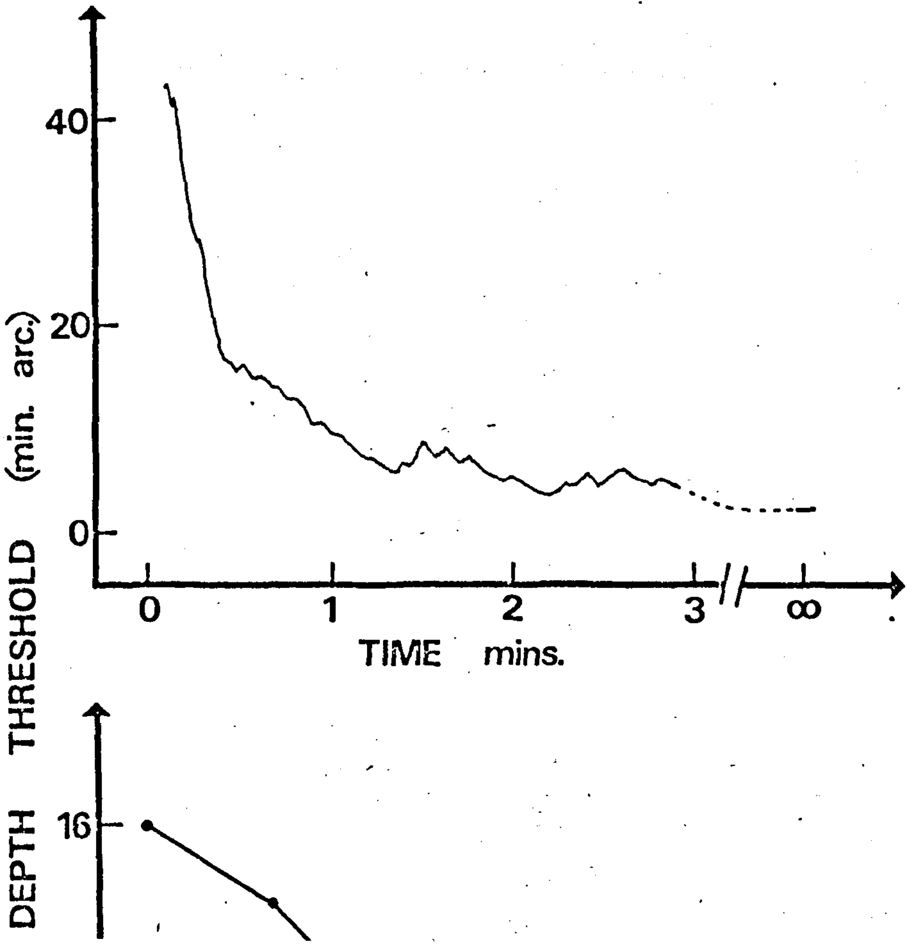


Figure 40. Timecourse of recovery of visual sensitivity to movement in depth after 15 minutes adaptation to a stimulus moving in depth. Upper - recording of depth threshold versus time in minutes after end of adaptation. Both axes are linear. Lower - long term recovery of stereoscopic depth sensitivity. Each point is the mean threshold set during a 30 second 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, abscissae are logarithmic.

RECOVERY FROM 15mins. ADAPTATION



5:2. Timecourse of Recovery from Adaptation.

When measuring the effect of adaptation to a particular stimulus, an important problem is that recovery from adaptation starts immediately the adapting stimulus is changed to the test stimulus. If the presentation time of the test stimulus is long (as for example when using the method of adjustments), then the magnitude of any adaptation effect will be decreased because some recovery from adaptation will occur. Since the method of adjustments is preferred by most subjects for measuring thresholds, it is important to know whether the method will give useful results. To this end, the timecourse of recovery of visual sensitivity to movement in depth was measured after adaptation to a stimulus moving in depth. This experiment is reported below. The method described in Section 2:3:6 was used.

5:2:1. Results.

Fig. 40 (upper) is a tracing of an on-line record of subject K.B.'s threshold for the detection of movement in depth *versus* the time in minutes after the end of adaptation. Prior to the start of this record the subject gazed for 15 minutes at the adapting stimulus (see Section 2:3:6).

At the start of recovery from adaptation the subject's depth threshold decreased rapidly. Within the first 20 to 60 seconds (the actual time varied widely from subject to subject and from one experiment to the next) the threshold had decreased from 10 or more times to about twice the pre-adaptation level. However, after this rapid decrease, the threshold decreased more slowly. This slow threshold decrease to the pre-adaptation level is shown more clearly in Fig. 40 (lower).

Fig 40 (lower) shows that recovery of stereoscopic depth sensitivity was not complete (where the two lines cross) until 210 minutes had elapsed since adaptation. The continuous line shows the depth threshold after adaptation to an adapting L/R ratio * identical to the test L/R ratio. The chain line shows the depth threshold for the control situation where the test L/R ratio was the inverse of the adapting L/R ratio. Both measurements were taken concurrently in one experiment with subject D.R..

It should be noted that 1) while the ordinates are linear the abscissae are logarithmic; 2) the control results form a horizontal straight line (other experiments which are not illustrated confirm this) as is to be expected; 3) the test results lie, more or less, along a straight line in this log.-lin. plot. This implies an exponential decay of the adaptation effect.

5:2:2. Discussion.

The above results confirm that the method of adjustments can be used to measure adaptation thresholds, but only if several conditions are observed.

Firstly, the subject may be only allowed a limited amount of time in which to set the depth threshold. From Fig. 40 (upper) it is clear that this time must be less than 20 seconds and should preferably be less than 10 seconds. Even so, the adapted threshold measured will be far less than the adapted threshold measured by

---

* The meaning of the term L/R ratio is explained in Section 5:3. In brief, it is the peak to peak stimulus oscillation amplitude seen by the left eye divided by the peak to peak stimulus oscillation amplitude seen by the right eye (this is also equal to the ratio of maximum stimulus velocities in the left and right eyes).

(for example) the 2 forced-choice psychophysical method. * Since it was intended only to make comparative measurements between (for example) the adaptation effect of different L/R ratios, then this decrease in measured adapted threshold is unimportant. It should be noted that this assumes that the timecourse of deadaptation is similar for different L/R ratios. No evidence that this is not true has been found. Similar results to the results of Fig. 40 were obtained when a L/R ratio of 1:1.5 was used instead of 1.5:1.

The second condition is that each test threshold setting must be prece~~e~~ded by a sufficiently long adaptation period to ensure that the threshold rises to an equivalent level at the start of each test period. If this is not done there will be extremely large variability in the results.

Thirdly, only two adaptation L/R ratios (or phase angles) may be used for any one subject on any one day. This is clearly shown in Fig. 40 (lower) where recovery from adaptation was not complete for 3½ hours. If two adaptation L/R ratios are to be used on any one day on one subject, then there should be at least a 6 hour (for safety) interval between them to avoid interaction effects. It is probably best to use only one adaptation L/R ratio per subject per day.

---

* In a control experiment, adapted thresholds measured by the 2 forced-choice method were 3 times larger than thresholds measured by the method of adjustments. See also Section 5:3:1.

5:3. Adaptation With Unequal Amplitudes of Stimulus Oscillation Seen by the Left and Right Eyes.

The term "left/right ratio" or L/R ratio, as used in this section and elsewhere, is defined as follows.

The left eye views a stimulus, part of which (the target) is oscillating sinusoidally from left to right. Let the peak to peak oscillation amplitude of this target be A (min. arc subtended at the left eye).

The right eye views a stimulus, part of which (the target) is oscillating sinusoidally from left to right. Let the peak to peak oscillation amplitude of this target be B (min. arc subtended at the right eye).

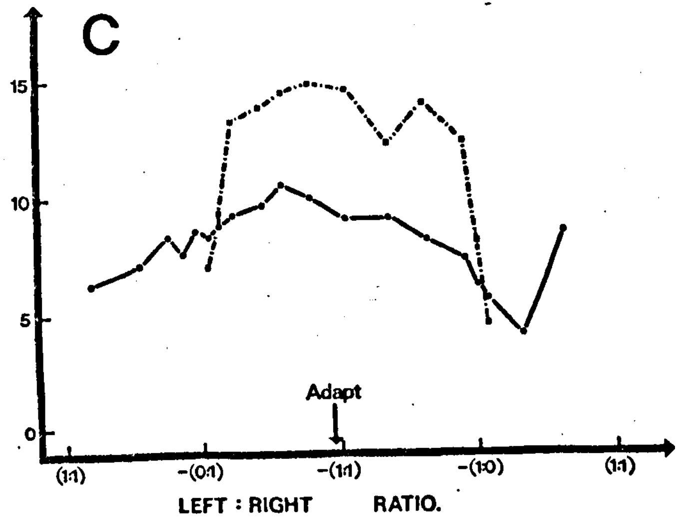
The L/R ratio is then A/B (or A:B).

If the left and right eyes' targets oscillate in phase, the L/R ratio is defined as being positive. If the left and right eyes' targets oscillate in antiphase, the L/R ratio is defined as being negative.

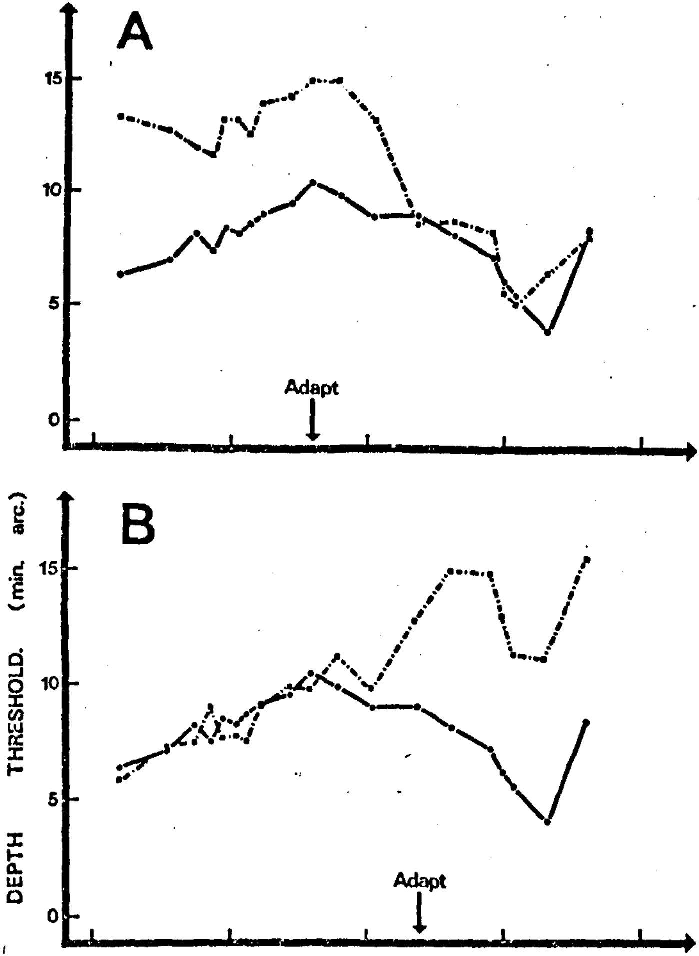
A complete description of actual and apparant stimulus movements for experiments reported in this Section is given in Appendix 2.

Values of L/R ratio can range from 0 to $+\infty$ and from 0 to $-\infty$. In order to plot this range of L/R ratios on a graph, the inverse tangent ($\tan^{-1}$) of the L/R ratio was used. The L/R ratio was therefore plotted along a linear scale of $\tan^{-1}$(L/R ratio).

The method of adjustments as described in Section 2:3:7 was used for all experiments reported in this Section (see also Section 5:2). Apparatus 3 and Stimulus 4 were used.



<u>Figure 41</u>. Adaptation to a particular direction of movement in depth. Ordinates are psychophysical thresholds (mins. arc) for movement in depth. Abscissae are left/right ratios of the test stimuli. The continuous lines are the pre-adaptation "baselines". The chain lines in <u>A</u>, <u>B</u> and <u>C</u> show thresholds measured after adaptation to moving stimuli with left/right ratios of -(1:2), -(2:1) and -(1:1.05) respectively, i.e. stimuli moving along lines directed respectively just to the right of the left eye, just to the left of the right eye and almost midway between the eyes. Ordinates are linear, abscissae are linear with respect to $\tan^{-1}$(left/right ratio).


A
B
DEPTH THRESHOLD. (min. arc.)
0
5
10
15
Adapt

5:3:1. Results.

Fig. 41 illustrates the effect of adapting to a particular direction of movement in depth (L/R ratio) upon stereoscopic depth threshold for subject K.B..

Before any adaptation experiments were performed, the subject's depth threshold was measured as a function of L/R ratio. This provided an unadapted "baseline" with which the effects of adaptation could be compared. The continuous line joining the data points in Fig. 41A shows this baseline. The baseline is also plotted in Fig. 41B and C for comparison purposes. It was impossible to measure the depth threshold when the L/R ratio approached (1:1) since the target then appeared to move solely from side to side and no motion in depth was seen.

The graph shows that the stereoscopic depth threshold was highest for L/R ratios close to -(1:1) (i.e. stimulus moving along a line directed towards the head). The stereoscopic depth threshold progressively decreased as the direction of stimulus movement was inclined away from the head. This finding held for all four subjects tested.

The chain line in Fig. 41A shows the stereoscopic depth threshold after the subject had adapted to a L/R ratio of -(1:2) for 15 minutes (i.e. to a stimulus moving along a line directed just to the right of the left eye). Stereoscopic depth threshold was elevated for all L/R ratios in the range (1:1) to -(0:1) to -(1:1) but was unaffected for the other L/R ratios. This means that the stereoscopic depth threshold was elevated for test stimuli which moved to the <u>left</u> of a point midway between the eyes, but was unaffected for test stimuli which moved to the <u>right</u>.

The chain line in Fig. 41B shows the stereoscopic depth threshold after the subject had adapted to a L/R ratio of -(2:1) for 15 minutes (i.e. to a stimulus moving along a line directed just to the left of the right eye). Stereoscopic depth threshold was elevated for all L/R ratios in the range (1:1) to -(1:0) to -(1:1) but was unaffected for the other L/R ratios. This means that the stereoscopic depth threshold was elevated for test stimuli which moved to the right of a point midway between the eyes, but was unaffected for test stimuli which moved to the left.

The chain line in Fig. 41C shows the stereoscopic depth threshold after the subject had adapted to a L/R ratio of -(1:1.05) for 15 minutes (i.e. to a stimulus moving along a line directed just to the right of the point midway between the two eyes). Stereoscopic depth threshold was elevated for all L/R ratios in the range -(0:1) to -(1:1) to -(1:0). This means that the stereoscopic depth threshold was elevated for test stimuli which moved towards the head, between the eyes.

Threshold elevations of no more than about 250% were recorded using the method of adjustments (Fig. 41). When a two forced-choice method was used, much larger threshold elevations occurred (see Section 5:2); in some cases they were as much as 600%. This difference in threshold elevation was probably due to the difference in the time which elapsed between the cessation of adaptation and the test threshold measurement (within 5 seconds for the two forced-choice method and up to 10 seconds for the method of adjustments). This difference in threshold elevation does not affect the conclusions of Section 5:3:2.

The subject's impressions of the stimulus were recorded during the experiments and can be summarized as follows. As the subject gazed at the adapting target, at first the target's oscillations in depth appeared large. However, as adaptation progressed, the oscillations in depth grew progressively smaller until, after several minutes, (the time varied from subject to subject and from day to day) no movement in depth was visible at all. It should be noted however, that the stimulus still appeared

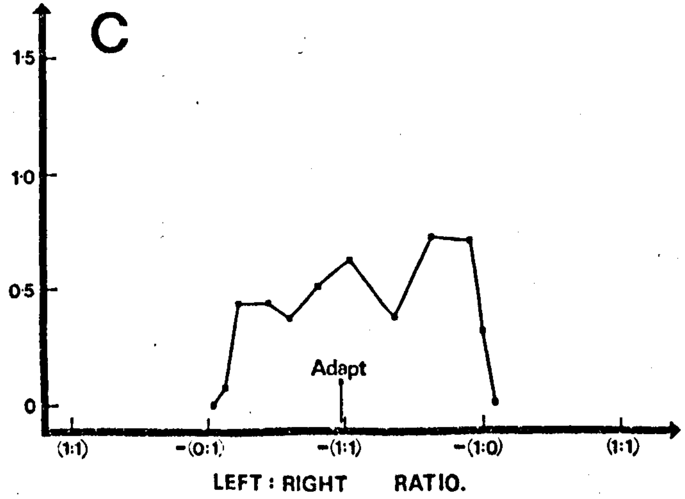
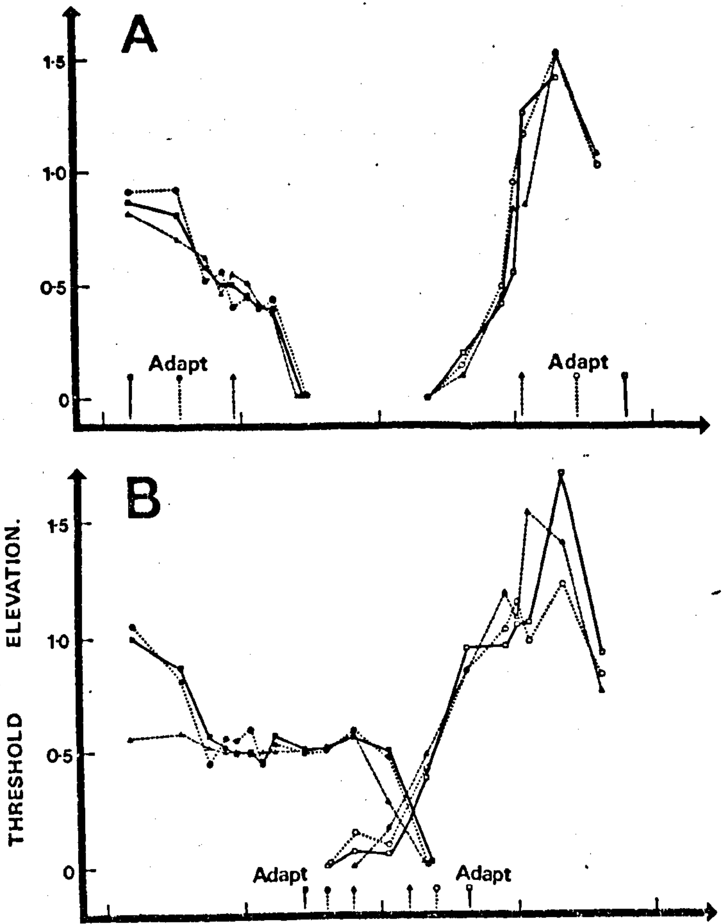
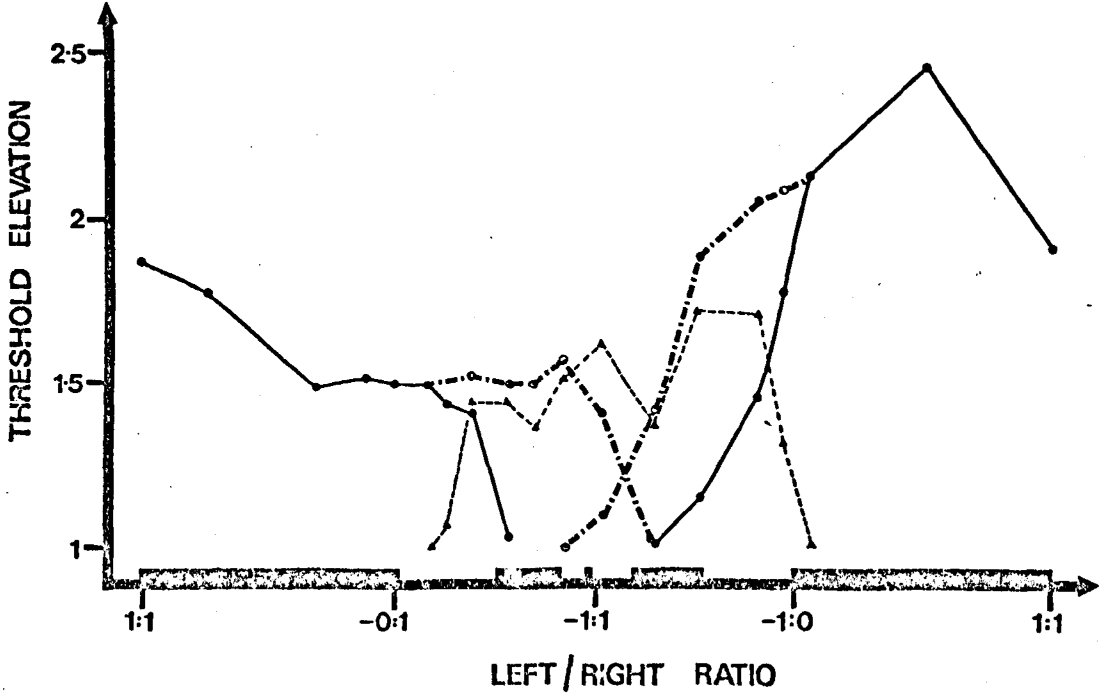


Figure 42. Fractional elevations of threshold for movement in depth caused by adapting to 13 different left/right ratios. A - continuous line at left, left/right ratio (1:1.3); continuous line at right, (1.3:1); dotted line at left, (1:2.8); dotted line at right, (2.8:1); dashed line at left, (1:29); dashed line at right, (29:1). B - continuous line at left, -(1:4.3); continuous line at right, -(4.3:1); dotted line at left, -(1:2); dotted line at right, -(2:1); dashed line at left, -(1:1.3); dashed line at right, -(1.3:1). C - continuous line, -(1:1.05). The - sign indicates that the left and right eye's stimuli are in antiphase. Ordinates are linear, abscissae are linear with respect to $\tan^{-1}$(left/right ratio).


A
1·5
1·0
0·5
0
Adapt
Adapt
B
THRESHOLD ELEVATION.
1·5
1·0
0·5
0
Adapt
Adapt

<u>Figure 43</u>. Fractional elevations of threshold for movement in depth caused by adapting to different left/right ratios. Each curve is the mean of a set of curves shown in Fig. 42. Continuous line at left, mean of threshold elevations for left/right ratios (1:1.3), (1:2.8) and (1:29). Continuous line at right, (1.3:1), (2.8:1) and (29:1). Chain line at left, -(1:4.3), -(1:2) and -(1:1.3). Chain line at right, -(4.3:1), -(2:1) and -(1.3:1). The dashed line is the threshold elevation for left/right ratio -(1:1.05). Ordinates are linear, abscissce are linear with respect to $\tan^{-1}$(left/right ratio).


THRESHOLD ELEVATION
2·5
2
1·5
1
1:1
-0:1
-1:1
-1:0
1:1
LEFT / RIGHT RATIO

to move from side to side, and that even after 30 minutes adaptation no noticible change in this side to side movement occurred.

Although several minutes adaptation were necessary to completely abolish the perception of movement in depth, a marked loss of sensitivity took place within the first few seconds of adaptation. When adaptation was complete and testing at different L/R ratios began, it was evident that a much greater stimulus oscillation amplitude was necessary to see depth for some L/R ratios than for others (this was apparent from the sideways motion of the stimulus). It was much more difficult to see oscillations in depth for stimulus oscillations directed to the same side of the head as the adapting stimulus oscillations. This was true for all adapting L/R ratios except -(1:1.05).

The above results were confirmed on three additional subjects (D.R., J.J. and S.H.).

Threshold elevation curves similar to those shown in Fig. 41 were measured for 13 different adapting L/R ratios. For ease of interpretation the threshold elevation (defined as (threshold after adaptation - threshold before adaptation)/(threshold before adaptation) for each L/R ratio) was plotted directly. Threshold elevations in the range ± 0.1 were considered to be insignificant and therefore were not plotted.

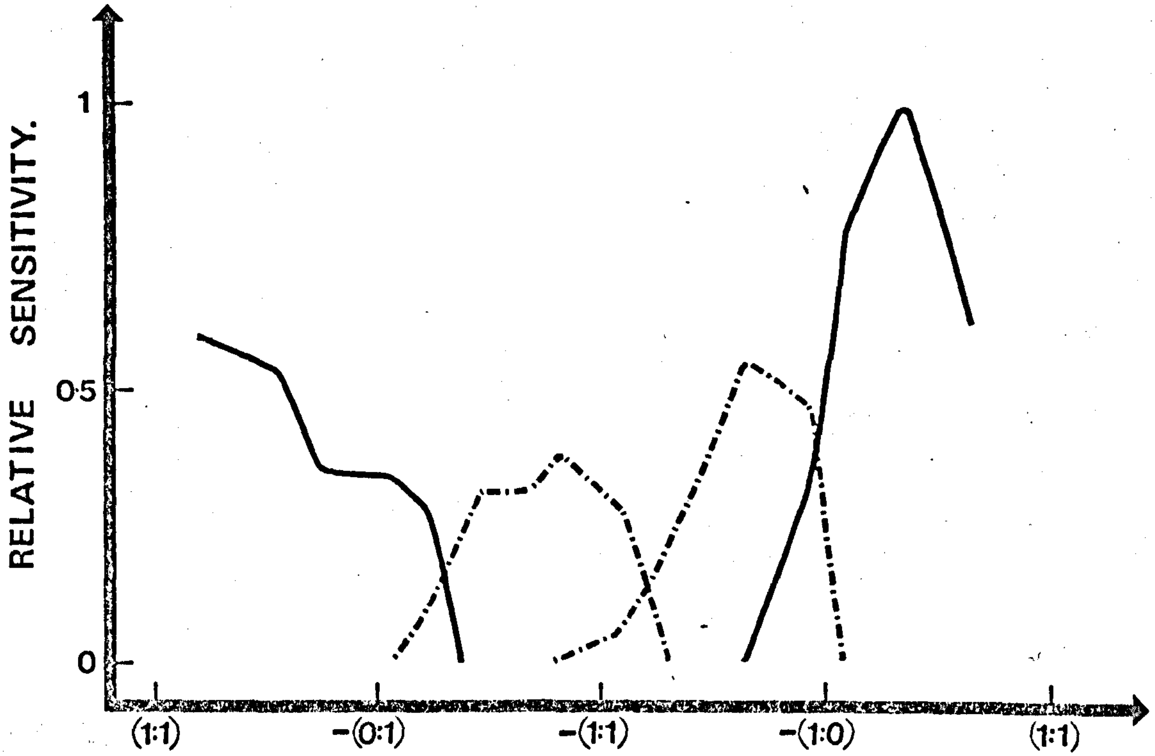
Fig. 42 shows these 13 curves for subject K.B..

It is clear that adaptation at L/R ratios of (1:1.3), (1:2.8) and (1:29) had the same effect upon stereoscopic depth threshold. The mean of these three curves is plotted as the continuous line to the left of Fig. 43.

Adaptation at L/R ratios of -(1:4.3), -(1:2) and -(1:1.3) produced similar threshold elevations. The mean of these three curves is plotted as the chain line to the left of Fig. 43. This

LEFT : RIGHT RATIO.

<u>Figure 44</u>. Sensitivity curves of the hypothesised 4 underlying mechanisms that describe the experimental curves of Figs. 42 and 43.


RELATIVE SENSITIVITY.
1
0·5
0
(1:1)
-(0:1)
-(1:1)
-(1:0)
(1:1)

line coincides with the continuous line on the left of Fig. 43 for L/R ratios in the approximate range (1:1) to -(0:1).

Adaptation at L/R ratios of (1.3:1), (2.8:1) and (29:1) had the same effect upon stereoscopic depth threshold. The mean of these three curves is plotted as the continuous line to the right of Fig. 43.

Adaptation at L/R ratios of -(4.3:1), -(2:1) and -(1.3:1) produced similar threshold elevations. The mean of these three curves is plotted as the chain line in Fig. 43 to the right. This line coincides with the continuous line on the right of Fig. 43 for L/R ratios in the approximate range -(1:0) to (1:1).

Adaptation at a L/R ratio of -(1:1.05) produced a threshold elevation curve different to any of the other curves. This curve is reproduced as the dashed line in Fig.43.

The above findings were confirmed on a second subject D.R..

5:3:2. Discussion.

Fig. 43 shows that only 5 different curves are necessary to describe the threshold elevations for depth movement produced by 13 different adapting L/R ratios. It is clear to informal visual inspection that these 5 curves can be summarised in terms of 4 hypothetical sensitivity functions. These 4 sensitivity functions are shown in Fig. 44.

This suggests that 4 neural mechanisms underlie visual sensitivity to depth movement, and that these mechanisms are "tuned" in terms of L/R ratio. Since L/R 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. One function of the multiple sensitivity functions shown in Fig. 44 might be to provide a basis for sensitively discriminating different L/R ratios that lie at or near the crossover points of the four sensitivity functions. These crossover points are near (though not exactly coincident with) L/R ratios of -(0:1), -(1:1) and -(1:0). * (Beverley and Regan, 1973B).

A L/R ratio of (1:1) means that the target was moving purely from side to side. A L/R ratio of -(1:1) means that the target was moving to and fro in depth aimed at a point midway between the eyes. L/R ratios of -(0:1) and -(1:0) mean that the target was moving towards (and away from) the left and right eyes respectively (see Appendix 3). Since the distance between the eyes is approximately 6cm., and as the target was located 63cm. in front of the eyes, the visual angle between lines directed from the target towards the left and right eyes was only 6°. This small angle of visual space is subserved by 2 out of the 4 hypothetical neural mechanisms. The other 2 hypothetical neural mechanisms subserve the remaining 174° of visual space.

This suggests that, when processing information about movement in three-dimensional space, the brain does not give equal weight to all visual directions. The narrow band of visual directions pointing towards the head, between the eyes, seems to be at least as important as the whole remaining range of other directions. This is not surprising, since the ability to finely judge whether an object (such as an arrow, a spear, or even a cricket ball) is going to hit, or just miss one's head is an obvious survival characteristic. The presence of 4 sensitivity functions would provide the means by which such a discrimination could be effected.

It seems unlikely that the site of the neural mechanisms responsible for adaptation to movement in depth is before the site of binocular convergence. There are several arguments supporting this conclusion. Firstly, adaptation to a target's movement in

* see overleaf.

depth is much greater than to its simultaneous sideways movement. Secondly, no test or adapting stimulus used in the experiments of Section 5:3:2 had any monocular directional bias. Both eyes always viewed a sinusoidally oscillating target, so that there was always an exact balance between movements in different directions. Thirdly, monocularly-indistinguishable adapting stimuli gave quite different threshold elevation curves. For example, the continuous line to the left of Fig. 42A (L/R ratio (1:1.3)) and the dashed line to the left of Fig. 42B (L/R ratio -(1:1.3)) show clearly different adaptation effects yet monocularly the two adaptation stimuli were identical. The only difference lay in the relative timing (phase) of the oscillations viewed by the left and right eyes. Relative timing (phase) is obviously meaningless if only one eye is used (see also Section 5:4:2).

If the site of the neural mechanisms responsible for adaptation to movement in depth is after the site of binocular convergence then there are several possible explanations for the observed threshold elevation curves. One possible explanation is discussed in Section 5:5.

In the experiments reported in Section 5:3:1, the targets seen by the left and right eyes both oscillated sinusoidally from side to side at a frequency of 0.8Hz.. This frequency was used as it was sufficiently low to avoid confounding the threshold for movement in depth with the threshold for sideways movement (see Sections 3:1 and 4:3).

---

* Regan and Beverley (1975 in preparation) have provided some evidence to support this assumption. They have shown that subjective judgements of the direction along which an object moves in three dimensions are more sensitive at L/R ratios close to the crossover points of the 4 hypothetical sensitivity functions.

The asymmetric threshold elevations of Figs. 41 and 42 were confirmed while both fixation and depth tracking were monitored by means of noni~~q~~us lines. Changes in ocular convergence of 0.5 mins. arc could be detected by this means. It seems unlikely that changes in fixation, or tracking of the stimulus, of this order of magnitude could account for the asymmetric threshold elevations which were observed.

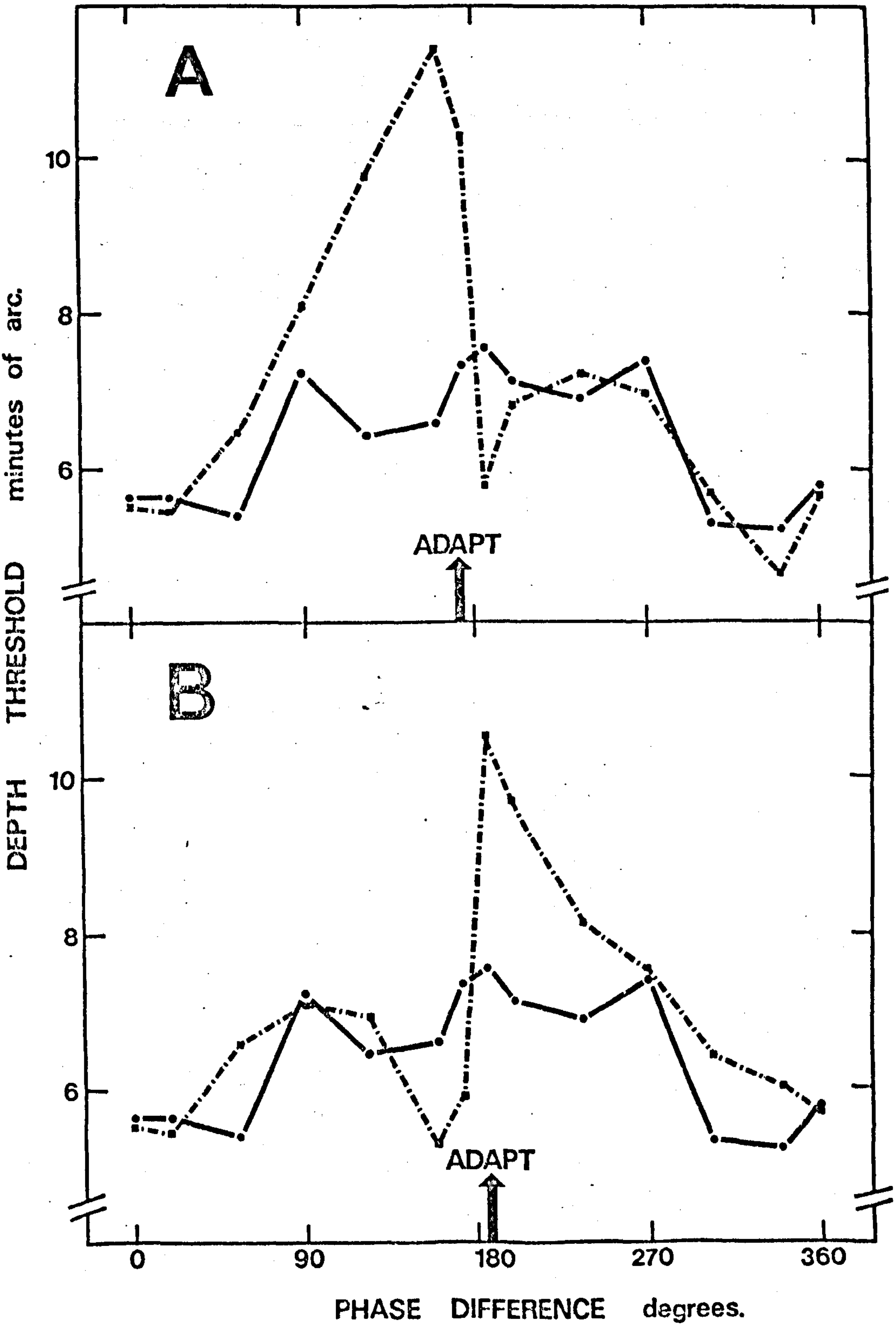


Figure 45. Depth threshold versus the phase difference between the target oscillations presented to the left and right eyes. The continuous lines are the pre-adaptation "baselines". The chain line in A shows the threshold measured after 15 minutes adaptation to a phase of 174° (arrowed). The chain line in B shows the threshold measured after 15 minutes adaptation to a phase of 186° (arrowed). Both axes are linear.

5:4. Adaptation as a Function of the Phase Difference Between the Stimulus Oscillations Seen by the Left and Right Eyes.

The method of adjustments as described in Section 2:3:7 was used for the experiments reported in this section. Apparatus 3 and Stimulus 4 were used. A complete description of actual and apparant stimulus movements for experiments reported in this section is given in Appendix 3.

5:4:1. Results.

Fig. 45 illustrates the effect of adapting to a particular phase difference between the left and right eyes' stimulus oscillations, upon stereoscopic depth threshold, for subject K.B..

Before any adaptation experiments were performed the subject's depth threshold was measured as a function of phase difference. This provided an unadapted "baseline" with which the effects of adaptation could be compared. The continuous line in Fig.45A shows this baseline. The baseline is also plotted in Fig. 45B for comparison purposes. It was possible to measure the depth threshold for a phase difference of 0° (or 360°) because there was a difference in stimulus oscillation amplitude seen by the left and right eyes. For Fig. 45 the L/R ratio was (1.5:1). Note that the L/R ratio was unchanged throughout the experiment.

For phase differences less than 180°, the stimulus appeared to move in an anticlockwise ellipse. For phase differences greater than 180°, the stimulus appeared to move in a clockwise ellipse. The graph shows that the stereoscopic depth threshold was symmetrical about 180°. Changing the L/R ratio did not affect this result.

The graph also shows that the stereoscopic depth threshold was highest for phase differences in the range 90° to 270° (i.e. for stimuli moving in an ellipse whose major axis pointed towards (or away from) the head). The stereoscopic depth threshold was lower for phase differences between 0° and 90° and between 270° and 360° (i.e. for stimuli moving in an ellipse whose major axis pointed from side to side). This finding was true for all three subjects tested and for all three L/R ratios used.

The chain line in Fig. 45A shows the stereoscopic depth threshold after the subject had adapted to a phase difference of 174° for 15 minutes (i.e. to a stimulus moving in an anticlockwise ellipse as viewed from above.). Stereoscopic depth threshold was elevated for all test phase differences less than 180°. In contrast, threshold was not significantly elevated for any test phase greater than 180°. * This means that stereoscopic depth threshold was elevated for all stimuli which appeared to move in an anticlockwise ellipse, but was not elevated for all stimuli which appeared to move in a clockwise ellipse.

The chain line in Fig. 45 B shows the stereoscopic depth threshold after the subject had adapted to a phase difference of 186° for 15 minutes (i.e. to a stimulus moving in a clockwise ellipse as viewed from above). Stereoscopic depth threshold was elevated for all test phase differences greater than 180°. In contrast, threshold was not significantly elevated for any test phase less than 180°. *

---

* For one subject (K.B.) out of the three tested, a <u>decrease</u> in threshold was produced when the test phase was just greater than 180° (for adaptation at 174°) or when the test phase was just less than 180° (for adaptation at 186°) (Fig. 45A). These decreases were less clear, however, when L/R ratios other than (1.5:1) were used.

This means that stereoscopic depth threshold was elevated for all stimuli which appeared to move in a clockwise ellipse, but was not elevated for all stimuli which appeared to move in an anticlockwise ellipse.

The subject's impressions of the stimulus were recorded during the experiment and can be summarized as follows. As the subject gazed at the adapting target, the target appeared to move in an ellipse extended in depth. However, as adaptation progressed, the oscillations in depth grew progressively smaller until, after several minutes (the time varied from subject to subject and from day to day) no movement in depth was visible at all. The target then appeared to move solely from side to side. Although several minutes adaptation were necessary to completely abolish the perception of movement in depth, a marked loss of sensitivity took place within the first few seconds of adaptation. When adaptation was complete and testing at different phase differences began, it was evident that a much greater stimulus oscillation amplitude was necessary to see depth for some phase differences than for others. It was much easier to see oscillations in depth for stimuli which appeared to move in the opposite direction to the adapting stimulus. This was true for all subjects tested and for all L/R ratios used.

The above experiment was repeated for subject K.B. for two further L/R ratios of (1:1) and (2:1). These L/R ratios produced similar adaptation effects to those shown in Fig. 45 for a L/R ratio of (1.5:1), although the threshold elevations were not as large.

The asymmetric threshold elevations shown in Fig. 45 were confirmed on two further subjects (D.R. and S.H.) using adapting phases of 90° and 270° and a L/R ratio of (2:1).

5:4:2. Discussion.

In the experiments reported in Section 5:4:1, the targets seen by the left and right eyes both oscillated from left to right at a frequency of 0.8Hz.. This frequency was used as it was sufficiently low to avoid confounding the threshold for movement in depth with the threshold for sideways movement (see Sections 3:1 and 4:3). Both targets oscillated sinusoidally with constant relative peak to peak amplitudes throughout the experiments. Only the phase difference (that is the relative timing) between the left and right targets' oscillations was altered in any one experiment. This means that adaptation at a site peripheral to binocular convergence cannot explain the asymmetric adaptation effects in the ability to see movement in depth.

To repeat, at all times the left eye viewed a sinusoidally-oscillating target, so that there was always an exact balance between movements in different directions. The same was true for the right eye. Phase difference (or relative timing) which alone distinguishes between the adapting and the various test stimuli is obviously meaningless if only one eye is used (see also Regan and Beverley, 1973C). Thus, adaptation of monocular, directionally-specific motion detectors cannot account for the above results in the same way that it can account for classical after-effects of seen motion such as the "Waterfall Effect" (Wohlgemuth, 1911; Barlow and Hill, 1963).

However, the asymmetric threshold elevations can be explained in terms of adaptation at, or central to the site of binocular convergence. This is discussed further in Section 5:5.

Finally, it should be noted that the asymmetric threshold elevations were confirmed while both fixation and depth tracking were monitored by means of nonius lines. Changes in ocular convergence of 0.5 min. arc could be detected by this means. It seems unlikely that changes in fixation, or tracking of the stimulus, of this order of magnitude could account for the asymmetric threshold elevations which were observed.

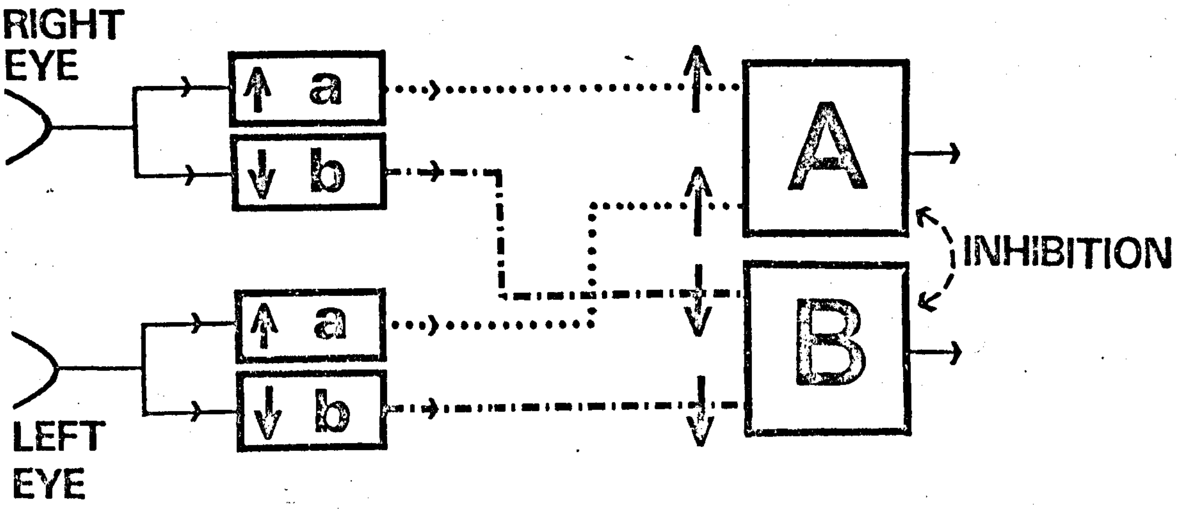


Figure 46. Suggested way in which directionally specific responses to movements of the retinal images in the left and right eyes are combined in stereoscopic depth perception.

5:5. Models.

The model shown in Fig. 46 can account for the findings of Section 5:4.

Suppose that for every point on the left retina there is a group of motion detectors which are most sensitive to stimuli moving from left to right (a_l) and a second group of motion detectors which are most sensitive to stimuli moving from right to left (b_l). Suppose also that for every point on the right retina there are two corresponding groups of motion detectors (a_r and b_r). Single neurones in the visual pathway of animals which show such directional selectivity have been reported (Barlow and Hill, 1963; Hubel and Wiesel, 1959, 1962; Pettigrew, Nikara and Bishop, 1968). This means that for each value of retinal disparity there could be four classes of disparity detectors; A (excited only when a_l and a_r excited), B ($b_l + b_r$), C ($a_r + b_l$) and D ($a_l + b_r$). These four classes would exist <u>only</u> if the directionally-sensitive outputs from both eyes are kept separate up to the level at which retinal disparity is computed.

Now consider the movement of the stimulus when there is a phase difference between the left and right eyes' stimulus oscillations (see Appendix 3). For phase differences less than 180°, when crossed disparity is greatest (i.e. when the target appears to be nearest the head) both left and right targets are moving from left to right so that class A disparity detectors are excited. If prolonged viewing produces appreciable adaptation of class A disparity detectors, but little adaptation of class B disparity detectors, then the finding that depth thresholds were elevated for test phases less than 180°, but not appreciably for test phases greater than 180°, would be explained.

For phase differences greater than 180°, the situation is

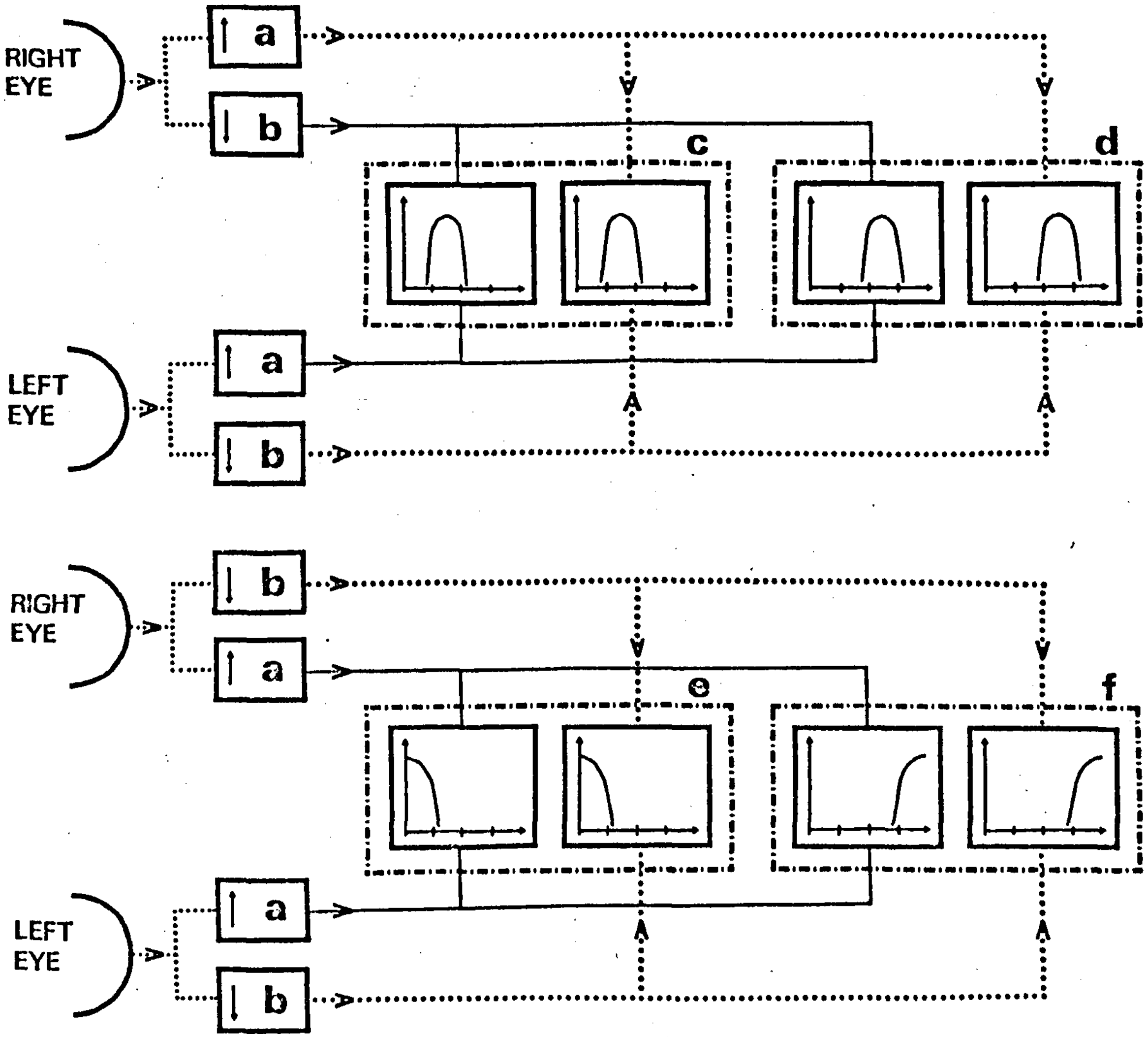


Figure 47. Model. a - monocular image position detector which responds preferentially to retinal image motion from left to right. b - monocular image position detector which responds preferentially to retinal image motion from right to left. c, d, e and f - stages which compute the retinal image disparity and which are "tuned" for left/right ratio. These disparity computers respond appreciably only when the left/right ratio falls within the following ranges: c - -(0:1) to -(1:1); d - -(1:1) to -(1:0); e - (1:1) to -(0:1); f - -(1:0) to (1:1).

reversed. Class B disparity detectors will adapt, and class A disparity detectors will be little affected. This could account for the finding that the asymmetry of the threshold elevation curve reverses when the adapting phase crosses 180° (Fig. 45) (see also Regan and Beverley, 1973C).

The small, localised reduction in depth threshold that one subject showed (K.B. Fig. 45) could be explained in terms of antagonism or mutual inhibition between class A and class B disparity detectors. Such a "sharpening-up" process might also be necessary to account for the fine sensitivity to small changes in phase angle around 180°. *

The model shown in Fig. 47 can account for the findings of Section 5:3.

This model is similar to the model shown in Fig. 46 in that two groups of motion detectors (a and b) are postulated which are selectively sensitive to stimuli moving from left to right (a) and right to left (b) on each retina. The outputs from these four groups of motion detectors (a_l, a_r, b_l and b_r) feed into disparity-computing stages. Four such disparity-computing stages are shown (C, D, E, F). Note that these are <u>entirely different</u> from the disparity-computing stages A and B shown in Fig. 46.

Stages C and D are excited only when the images in the left and right eyes are moving in opposite directions. Stages E and F are excited only when the images in the left and right eyes are moving in the same direction.

---

* This model was formulated in discussion with D. Regan and is also described in Regan and Beverley 1973C.

Stage C is shown as responding over a range of L/R ratios from -(0:1) to -(1:1) i.e. from a direction that passes through the left eye to a direction through a point midway between the eyes. This corresponds to a visual angle of some 3° (see Section 5:3). Stage D is shown as responding over a range of L/R ratios from -(1:1) to -(1:0) i.e. from a direction that passes through a point midway between the eyes to a direction that passes through the right eye. This also corresponds to a visual angle of some 3°. Stage E is shown as responding over a range of L/R ratios from (1:1) to -(0:1) i.e. from sideways motion to a direction that passes through the left eye. This corresponds to a visual angle of some 87°. Stage F is shown as responding over a range of L/R ratios from -(1:0) to (1:1) i.e. from a direction that passes through the right eye to sideways motion. This also corresponds to a visual angle of some 87°.

These four disparity-computing stages correspond to the four neural mechanisms "tuned" in terms of L/R ratio that underlie the four sensitivity functions shown in Fig. 44.

Section 5:4 has shown that for a given L/R ratio adaptation to movement is specific to the phase difference between the stimulus oscillations seen by the left and right eyes. This was modelled in Fig. 46. It seems likely, therefore, that each of the disparity-computing stages (C, D, E and F) of Fig. 47 may be subdivided into two parts.

For example, each part of stage E receives an input from either type a or type b motion detectors, but not both a and b motion detectors. Thus some of the disparity-computing mechanisms are excited only when the left and right retinal images are moving from <u>left to right</u> in both eyes. The remainder are excited only when both retinal images are moving from <u>right to left</u>.

The evidence of Section 5:4 and Fig. 46, however, only applies directly to stages E and F. As yet, there is no direct evidence to suggest an analogous subdivision of stages C and D, although this seems plausible (in fact it would be difficult to draw the model without this segregation). *

It should be noted that, since retinal image position was varied sinusoidally in these experiments, the peak to peak oscillation amplitude was proportional to the maximum velocity of the retinal image. Consequently the L/R ratio confounds the ratio of maximum displacements of the left and right retinal images with the ratio of maximum image velocities. Therefore, it is not yet clear whether the sensitivity curves shown in Fig. 44 or the retinal disparity computers of Fig. 47 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.

Finally, the existence of the several types of disparity computing mechanisms shown above, is sufficient to explain the effects of ΔF upon depth movement sensitivity (Chapter 4).

---

* This model was formulated in discussion with D. Regan and is also described in Beverley and Regan, 1973B.

5:6. Summary.

This chapter reports experiments performed in order to test the predictions made in Chapter 4. The model described in Section 4:4:2 assumed the existence of several phase-selective mechanisms tuned to different phase differences between the left and right eyes' stimulus oscillations. This would mean that selective adaptation should occur to phase differences between the two eyes' stimulus oscillations. The results of Section 5:4 show that such phase selective adaptation does indeed occur. Adaptation to a stimulus with an inter-ocular phase difference of less than 180° produced a threshold elevation for test stimuli with phase differences less than 180°. In contrast, the threshold for test stimuli with phase differences greater than 180° was unaffected. Adaptation to a stimulus with a phase difference greater than 180° produced the reverse effect. This finding was true for all subjects tested and for all L/R ratios used, although the effect was greatest for a L/R ratio of (1.5:1). (Note that the L/R ratio was unchanged throughout each experiment, and that both eyes at all times viewed unvarying sinusoidal stimulus oscillations).

This finding cannot be explained by adaptation at a site <u>peripheral</u> to binocular convergence.

A model is proposed in which the adaptation occurrs at or after the disparity computing stage. (At least) Two classes of disparity detectors are postulated. Each eye's input to a single class of disparity detector consists of the physiological responses to a single direction of stimulus movement on the retina.

The model described in Section 4:4:2 also predicted that it should be possible to selectively adapt to one direction of motion in space of the stimulus, but leave the sensitivity to other directions of motion unaffected. The results of Section 5:3 show that such direction-selective adaptation occurrs. Varying the relative amplitudes of stimulus oscillation in the left and right eyes (L/R ratio) varies the apparent direction of motion in space of the stimulus. Adaptation to a stimulus which moved along one particular direction in space produced a threshold elevation for test stimuli moving close to that direction. For other directions of movement the threshold was unaffected. This finding was true for all four subjects tested. (Note that both eyes at all times viewed unvarying sinusoidal stimulus oscillations.) Any adapting stimulus whose L/R ratio fell within a definite range gave similar threshold elevations. The results for 13 different adapting L/R ratios produced evidence for 5 such ranges. This finding was confirmed on a second subject. The 5 different threshold elevation curves could be summarized in terms of 4 hypothetical sensitivity functions.

These findings cannot be explained by adaptation at a site <u>peripheral</u> to binocular convergence.

A model is proposed in which the adaptation occurrs at or after the disparity computing stage. Eight classes of disparity detector are postulated. These classes are grouped into four pairs. Each pair is tuned to one direction of motion in three-dimensional space, thus reflecting the 4 postulated sensitivity functions. Each pair of classes of disparity detector is subdivided in terms of phase difference. One being selectively sensitive to phase differences less than 180°, the other selectively sensitive to phase differences greater than 180°.

Four of the eight classes of disparity detector are wholly concerned with movements along directions which pass very close to the head. These four classes subserve a visual angle of less than 6° and might go some way to explain man's excellent ability to judge the direction of movement in space of any object likely to hit his head (or body).

The existence of the several types of disparity detector is sufficient to explain the effects of ΔF upon depth movement sensitivity, reported in Chapter 4.

Section 5:2 reports on the timecourse of adaptation and recovery from adaptation to stimuli moving in depth. The threshold for movement in depth decreased rapidly from ten or more times to about twice the pre-adaptation level within 20 to 60 seconds from the start of recovery from adaptation. This is similar to the recovery from adaptation to gratings reported by Blakemore and Campbell (1969). However, recovery was not complete until 100 to 300 minutes had elapsed.

6/ CONCLUSIONS.

The conclusions that can be drawn from the experiments reported in this thesis can be summarized as follows.

For both sinewave and squarewave stimulation,* disparity cues affected a subject's ability to detect movement only when the stimulus oscillation frequency was less than 1Hz. (Sections 3:1:1, 3:1:3 and 3:2:1). Disparity cues then increased sensitivity for targets close to the fixation plane (within 7.5 min. arc), but decreased sensitivity for targets whose disparities were greater. Binocular sensitivity to sideways movement was higher for targets in the fixation plane than for targets with finite disparities (Section 3:1:2). The above findings mean that precise control of fixation (convergence) is of central importance in any experiment on stereopsis. One way of checking that convergence remains constant is to use nonius lines. Convergence on the fixation plane can be held to within 0.5 min. arc for 5 to 20 seconds by this means. Displacing the moving part of the stimulus pattern to one side of the fixation point, also helps maintain a steady convergence. Fig. 12 and Fig. 27 give some evidence that convergence errors were very small.

---

* It should be noted that, in the experiments of Chapter 3, changes in disparity were accompanied by movements of one or both retinal images. Because of this, all threshold measurements referred to the detection of "movement" of the target, and did not involve any discrimination as to whether the target moved in depth. The question as to whether the subjects could discriminate movements in depth from sideways movements, at threshold, is left open.

The effect of frequency upon depth sensitivity was different for crossed, uncrossed and zero disparities (Sections 3:1:3 and 3:2:1). Suprathreshold depth sensitivity had a steeper high-frequency attenuation for uncrossed than for crossed disparities (Section 3:4:1). One "stereoanomolous" subject could see depth for crossed disparities but gave no depth responses at all for uncrossed disparities of more than 5 min. arc (Section 3:4:2). This is consistent with Richards' (1970, 1971) hypothesis that there are three pools of disparity detectors responding respectively to crossed, uncrossed and near-zero disparities.

There was a discontinuity at about 3Hz. in the matched depth curves for suprathreshold squarewave stimulation (Section 3:5:1). Above this discontinuity, the sensation of depth did not vary with frequency. The appearance of a single target moving to and fro in depth changed to an appearance of two stationary targets. This can be likened to an analog, in the depth dimension, of the phi phenomenon.

When a target's retinal disparity changes with a pulsed waveform, the target appears to execute a pulsed movement in depth (Sections 3:3:1, 3:3:2 and 3:6:1). Visual sensitivity to such disparity changes was plotted as a function of pulse duration. These curves resembled low-pass filter characteristics. For a given direction of movement in depth, different sensitivity curves were obtained for targets located in front of and behind the plane of binocular fixation. However, depth sensitivities were similar for pulses directed from either location towards the fixation plane or directed from either location away from the plane. This suggests that movements in depth directed towards and away from the fixation plane are handled by different neural mechanisms in man in accord with single-neurone evidence in cat and monkey (Pettigrew, 1973; Zeki, personal communication to D. Regan). This is also consistent with Richards' (1970, 1971) hypothesis of three pools of disparity detectors.

sideways oscillations were less than 5Hz. in *both* eyes, depth oscillations could be seen; (b) when the frequency of sideways oscillation lay between 5 and 10Hz. in *either* eye, depth oscillations could not be seen; (c) when the frequency of sideways oscillation exceeded 10Hz. in one eye and was less than 3Hz. in the other eye, depth oscillations could be seen. Although the stimulus disparity waveforms could also be described in terms of three frequency regions, these three regions *did not coincide* with the three psychophysical regions. The existance of depth perception in the high-frequency region can be explained in terms of temporal integration ($\tau_A \doteq 30$ milliseconds) before the signals from the two eyes unite, at a point common to both disparity and sideways motion channels.

Sensitivity to oscillations in depth fell off when depth oscillated faster than 1Hz. at most, and failed completely at 2 to

It is possible to discriminate between sideways movements and movements in depth of a fused target at threshold. One method (described in Chapter 4) is to cause the timecourse of sideways motion to differ from the timecourse of motion in depth.

Using this method with squarewave stimulation, there was a rapid decrease in sensitivity to movement in depth as both F and ΔF were increased (Section 4:2:1). No movement in depth could be seen at all when either F or ΔF was greater than 7Hz.. To a first approximation, these results can be described in terms of the single parameter ($F+\Delta F$), where $1/(F+\Delta F)$ was the maximum "dwell time" of the fused target at any one disparity. As the dwell time was increased, depth sensitivity was increased. This relationship failed at a dwell time of approximately 500 milliseconds.

Using this method with sinewave stimulation, the perception of depth oscillations could be classified into three frequency regions (Section 4:3:1). These were (a) when the frequencies of

5Hz.. Sideways oscillations could be seen at much higher frequencies than oscillations in depth, up to at least 20 to 25Hz..

One's ability to see oscillations in depth was reduced by an unexpectedly large degree when ΔF was increased. This means that some form of temporal integration ($\tau_B \bumpeq 50$ milliseconds) must occur at a site central to binocular convergence.

A model is proposed (Section 4:4:2) to account for the above findings. This model assumes the existance of 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. These classes of disparity detector would also be tuned to different phase differences between the left and right eyes' stimulus oscillations. Some evidence, which points to the existance of directionally-selective mechanisms, has recently been found in cat (Pettigrew, 1973), monkey (Zeki, personal communication to D. Regan) and man (Regan and Beverley, 1974A).

The relative distance through which the left and right retinal images move (L/R ratio) provides a sensitive cue to the direction along which a target moves in three-dimensional space (Section 5:3:1).

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 (Section 5:3:1). Sensitivity to depth movement rapidly rose almost to the pre-adaptation level within the first 20 to 60 seconds after removing the adapting target, but recovery was not complete until 2 to 5 hours had elapsed (Section 5:2:1). Any adapting target whose L/R ratio fell within a definite range gave similar reductions of visual sensitivity to movements in depth (Section 5:3:1). There were five such ranges. These five ranges can be summarized in terms of four hypothetical sensitivity functions (Section 5:3:2). Regan and Beverley (1975) have provided further evidence for these four sensitivity functions. All this points to four classes of disparity detector, each tuned to one direction of motion in three-dimensional space.

In Chapter 5 it was also shown that viewing a target moving in depth depressed visual sensitivity to depth when test and adapting stimuli simulated motion along closed paths with the same directions of rotation (i.e. when the inter-ocular phase difference was either less than 180° for both test and adapting stimuli, or was greater than 180° for both test and adapting stimuli) (Section 5:4:1). However for opposite directions of motion, sensitivity was either unaffected or increased. This points to two classes of disparity detector tuned with respect to the inter-ocular phase difference. Either eye's input to a single class of disparity detector consists of the physiological responses to a single direction of horizontal movement.

The findings of Chapter 5 cannot be explained by adaptation at a site <u>peripheral</u> to binocular convergence. Instead, a model is proposed in which the adaptation occurrs at or after the disparity computing stage (Section 5:5). Eight classes of disparity detector are postulated. These classes are grouped into four pairs. Each pair is tuned to one direction of motion in three-dimensional space (Section 5:3:2). Each pair of classes of disparity detector is subdivided in terms of phase difference (Section 5:4:2). One being selectively sensitive to phase differences less than 180° , the other selectively sensitive to phase differences greater than 180°. Four of the eight classes of disparity detector 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. This might go some way to explain man's excellent ability to judge the direction in which an object moves in three-dimensional space.

The existance of the several classes of disparity detector is sufficient to explain the effects of ΔF upon depth movement sensitivity (Section 4:3:1).

It is possible that each of these eight classes of disparity detector is further subdivided in terms of the static disparity over which they operate. Richards (1970, 1971) has postulated the existance of three pools of disparity detectors responding respectively to crossed, uncrossed and near zero disparities. Further evidence for the existance of these pools was found in Sections 3:1:3, 3:2:1, 3:3:2, 3:4:1, 3:4:2, 3:5:1 and 3:6:1. Regan and Beverley (1974A) have found differences in the electrophysiological responses to crossed and uncrossed disparities which further supports this supposition.

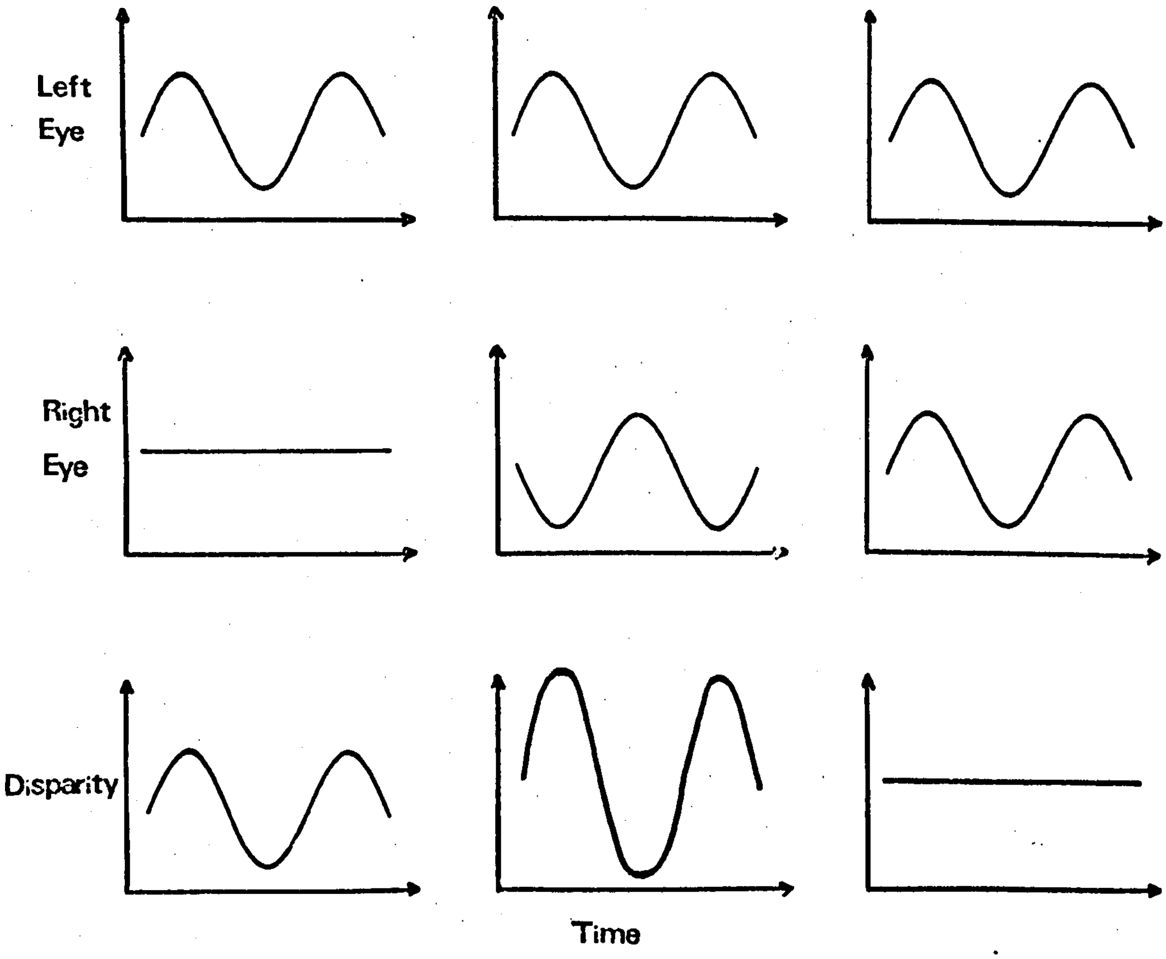


Figure 48. Sideways displacements of the stimulus patterns and the resulting changes in disparity for sinusoidal stimulation (chapter 3). Upper row. Sideways displacement of the stimulus seen by the left eye. Middle row. Sideways displacement of the stimulus seen by the right eye. Lower row. Resulting disparity changes. Left column. Movement of the stimulus pattern in only one eye. Centre column. Movement of both stimulus patterns in antiphase. Right column. Movement of both stimulus patterns in phase.

APPENDICES.

Appendix 1. Stimulus Motion With Sinewave, Squarewave or Pulsed Movements.

Sinewave Stimulation.

It is possible to generate an illusion of depth by using disparity cues alone (Wheatstone, 1838, 1852). Regan and Spekreijse (1970) have shown that by rhythmically changing the retinal disparity of part of a stimulus pattern, a compelling illusion of movement in depth can be created (see also Appendix 4). This illusion occurs even though no part of the stimulus pattern moves in depth either towards or away from the subject (i.e. when only sideways displacements of the stimulus patterns occur).

Fig. 48 shows the sideways displacements of the stimulus patterns and the resulting changes in disparity that occurred when using sinusoidal stimulation for the experiments of Sections 3:1 and 3:4. The upper row shows the sideways displacements of the moving part of the stimulus patterns (target) seen by the left eye (Stimulus 1, S1; Stimulus 2, S1; Stimulus 3, S3; or Stimulus 5, Q3). The target seen by the left eye always moved sinusoidally. The middle row shows the sideways displacements of the target seen by the right eye. In the left-hand column no displacement occurs (Stimulus 1, S2; Stimulus 2 S2; or Stimulus 3, S1), whereas in the centre and right hand columns sinusoidal displacements occur (Stimulus 5, Q4). The lower row shows the resulting changes in disparity that occurred when the targets were displaced in this way.

The left column, in which there is sideways movement of the target in one eye only, refers to the experiments of Sections 3:1:1, 3:1:2, 3:1:3, 3:1:4, 3:4:1 and 3:4:2. The left eye viewed a target oscillating sinusoidally from side to side and the right eye viewed an identical stationary target. When fused, the subject saw a single target oscillating sinusoidally to and fro in depth; the direction of motion being towards the right eye. * The centre column, in which there are sideways movements of the targets in both eyes, refers to the experiments of Section 3:1:2. Here sinusoidal displacements of the identical targets occurred in antiphase in the two eyes. Since a change in disparity refers to the <u>difference</u> between movements in the left and right eyes, the peak to peak change in disparity was twice that for the situation shown in the left column. When fused the subject saw a single target oscillating sinusoidally to and fro in depth; the direction of motion being towards a point midway between the eyes. The right column, in which there are sideways movements of the targets in both eyes, refers to the experiments of Sections 3:1:1, 3:1:2 and 3:1:3. Here sinusoidal displacements of the identical targets occurred in phase in the two eyes. Since a change in disparity refers to the <u>difference</u> between movements in the left and right eyes, there was no change in disparity for this condition. When fused the subject saw a single target oscillating sinusoidally from side to side. The subject saw no motion in depth.

The three columns refer to the three stimulation conditions of monocular-stereoscopic movement (left column), stereoscopic movement (centre column) and binocular movement (right column). A fourth stimulation condition (monocular movement) occurred when one eye was occluded. The non-occluded eye viewed the left eye's

---

* When using Stimulus 3, the left eye viewed the stationary target and the right eye the moving one. This, however, makes no difference to the argument except that "left" and "right" should be interchanged.

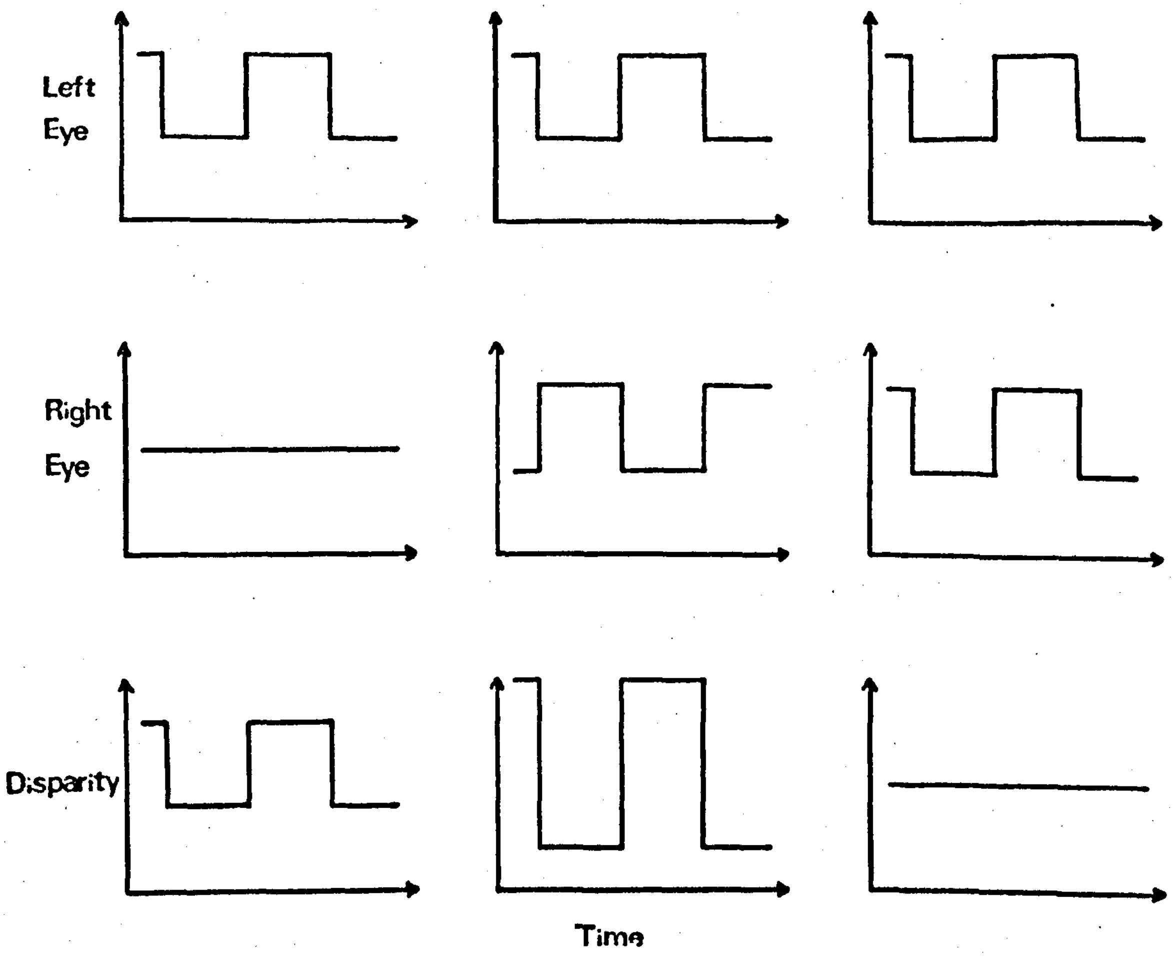


Figure 49. As Fig. 48 but for squarewave stimulation.

stimulus shown in Fig. 48, and the subject saw the target move only from side to side.

It should be emphasised that, although the subject had an illusion that the fused target moved to and fro in depth, at no time did any part of the actual stimulus pattern move in depth. The illusion of movement in depth was generated entirely by changing the retinal disparity of part of the stimulus by means of side to side movements.

Squarewave Stimulation.

Fig. 49 shows the sideways displacements of the stimulus patterns and the resulting changes in disparity that occurred when using squarewave stimulation for the experiments of Sections 3:2 and 3:5. The actual side to side movements of the targets and the resulting changes in disparity, shown in Fig. 49 for squarewave stimulation, can be explained in exactly the same way as for sinewave stimulation (shown in Fig. 48).

Stimulus 1 and Stimulus 2 were used in Section 3:2, and Stimulus 3 was used in Section 3:5.

At threshold, the subjective appearance of the fused stimulus with squarewave stimulation was similar to the subjective appearance of the movements of the fused stimulus with sinewave stimulation (Sections 3:1 and 3:2). However, with suprathreshold (matched depth) stimulation (Sections 3:4 and 3:5)the appearance of the movements differed.

With suprathreshold sinewave stimulation, the fused target appeared to sinusoidally oscillate to and fro in depth. The movement of the fused target was continuous. With suprathreshold squarewave stimulation, however, the fused target appeared to jump from one position in depth to a second position at a different depth. At

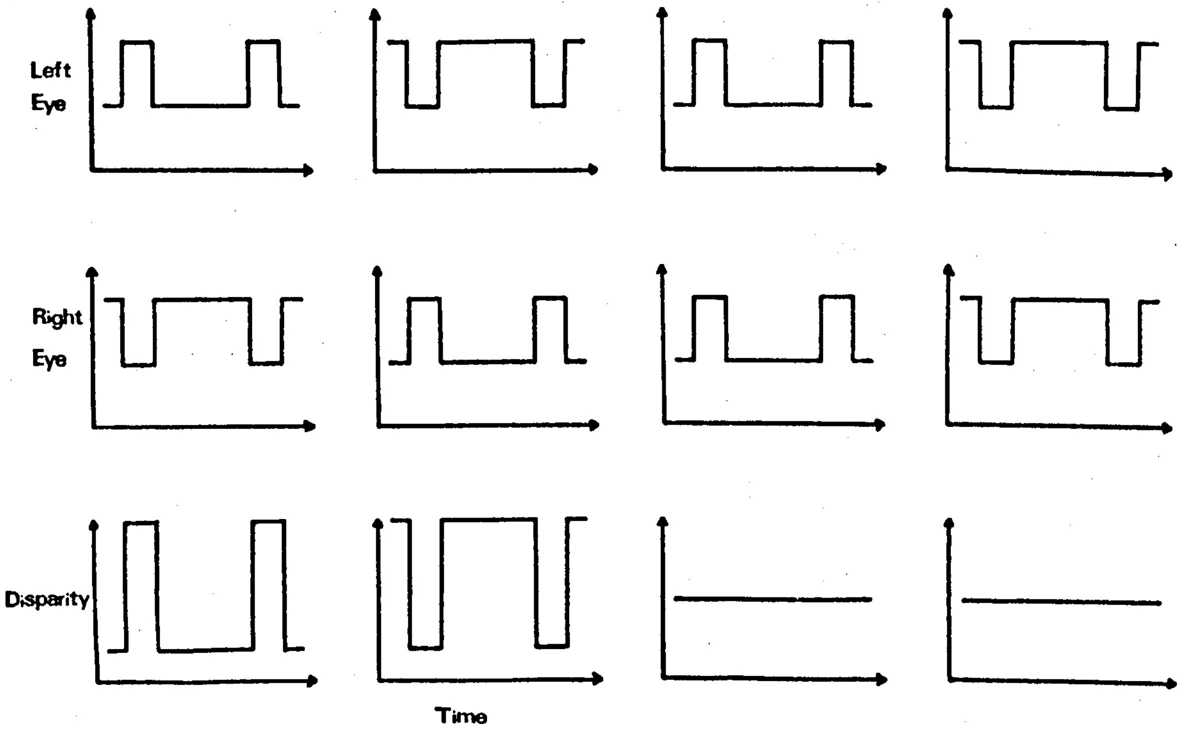


Figure 50. Sideways displacements of the stimulus patterns and the resulting changes in disparity for pulse stimulation (chapter 3). First two rows. Sideways displacements of the stimuli seen by the left and right eyes. Lower row. Resulting disparity changes. First column. Apparant movement of the stimulus towards the subject (P). Second column. Apparant movement of the stimulus away from the subject (N). Third column. Apparant movement of the stimulus to the right (R). Fourth column. Apparant movement of the stimulus to the left (L).

each of the two positions, the fused target remained for a short period. This period varied inversely with the frequency of the squarewave oscillation. This is to be expected from a consideration of Fig. 49.

However, as the squarewave oscillation frequency was increased to, roughly, 3Hz. there was an abrupt perceptual change in the appearance of the stimulus. Instead of a single fused target abruptly moving between two positions in depth, the appearance of the stimulus changed to that of two stationary targets, one at each of the two depth positions. These two targets appeared slightly "blurred". This abrupt perceptual change always occurred at about the same frequency (for increasing frequencies the change occurred at a slightly higher frequency than for decreasing frequencies - i.e. there was some hysterisis). Above this frequency, altering the stimulus oscillation amplitude altered the positions of the "two" bars. Consequently, matched depth settings were easily made at these high frequencies. This perceptual change in the appearance of the stimulus occurred for all subjects and under all experimental conditions.

A possible explanation for this change in the appearance of the stimulus is given in Section 3:5:2.

A similar abrupt change in the appearance of the stimulus occurred for side to side movements when squarewave stimulation was used. In this case the frequency at which the abrupt change occurred was roughly 20Hz..

Pulsed Movement Stimulation.

Fig. 50 shows the sideways displacements of the stimulus patterns and the resulting changes in disparity that occurred when using pulsed movement stimulation for the experiments of Sections 3:3 and 3:6.

The upper row shows the sideways displacements of the target seen by the left eye (Stimulus 6, Q3). The middle row shows the contemporaneous sideways displacements of the target seen by the right eye (Stimulus 6, Q4). The lower row shows the resulting changes in disparity that occurred when the targets were displaced in this way.

In the first two columns, sideways displacements of the identical targets occurred in antiphase in the two eyes. The timecourses of the targets' movements shown in the first column were as follows. After a variable interval (averaging about 1 second) the left eye's target moved suddenly to the right. It remained in this second position for a preset interval (the experimental variable - range 7 milliseconds to 1 second), and then it suddenly returned to its original position. The cycle was then repeated. The right eye's target, initially at the left, moved suddenly to the right and then returned. These movements caused a resulting change in disparity. The disparity, initially negative (uncrossed) changed abruptly to a more positive value (crossed) and then returned. The appearance of the fused target was as follows. After a variable interval the fused target moved suddenly towards the subject. After a preset interval the target suddenly returned to its original position. This cycle was then repeated. For any one measurement the preset interval was constant. The variable interval, however, varied irregularly so that the subject could not guess when the target would move.

The timecourses of the targets' movements shown in the second column were the reverse of the timecourses shown in the first column. The left eye's target moved to the left and then returned; the right eye's target moved to the right and then returned; disparity changed from a positive to a more negative value and then returned; and the fused target appeared to move suddenly away from the subject and then it returned.

In the last two columns, sideways displacements of the two identical targets occurred in phase in the two eyes. Thus, in the third column, the left eye's target moved suddenly to the right and then returned. The right eye's target also moved suddenly to the right and then returned. There was no change in disparity. The fused target appeared to move suddenly to the right and then it returned. There was no apparant movement in depth. In the fourth column, the left eye's target moved suddenly to the left and then returned. The right eye's target also moved suddenly to the left and then returned. There was no change in disparity. The fused target appeared to move suddenly to the left and then it returned. There was no apparant movement in depth.

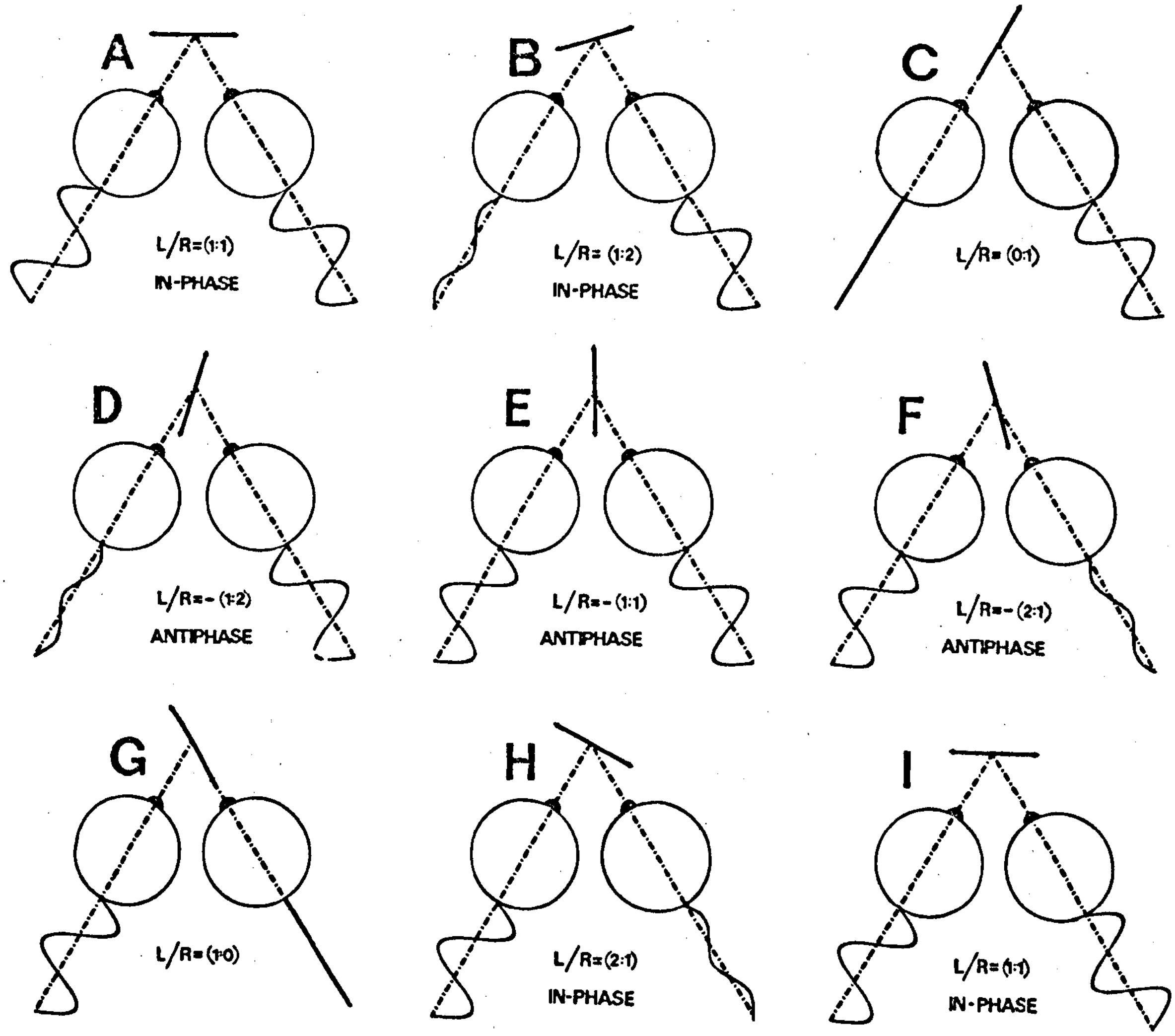


Figure 51. Schematic diagram illustrating the motion of the images on the left and right retinae of a binocularly-fixated stimulus which oscillates sinusoidally in various directions in three-dimensional space. See text.

Appendix 2. Stimulus Motion With an Amplitude Difference Between the Left and Right Eyes' Stimulus Oscillations.

It is possible to generate a stimulus which appears to oscillate along a straight line whose direction in space can be predetermined by varying the relative amplitude of stimulus oscillation seen by the left and right eyes (using Apparatus 3 and Stimulus 4)(see also Appendix 4). The term "L/R ratio", which refers to the relative amplitudes of oscillation of the left and right stimulus targets, is defined in Section 5:3.

It should be noted that, since the oscillations of the stimulus targets were sinusoidal, the L/R ratio does not distinguish between the relative peak to peak amplitudes of the stimulus movements, and the relative maximum velocities of the stimulus movements.

Both the left and right eyes viewed unvarying sinewave stimulus oscillations at 0.8Hz.. This low oscillation frequency was chosen since other experiments (Regan and Beverley, 1973A; Section 3:1:1) had shown that at higher oscillation frequencies thresholds for sideways motion were confounded with thresholds for motion in depth.

The use of sinusoidal stimulation meant that for both left and right eyes the leftwards and rightwards motions of the stimulus targets were exactly balanced.

Fig. 51 illustrates the motion of the images on the left and right retinae of a binocularly-fixated stimulus which oscillates sinusoidally in various directions in three-dimensional space. The arrowed lines immediately in front of the eyes represent the directions along which a real target oscillates.

In Fig. 51A, the target oscillates from side to side and does not move in depth. Consequently, the retinal image positions oscillate <u>in phase</u> with equal amplitudes (L/R ratio = (1:1)). 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 in phase (L/R ratio = (1:2)). 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 (L/R ratio = (0:1)).

When the target's direction of motion is directed to any point between the eyes, the two retinal image positions oscillate in <u>antiphase</u> (L/R ratio is negative). 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 (L/R ratio = -(1:2)). 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 (L/R ratio = -(1:1)). Fig. 51F, G, H and I show how the sequence D, C, B and A is paralleled 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. 51 is that the very large change in the L/R ratio going from C to G may refer to only a very small change in the direction of the target's motion. For the experiments reported in Chapter 5, the viewing distance was 63cm. so that the change in L/R ratios from C to G represented a change of only 6° of visual angle. For longer viewing distances, the same change in L/R ratio would represent a correspondingly smaller angular change. Thus, L/R ratio is a very sensitive indication of the direction of target movement provided that the direction is within a few degrees of the line which cuts midway between the eyes.

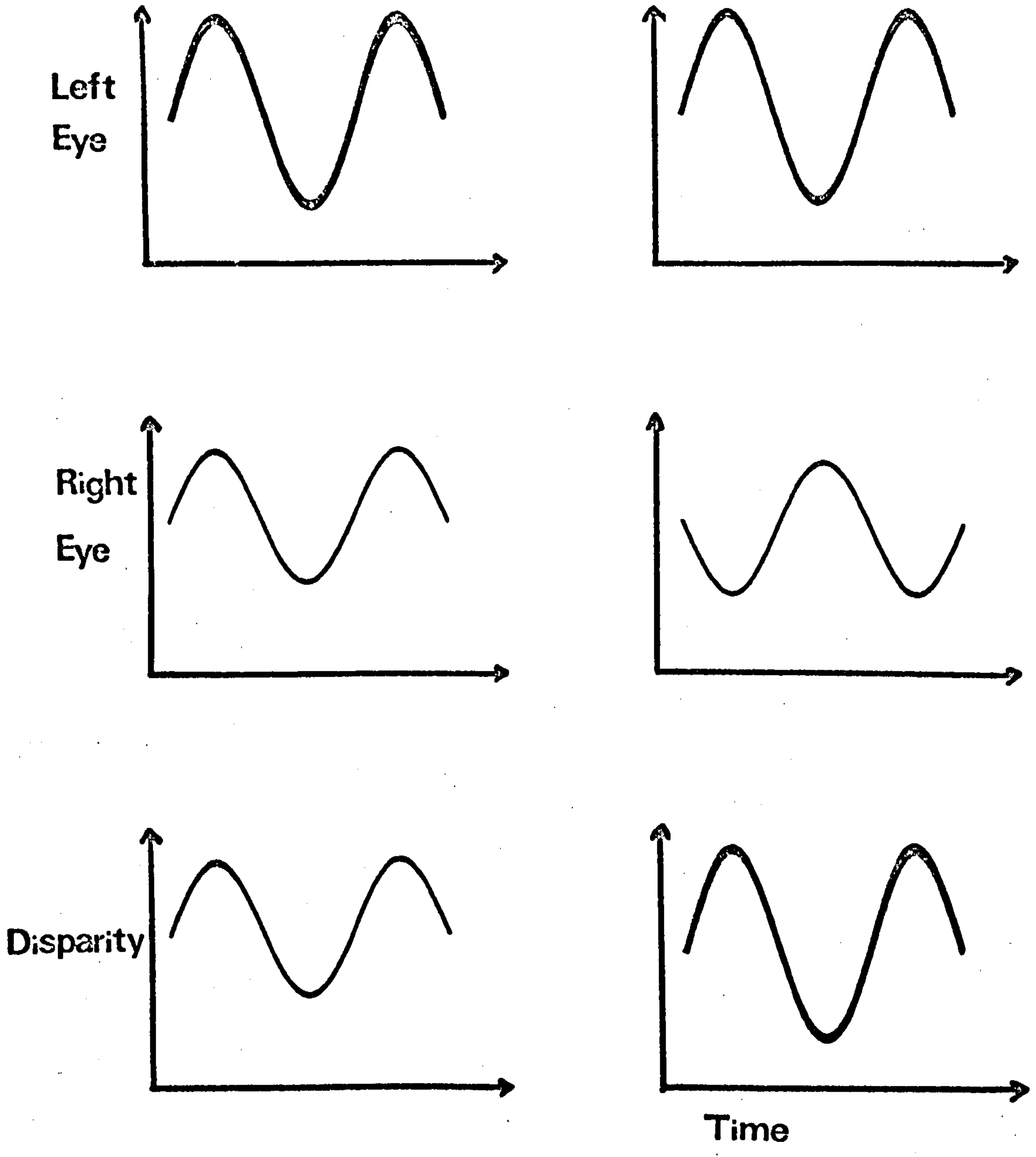


Figure 52. Sideways displacements of the stimulus patterns and the resulting changes in disparity for different L/R ratios (chapter 5). First two rows. Sideways displacements of the stimuli seen by the left and right eyes. Lower row. Resulting disparity changes. Left column. L/R ratio of +(1.5:1). Right column. L/R ratio of -(1.5:1).

The effect of changing the direction along which a target moves in space (as shown in Fig. 51) can be simulated by presenting separate patterns to the left and right eyes, and by moving these patterns from side to side so that the resulting retinal image movements are the same as those shown in Fig. 51. This was in fact the method used for the experiments of Chapter 5. The significance of the L/R ratio can be visualised, however, along the lines illustrated in Fig.51.

Fig. 52 gives a further illustration of the difference between a L/R ratio of +(1.5:1) and a L/R ratio of -(1.5:1). The upper row shows 1½ cycles of the stimulus waveform representing the side to side movement seen by the left eye. The oscillation amplitude is 1.5. The middle row shows 1½ cycles of a contemporaneous stimulus waveform representing the side to side movement seen by the right eye. The oscillation amplitude is 1. The lower row shows the resulting change in disparity. In the left column, the left and right eyes' stimulus oscillations are in phase (i.e. the L/R ratio is positive). In the right column, the left and right eyes' stimulus oscillations are in antiphase (i.e. the L/R ratio is negative). Note that the peak to peak disparity change is greater when the two eyes' stimulus oscillations are in antiphase. Note also that the phase of the disparity oscillation is the same as the left eye's side to side oscillation in both cases i.e. the phase of the disparity oscillation is the same as the side to side oscillation in whichever eye the greater peak to peak oscillation amplitude occurrs.

When the two targets were viewed in binocular fusion, the subjective appearance was that of a single target moving in space. The fused target appeared to sinusoidally oscillate along a single direction in space. This direction varied in the manner described in Fig. 51 as the L/R ratio was varied.

The subjective appearance of the movements of the fused target during an adaptation experiment was as follows. As the subject gazed at the adapting target, at first the target's oscillations in depth appeared large. However, as adaptation progressed, the oscillations in depth grew progressively smaller, until, after several minutes (the time varied from subject to subject and from day to day), no movement in depth was visible at all. It should be noted, however, that the stimulus still appeared to move from side to side, and that even after 30 minutes adaptation no noticable change in this side to side movement occurred. Thus, the angle between the direction of the target's apparant movement in space and the direction to the point midway between the eyes, appeared to increase as adaptation progressed.

Although several minutes adaptation were necessary to completely abolish the perception of movement in depth, a marked loss of sensitivity took place within the first few seconds of adaptation. When adaptation was complete and testing at different L/R ratios began, it was evident that a much greater stimulus oscillation amplitude was necessary to see depth for some L/R ratios than for others (this was apparant from the sideways motion of the stimulus). It was much more difficult to see oscillations in depth for stimulus oscillations directed to the same side of the head as the adapting stimulus oscillation. This was true for all adapting L/R ratios except -(1:1.05).

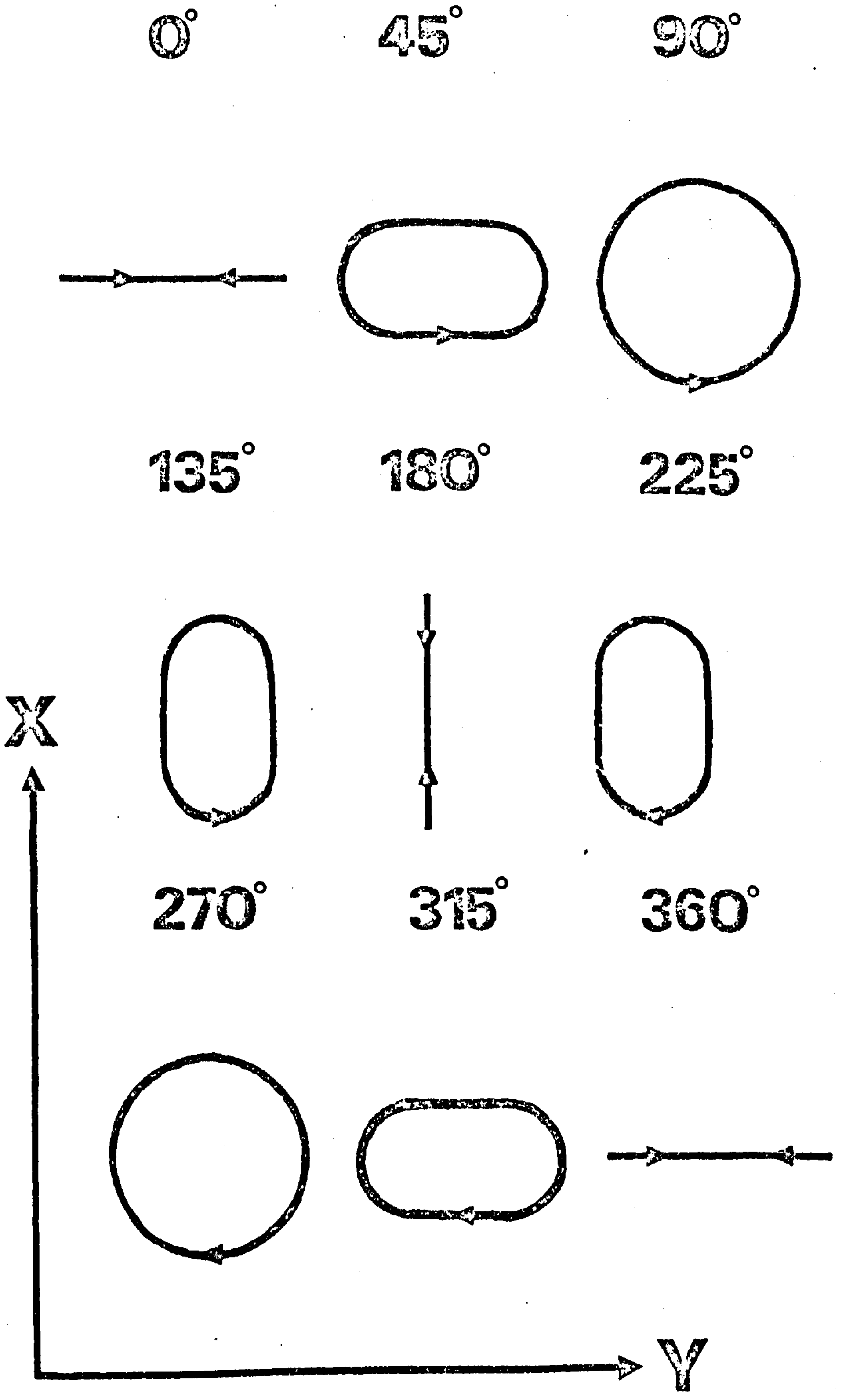


Figure 53. Schematic diagram illustrating the illusiory motion in depth of a binocularly-fixated target where there is a constant phase difference between the left and right eyes stimulus oscillations. X is the depth axis and Y the sideways movement axis. The numbers give the phase difference (degrees) between the oscillations seen by the two eyes.

Appendix 3. Stimulus Motion With a Phase Difference Between the Left and Right Eyes' Stimulus Oscillations.

It is possible to generate a stimulus which appears to move in depth by varying the relative phase difference between the stimulus oscillations seen by the left and right eyes (see also Appendix 4) (using Apparatus 3 and Stimulus 4).

Both left and right eyes viewed unvarying sinewave stimulus oscillations at 0.8Hz.. This low oscillation frequency was chosen since other experiments (Regan and Beverley, 1973A; Section 3:1:1) had shown that at higher oscillation frequencies thresholds for sideways motion were confounded with thresholds for motion in depth. The use of sinusoidal motion meant that the leftwards and rightwards motions of the stimulus targets were exactly balanced in either eye.

Fig. 53 is a schematic diagram illustrating the apparant motion in space of a binocularly-fixated target where there is a constant phase difference between the left and right eyes' stimulus oscillations. When the phase difference was 0° (left and right eyes' stimuli oscillating in phase), the fused target appeared to oscillate from side to side and did not move in depth at all. When the phase difference was 45° the fused target pursued an elliptical orbit in depth. The major axis of the ellipse was from side to side and the minor axis was to and fro in depth. The sense of rotation around the orbit meant that the target was moving from left to right when it appeared nearest to the eye (largest crossed disparity) and from right to left when it appeared furthest from the eye (largest uncrossed disparity). As the phase difference was progressively increased, the orbit of the fused target grew more elongated in depth. When the phase difference was 90° the fused target pursued a circular orbit in depth. When the phase difference was 135° the fused target pursued an elliptical orbit in depth. The major axis of the ellipse

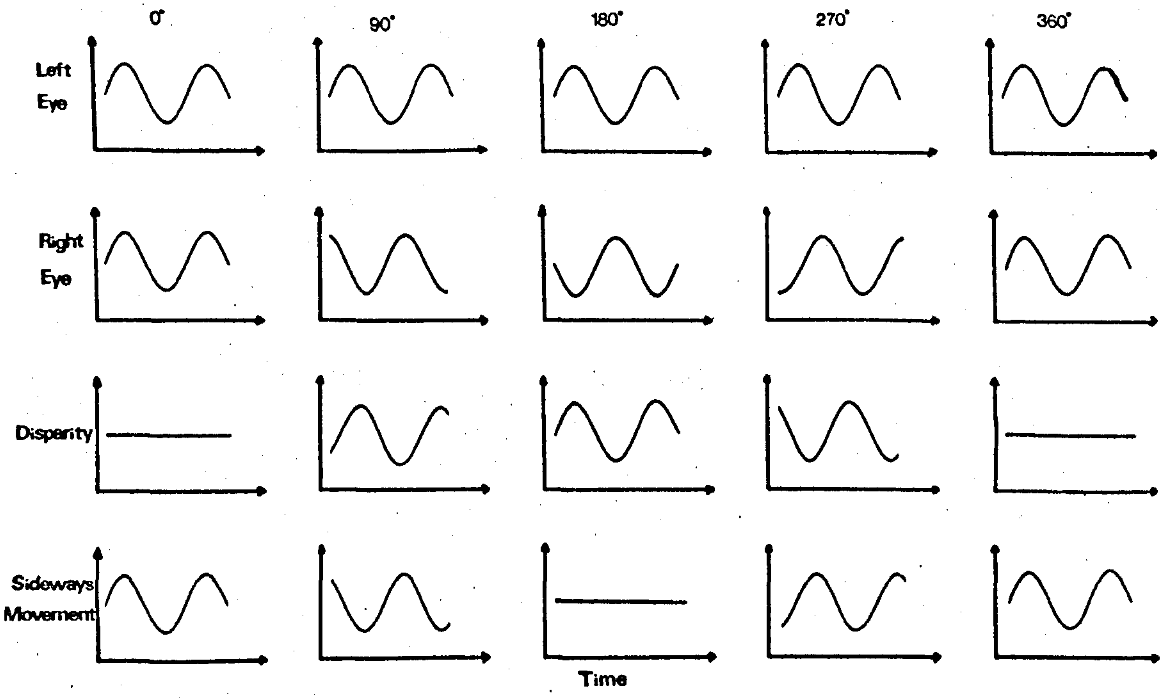


Figure 54. Sideways displacements of the stimulus patterns and the resulting changes in disparity and sideways movement for various phase differences between the left and right eyes stimulus oscillations (chapter 5). First two rows. Sideways displacements of the stimuli seen by the left and right eyes. Third row. Resulting disparity changes. Fourth row. Resulting sideways movements. The columns show the effects of various phase differences between the two eyes stimulus oscillations.

was to and fro in depth and the minor axis was from side to side. When the phase difference was 180° the fused target appeared to oscillate along a straight line directed at a point midway between the eyes. Further increases in phase angle caused the orbit of the fused target first to open out to an ellipse with its major axis extended in depth (225°), then to a circular orbit in depth (270°), then to an ellipse with its minor axis extended in depth (315°), until, for a phase of 360°, the situation was the same as for 0°.

These illusions were just what would have been expected from the known facts of binocular disparity. Fig. 53 also illustrates the central point that the sense of rotation of the fused target around the orbit was opposite for phase angles less than 180° than for phase angles greater than 180°. Thus the orbit of the fused target was identical for phase angles of 135° and 225° but the target moved <u>anticlockwise</u> for a phase angle of 135° and <u>clockwise</u> for a phase angle of 225°.

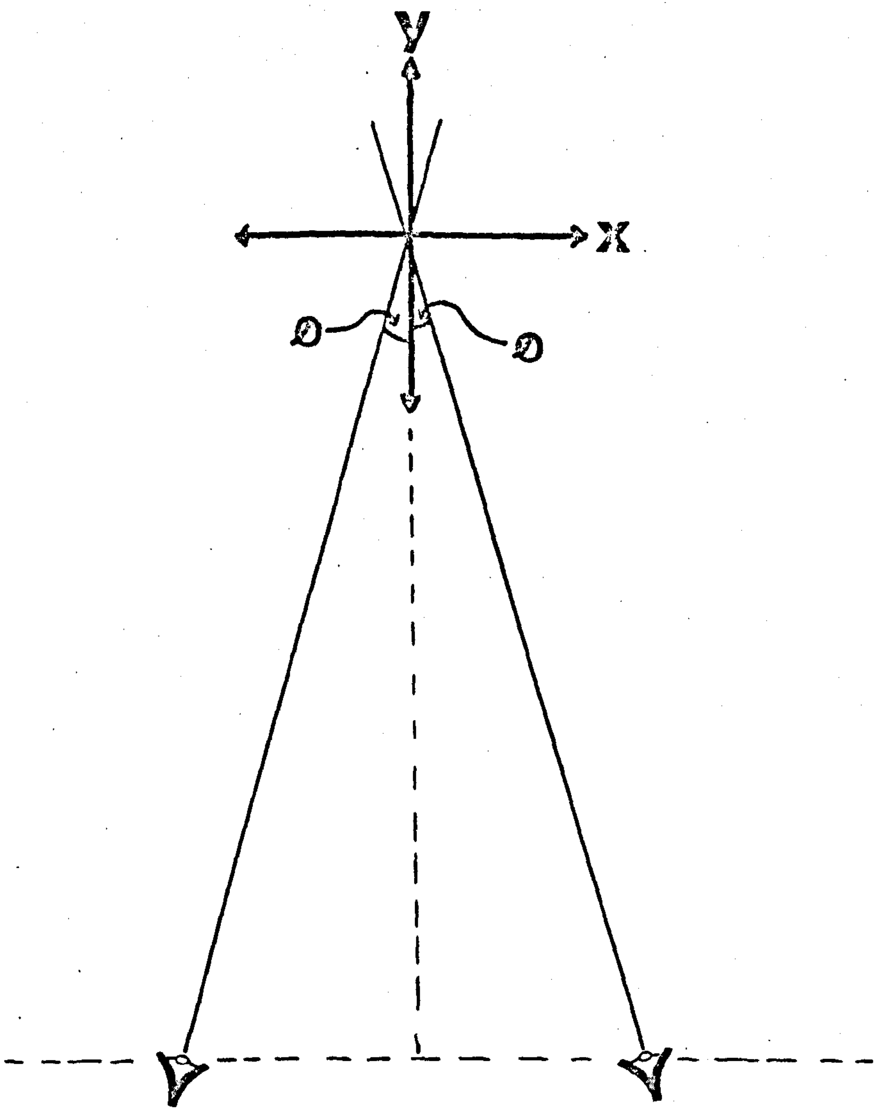
Fig. 54 shows the sideways displacements of the stimulus patterns and the resulting changes in disparity and sideways movement for various phase differences between the left and right eyes' stimulus oscillations. The upper row shows 1½ cycles of the stimulus waveform representing the side to side movement seen by the left eye. The second row shows 1½ cycles of a contemporaneous stimulus waveform representing the side to side movement seen by the right eye. The third row shows the resulting changes in disparity. The bottom row shows the resulting sideways movements of the fused target.

In the first column, the left and right eyes' stimulus oscillations are in phase (phase difference = 0°). There was no change in disparity when the phase difference was 0°. The fused target, therefore, moved purely from side to side. In the second column, the right eye's stimulus leads the left eye's stimulus

(phase difference = 90°). There was a change in disparity and also a change in sideways movement. The fused target, therefore, moved both from side to side and in depth. In the third column, the stimulus oscillations are in antiphase (phase difference = 180°). There was no change in sideways movement when the phase difference was 180°. The fused target, therefore, moved purely in depth. In the fourth column, the left eye's stimulus leads the right eye's stimulus (phase difference = 270°). This was the same as for a phase difference of 90° except that the movements in the left and right eyes were interchanged. The fused target moved both from side to side and in depth. In the fifth column, the left and right eyes' stimulus oscillations are again in phase (phase difference = 360° = 0°) which is the same as in column one. Note that the situation for phase differences less than 180° was the same as for phase differences greater than 180° but with the left and right eyes' stimulus movements interchanged.

For some experiments there was both a phase difference and an amplitude difference between the left and right eyes' stimulus oscillations. Under these conditions, the major and minor axes of the elliptical movements in depth (Fig. 53) were no longer in the X (to and fro in depth) and Y (side to side) directions but were inclined away from these directions by an amount depending on the L/R ratio. It should be noted also, that the direction of movement for a phase difference of 0° was no longer orthogonal to the direction of movement for a phase difference of 180°. For example, consider a L/R ratio of 2:1. For a phase difference of 0°, the fused target moved along a line directed just to the right of the right eye. For a phase difference of 180°, the fused target moved along a line directed just to the left of the right eye (see Fig. 51). For phase differences in the range 0° to 180°, the fused target moved in an anticlockwise ellipse, while for phase differences in the range 180° to 360°, the fused target moved in a clockwise ellipse. The central point, that the direction of motion of the fused target around its elliptical orbit was anticlockwise for phase differences less than 180°, and clockwise for phase differences greater than 180°, remained true whatever the L/R ratio.

The subjective appearance of the movements of the fused target during a phase adaptation experiment was similar to that reported in Appendix 2 for a L/R ratio adaptation experiment. Adaptation caused the target's movements in depth to decrease, whilst the target's sideways movements were unaffected. After adaptation was complete, testing with different phase differences showed an asymmetric adaptation effect. It was evident that a much greater stimulus oscillation amplitude was necessary to see depth for some phase differences than for others (this was apparant from the sideways motion of the stimulus). It was much more difficult to see movements in depth for movements in the same direction (clockwise or anticlockwise) as the adapting stimulus. This was true for all adapting phase differences and for all L/R ratios that were used. The effect was quite small however for a L/R ratio of (1:1).



$X_l = A_l \mathrm{sine}(2\pi ft)$ $X_r = A_r \mathrm{sine}(2\pi ft + \Phi)$

$$X_l = A_l \mathrm{sine}(\theta)\mathrm{sine}(2\pi ft)$$
$$X_r = A_r \mathrm{sine}(\theta)\mathrm{sine}(2\pi ft + \Phi)$$
$$Y_l = A_l \cos(\theta)\mathrm{sine}(2\pi ft)$$
$$Y_r = A_r \cos(\theta)\mathrm{sine}(2\pi ft + \Phi)$$

<u>Figure 55</u>. See text.

Appendix 4. Stimulus Motion With a Frequency Difference Between The Left and Right Eyes' Stimulus Oscillations - Sinewave.

It is possible to measure depth movement thresholds which are uncontaminated by the effects of sideways movements of the retinal images, by making the timecourse of sideways motion and motion in depth different. One way in which this can be done is to present a stimulus in which the frequencies of oscillation in the left and right eyes differ (see Section 4:1).

The frequency of sideways oscillation of the stimulus target seen by the left eye was FHz., and by the right eye was $(F+\Delta F)$Hz.. The movement of the fused stimulus can be understood by considering the frequency of sideways oscillation of the two targets to be the same, but with a continuously changing phase difference (ϕ) of 360° per $1/\Delta F$ seconds.

First, consider the case for $\Delta F = 0$Hz. (that is ϕ is constant). Let the equation of motion of the left eye's retinal image of the target be

$$X_L = A_L \sin(2\pi f t) \qquad -(1)$$

and of the right eye's retinal image be

$$X_R = A_R \sin(2\pi f t + \phi) \qquad -(2)$$

In terms of the depth direction (Y) and the sideways direction (X) shown in Fig. 55, these equations become, for the left eye

$$X = A_L \sin(\theta)\sin(2\pi f t)$$

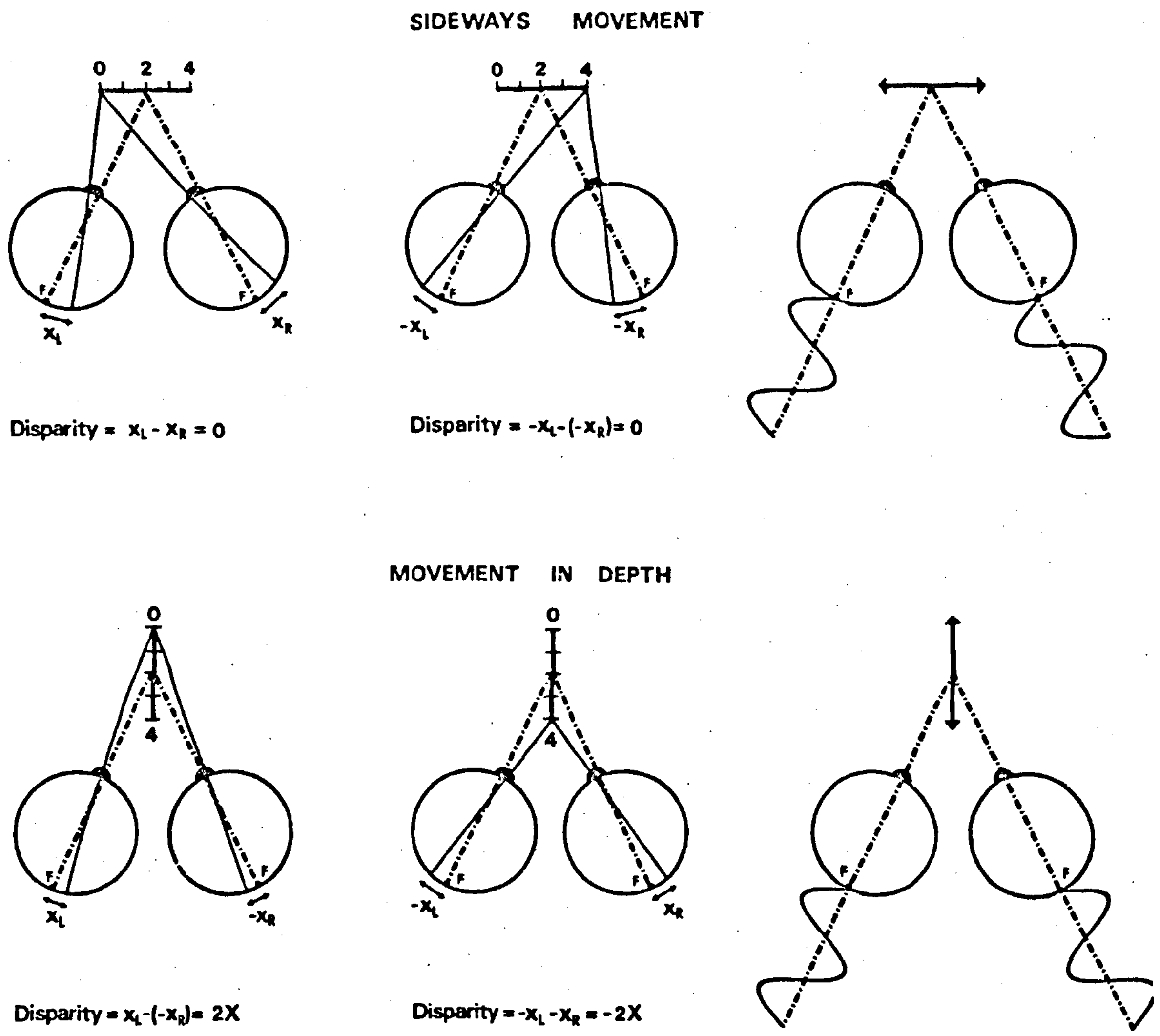
$$Y = A_L \cos(\theta)\sin(2\pi f t)$$

and for the right eye

$$X = A_R \sin(\theta)\sin(2\pi f t + \phi)$$

$$Y = A_R \cos(\theta)\sin(2\pi f t + \phi)$$

The equations of motion of a single, binocularly-fused target which generates the retinal image movements given by equations (1) and (2) above, are


SIDEWAYS MOVEMENT

MOVEMENT IN DEPTH

Figure 56. The upper half illustrates how a target which oscillates from side-to-side gives retinal images whose positions oscillate from side-to-side in phase, while the lower half illustrates how 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.

$$X = A(\sin(2\pi ft) + \sin(2\pi ft + \Phi)) \qquad - (3)$$

$$y = B(\sin(2\pi ft) - \sin(2\pi ft + \Phi)) \qquad - (4)$$

for $A_L = A_R$, A and B being constants.

For $\Phi = 0°$, that is for retinal images oscillating in phase, equations (3) and (4) reduce to

$$X = 2A\sin(2\pi ft)$$

$$y = 0.$$

These are the equations of motion of a target (viewed in binocular fusion) which oscillates, in a straight line, from side to side (Fig. 56 upper). Thus, a target will appear to oscillate from side to side if the left and right eyes' retinal images oscillate in phase.

For $\Phi = 180°$, that is for retinal images oscillating in antiphase, equations (3) and (4) reduce to

$$X = 0$$

$$y = 2B\sin(2\pi ft).$$

These are the equations of motion of a target (viewed in binocular fusion) which oscillates, in a straight line, to and fro in depth (Fig. 56 lower). Thus, a target will appear to oscillate to and fro in depth if the left and right eyes' retinal images oscillate in antiphase.

For all other values of Φ equations (3) and (4) become

$$X = A(2\sin(2\pi ft + \Phi/2)\cos(-\Phi/2))$$

$$y = B(2\cos(2\pi ft + \Phi/2)\sin(-\Phi/2))$$

Therefore, putting $Z = 2\pi ft + \Phi/2$

$$X = C\sin(Z) \qquad - (5)$$

$$y = D\cos(Z) \qquad - (6)$$

where C and D are constants.

Equations (5) and (6) are the equations of motion of a target (viewed in binocular fusion) which moves in an ellipse.

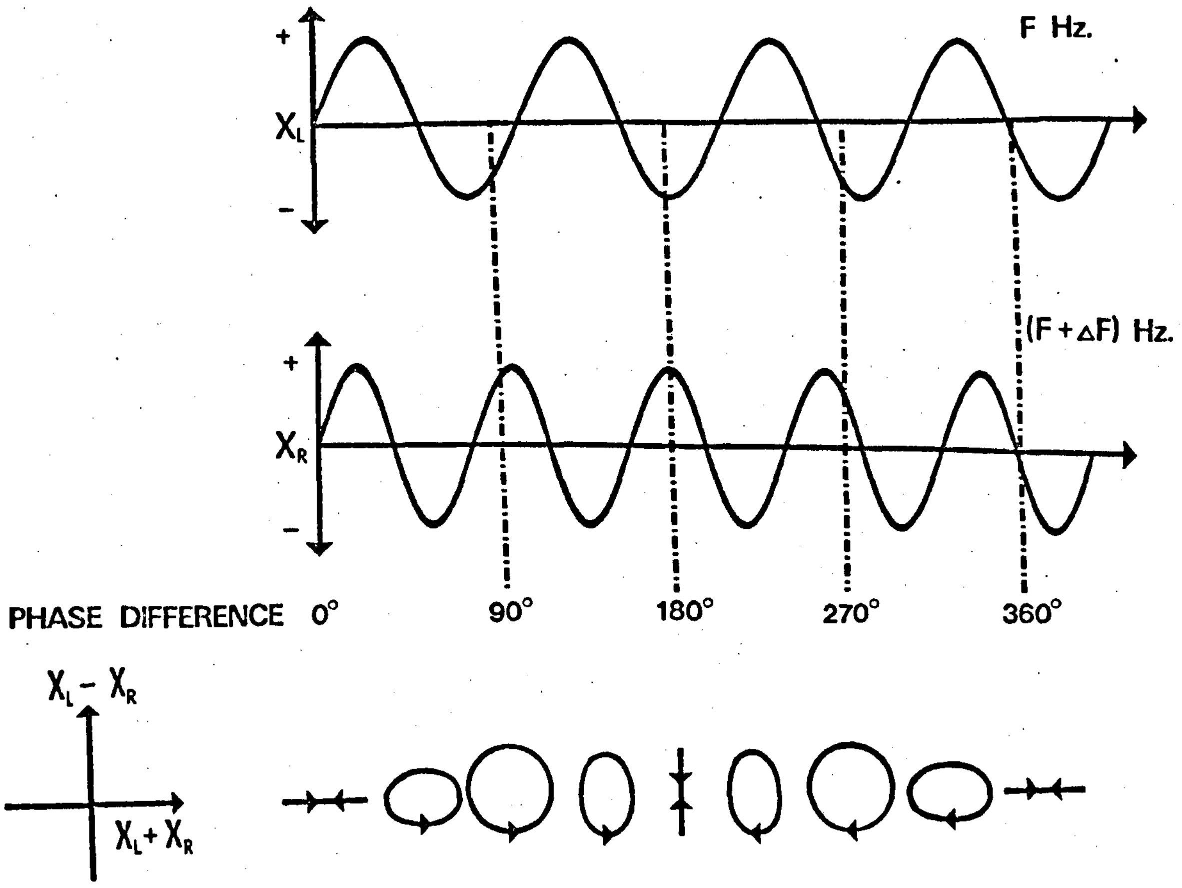


Figure 57. The upper part illustrates the sideways displacements of the stimulus patterns (targets) Q3 and Q4. X_L, X_R - positions of target images on left and right retinae respectively. Abscissae are time. The left eye's target oscillates at FHz., the right eye's at (F+ΔF)Hz.. The lower part illustrates the illusory motion in depth of the binocularly-fused target for various phase differences between the oscillatory displacements of the left and right eyes' targets. The plots are of retinal disparity (ordinates) versus retinal image position (abscissae).

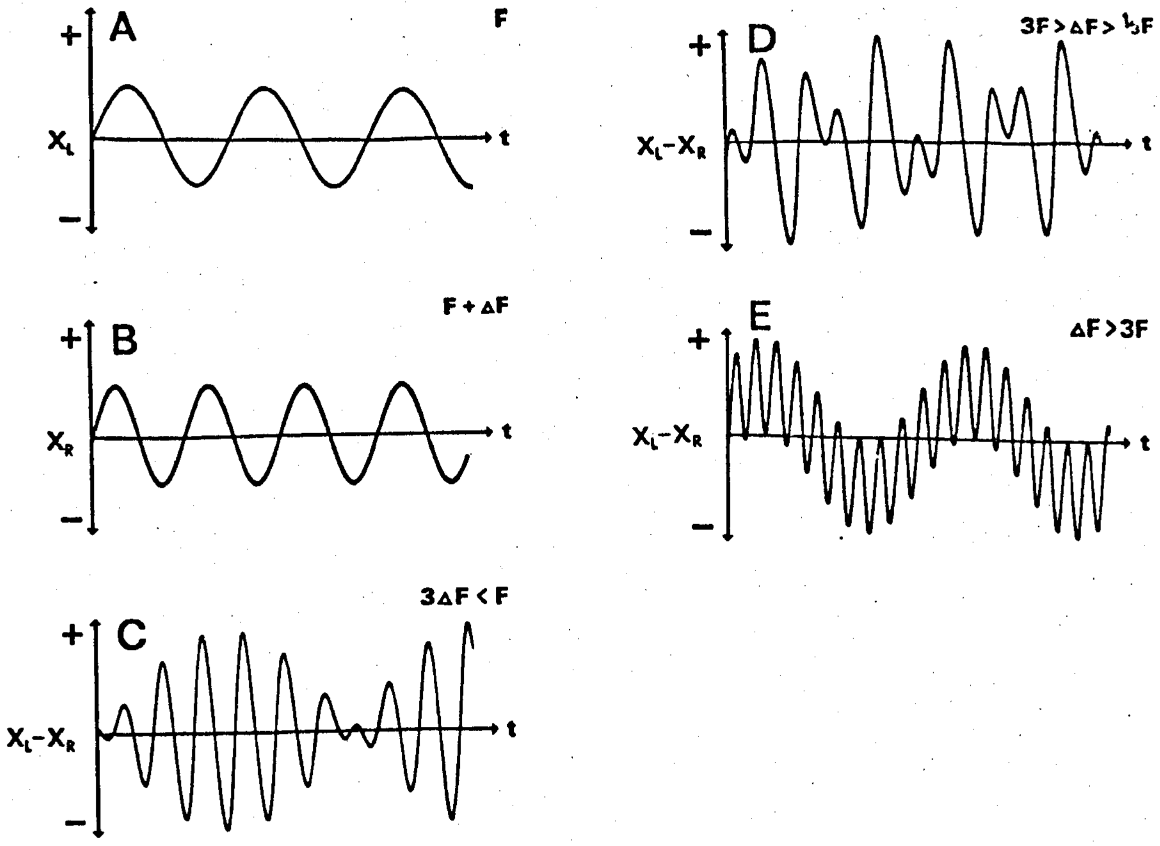


Figure 58. A and B show how the left and right eye's stimulus targets moved with time. The motion is sinusoidal. X_L, X_R - position of the retinal images in the left and right eyes. t - time. The oscillation frequency for the left eye's stimulus was FHz., and for the right eye's stimulus was (F+ΔF)Hz.. 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 $3F > \Delta F > F/3$; in E $\Delta F > 3F$.

Now, consider the case for $\Delta F \neq 0$Hz. (that is Φ varies continuously). For low ΔF ($3\Delta F$ less than F) the appearance of the target is shown in Fig. 57. At any instant in time the stimulus will appear to move as if there was a constant phase difference between the two eyes' stimuli (see Appendix 3). Thus when the instantaneous phase difference is 0° the fused target will appear to move in a straight line from side to side. When Φ is 45° the fused target will appear to move in an anticlockwise ellipse with its major axis sideways. When Φ is 90° the fused target will appear to move in an anticlockwise circle. When Φ is 135° the fused target will appear to move in an anticlockwise ellipse with its major axis in depth. When Φ is 180° the target will appear to move in a straight line to and fro in depth. For Φ greater than 180° the target's motion becomes clockwise and is elliptical in depth (for 225°), circular (for 270°), elliptical sideways (for 315°) and in a straight line from side to side (for 360°).

This whole sequence is continuously repeated and takes $1/\Delta F$ seconds for 1 cycle. 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 orbit continually merged into the next.

Fig. 58C shows the form of the retinal disparity function with time. The function appears as an amplitude-modulated sinewave; the carrier frequency being FHz. and the frequency of the amplitude modulation being ΔFHz. The appearance of the motion of the fused target was thus that of a stimulus moving to and fro in depth and at the same time moving from side to side, as described above. The side to side oscillations of the fused target occurred at a frequency of FHz.. The to and fro oscillations in depth of the fused target waxed and waned at a frequency of ΔFHz. (Fig. 58C). Since the frequency of the waxing and waning of the oscillations in depth (at

ΔFHz.) was uncorrelated with the frequency of the side to side oscillations of the fused target (at FHz.), and was also uncorrelated with the frequencies of side to side oscillations of the retinal images in the left and right eyes (FHz. and $(F+\Delta F)$Hz.), depth threshold measurements could be made independently of the sideways movements of the stimuli. Considerable sideways movements of the stimulus could in fact be seen in either eye.

All the above applies to the situation when $3\Delta F$ was less than F.

For the situation where $3F>\Delta F>\frac{1}{3}F$, the situation was somewhat different. In this case $\Delta F \mathrel{\hat{=}} F$ and the form of the retinal disparity function with time is shown in Fig. 58D. The carrier frequency is approximately the same as that of the modulating frequency. In consequence the retinal disparity function is complicated. The subjective appearance of the fused target reflected this complication. The fused target appeared to move irregularly (but continuously) both from side to side and to and fro in depth. The depth impression was very poor, and was only visible over a limited range of stimulus oscillation amplitudes; too great a stimulus oscillation amplitude and fusion was lost, too small an oscillation amplitude and the movements were below threshold. The impression of depth was often completely absent though considerable sideways movement of the stimulus could be seen in either eye.

For the situation where $\Delta F > 3F$, the situation was different again. In this case the form of the retinal disparity function with time is shown in Fig. 58E. The carrier frequency and the modulating frequency have changed places - the carrier frequency is now ΔF and the modulating frequency is F. The fused target appeared to oscillate sinusoidally in depth at FHz. along a straight line directed towards the right eye. The left eye's stimulus appeared to oscillate from side to side at FHz.. The right eye's stimulus appeared stationary but blurred. Increasing the stimulus oscillation amplitude until sideways movement became visible in the right eye caused the sensation of depth to break down. A possible explanation for this effect is given in Section 4:3:2.

It should be noted that the (somewhat arbitrary) changeover points between the three types of retinal disparity function ($3\Delta F < F$ and $3F < \Delta F$) shown in Fig. 58 do not correlate with the three regions of the psychophysical depth threshold function reported in Section 4:3:1 (see Section 4:3:2).

It should be emphasised that, although the subject saw an illusion of the fused target moving in depth, at no time did any part of the actual stimulus pattern move in depth. The illusion of movement in depth was generated entirely by changing the retinal disparity of part of the stimulus by means of side to side movements.

It should also be emphasised that, at all times, both left and right eyes viewed unvarying sinusoidal oscillations of the stimulus patterns.

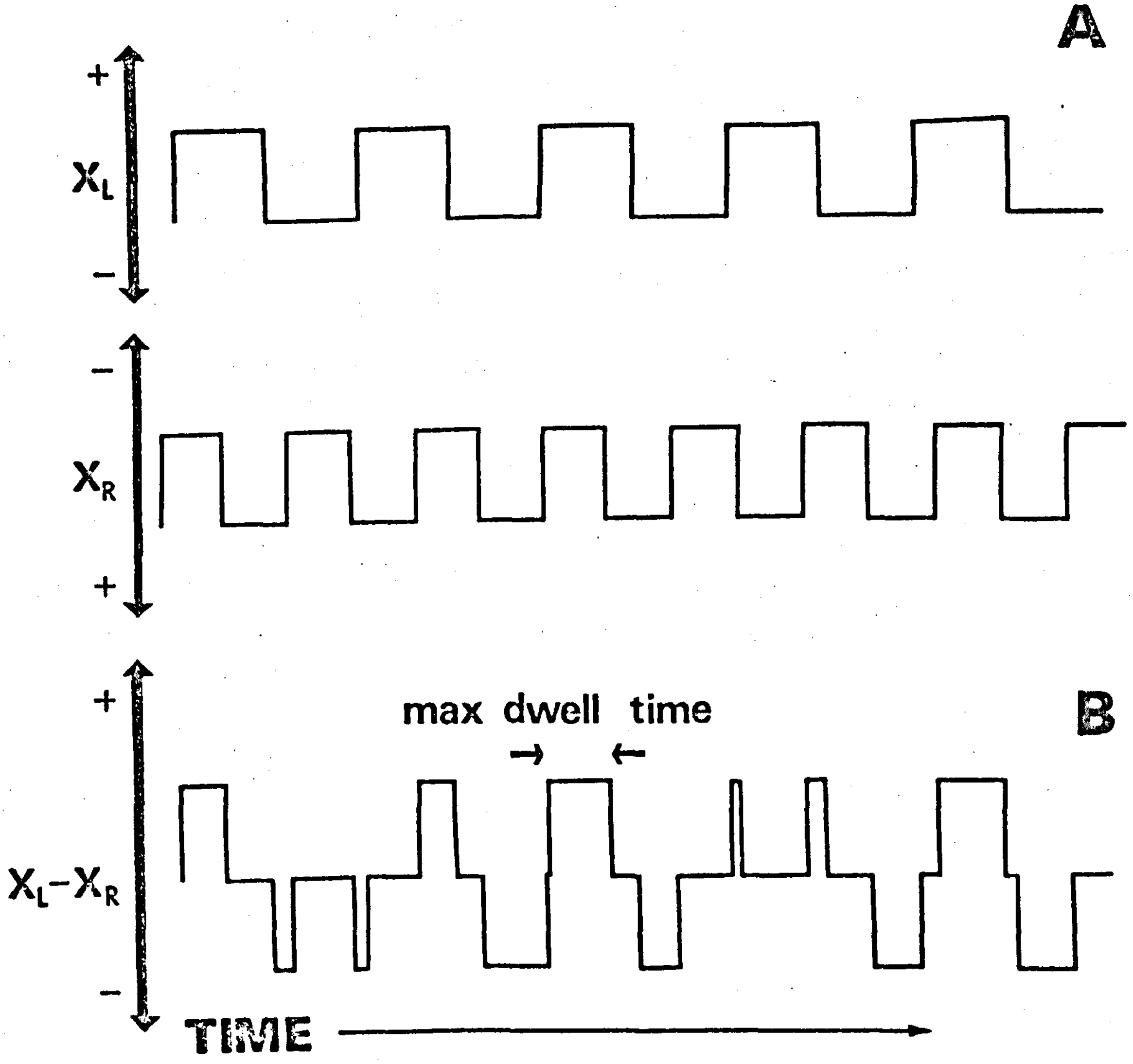


Figure 59. A shows the squarewave displacements of the positions (X_L and X_R) of the left and right eyes' retinal images. The left eye's target oscillated at F Hz. and the right eye's at (F+ΔF)Hz.. B shows the way in which retinal disparity ($X_L - X_R$) changed as a function of time. Note that only three values of retinal disparity were possible and that the longest time spent in any one of these three states (maximum dwell time) was 1/(F+ΔF) seconds.

Appendix 5. Stimulus Motion With a Frequency Difference Between The Left and Right Eyes' Stimulus Oscillations - Squarewave.

Fig. 59 shows the sideways displacements (X_L and X_R) of the stimulus patterns seen by the left and right eyes and the resulting changes in disparity ($X_L - X_R$) that occurred when using squarewave stimulation for the experiments of Section 4:2.

The left eye's target oscillated from side to side at a frequency of FHz. (Fig. 59 upper). The right eye's target oscillated from side to side at a frequency of $(F+\Delta F)$Hz. (Fig. 59 middle). Fig. 59 (lower) shows the resulting changes in disparity when the targets were displaced in this way. It can be seen that only three values of retinal disparity were possible, and that retinal disparity altered irregularly between these three values. The longest time spent in any one of these three states (maximum dwell time) was $1/(F+\Delta F)$ seconds. Thus as F or ΔF was increased the maximum dwell time decreased.

The subjective appearance of the fused target was as follows. The target appeared to jump, irregularly, to and fro in depth between any one of three positions, remaining at each position for a variable amount of time. Note that as the frequencies F and ΔF were increased there was no marked discontinuity as there was with a single frequency of stimulation (Appendix 1 squarewave stimulation). No doubling (or tripling) of the target occurred and at a sufficiently high frequency (about 7Hz.) all apparant movement in depth ceased, although side to side movements could still be seen in both eyes.

It should be noted that the stimuli viewed by both the left and right eyes moved in a regularly periodic manner (squarewave oscillations) so that the irregular changes of disparity had no counterpart in the monocular stimulation of either eye.

References.

Barlow, H.B., Blakemore, C. and Pettigrew, J.D. (1967). "The neural mechanism of binocular depth discrimination". Journal of Physiology, London, 193, 327-342.

Barlow, H.B. and Hill, R.M. (1963). "Evidence for a physiological explanation of the waterfall phenomenon and figural after-effects". Nature, London, 200, 1345-1347.

Beverley, K.I. and Regan, D. (1973A). "Selective adaptation in stereoscopic depth perception". Journal of Physiology, London, 232, 40P-41P.

Beverley, K.I. and Regan, D. (1973B). "Evidence for the existance of neural mechanisms selectively-sensitive to the direction of movement in space". Journal of Physiology, London, 235, 17-29.

Beverley, K.I. and Regan, D. (1974A). "Visual sensitivity to disparity pulses: evidence for directional selectivity". Vision Research, 14, 357-361.

Beverley, K.I. and Regan, D. (1974B). "Temporal integration of disparity information in stereoscopic perception". Experimental Brain Research, 19, 228-232.

Blakemore, C. (1967). "The neural mechanism of binocular depth discrimination". Journal of Physiology, London, 193, 327-342.

Blakemore, C. (1970A). "The range and scope of binocular depth discrimination in man". Journal of Physiology, London, 211, 599-622.

Blakemore, C. (1970B). "The representation of three-dimensional visual space in the cat's striate cortex". Journal of Physiology, London, 209, 155-178.

Blakemore, C. and Campbell, F.W. (1969). "On the existance of neurones in the visual system selectively sensitive to the orientation and size of retinal images". Journal of Physiology, London, 203, 237-260.

Bloch, A.M. (1885). "Expériences sur la vision". C.R. Soc. Biol. (Paris), 37, 493-495, quoted in "Handbook of Sensory Physiology" VII/4 - "Visual Psychophysics" pp 39. (Springer-Verlag, Berlin)

Bough, E.W. (1970). "Stereoscopic vision in the macaque monkey: a behavioural demonstration". Nature, London, 225, 42-44.

Fiorentini, A. and Maffei, L. (1970). "Electrophysiological evidence for binocular disparity detectors in human visual system". Science, 169, 208-209.

Fisher, R.A. (1963). "Statistical Methods for Research Workers". 13th. Edition, Oliver and Boyd, Edinburgh.

Hubel, D.H. and Wiesel, T.N. (1959). "Receptive fields of single neurones in the cat's striate cortex". Journal of Physiology, London, 148, 574-591.

Hubel, D.H. and Wiesel, T.N. (1962). "Receptive fields, binocular interaction and functional architecture in the cat's striate cortex". Journal of Physiology, London, 160, 106-154.

Hubel, D.H. and Wiesel, T.N. (1970). "Cells sensitive to binocular depth in area 18 of the macaque monkey cortex". Nature, London, 225, 41-42.

Julesz, B. (1960). "Binocular depth perception of computer generated patterns". Bell System Technical Journal, 39, 1125-1162.

Julesz, B. (1961). "Binocular depth perception and pattern recognition". in "Information Theory, 4th. London Symposium". Cherry, C. Ed. (Butterworths, London), pp 212-224.

Julesz, B. (1965). "Texture and visual perception". Scientific American, 212, 38-48.

Julesz, B. (1971). "Foundations of Cyclopean Perception". University of Chicago Press, Chicago.

Kahneman, D. and Norman, J.J. (1964). "The time-intensity relation in visual perception as a function of observer task". Journal of Experimental Psychology, 68, 215-220.

Nikara, T., Bishop, P.O. and Pettigrew, J.D. (1968). "Analysis of retinal correspondence by studying receptive fields of binocular single-units in the cat striate cortex". Experimental Brain Research, 6, 353-372.

Ogle, K.N. (1950). "Researches in Binocular Vision". W.B. Saunders Company, Philadelphia.

Ogle, K.N. (1953). "Precision and validity of stereoscopic depth perception from double images". Journal of the Optical Society of America, 43, 906-913.

Pettigrew, J.D. (1973). "Binocular neurones which signal change of disparity in area 18 of cat visual cortex". Nature, New Biology, 241, 123-124.

Pettigrew, J.D., Nikara, T. and Bishop, P.O. (1968). "Binocular interaction on single units in cat striate cortex: simultaneous stimulation by single moving slit with receptive fields in correspondence". Experimental Brain Research, 6, 391-410.

Regan, D. (1970). "Evoked potential and psychophysical correlates of changes in stimulus colour and intensity". Vision Research, 10, 163-178.

Regan, D. and Beverley, K.I. (1973A). "Some dynamic features of depth perception". Vision Research, 13, 2369-2379.

Regan, D. and Beverley, K.I. (1973B). "The dissociation of sideways movements from movements in depth: psychophysics". Vision Research, 13, 2403-2415.

Regan, D. and Beverley, K.I. (1973C). "Disparity-detectors in human depth perception: evidence for directional selectivity". Science, 181, 877-879.

Regan, D. and Beverley, K.I. (1973E). "Electrophysiological evidence for the existance of neurones sensitive to the direction of movement in depth". Nature, London, 246, 504-506.

Regan, D. and Beverley, K.I. (1975). in preperation.

Regan, D. and Cartwright, R.F. (1970). "A method of measuring the potentials evoked by simultaneous stimulation of different retinal regions". Electroencephalography and Clinical Neurophysiology, 28, 314-319.

Regan, D. and Spekreijse, H. (1970). "Electrophysiological correlate of binocular depth perception in man". Nature, London, 225, 92-94.

Regan, D. and Tyler, C.W. (1971). "Temporal summation and its limit for wavelength changes: an analog of Bloch's law for colour vision". Journal of the Optical Society of America, 61, 1414-1421.

Richards, W. (1970). "Stereopsis and stereoblindness". Experimental Brain Research, 10, 380-388.

Richards, W. (1971). "Anomolous stereoscopic depth perception". Journal of the Optical Society of America, 61, 410-414.

Richards, W. (1972). "Response functions for sine- and square-wave modulations of disparity". Journal of the Optical Society of America, 62, 907-911.

Tyler, C.W. (1971). "Stereoscopic depth movement: two eyes less sensitive than one". Science, 174, 958-961.

Wheatstone, C. (1838). "Contributions to the physiology of vision - 1. On some remarkable and hitherto unobserved phenomena of binocular vision". Philosophical Transactions of the Royal Society, 13, 371-394.

Wheatstone, C. (1852). "Contributions to the physiology of vision - 2. On some remarkable and hitherto unobserved phenomena of binocular vision (continued)". Philosophical Transactions of the Royal Society, 142, (II), 1-18.

Wohlgemuth, A. (1911). "On the aftereffect of seen movement". British Journal of Psychology, Supplement 1.

Zeki, S. Personal communication to D. Regan.