Vision Res. Vol. 15, pp. 583–590. Pergamon Press 1975. Printed in Great Britain.

SPATIAL ORGANIZATION OF BINOCULAR DISPARITY SENSITIVITY

C. WILLIAM TYLER*
Department of Psychology, Northeastern University, Boston, Massachusetts, U.S.A.

(*Received* 19 *July* 1974; *in revised form* 28 *August* 1974)

Abstract—The range of sensitivity to spatial modulation of disparity in a vertical line was investigated. The function obtained was not greatly altered by conditions of fixed aperture, constant number of cycles, high resolution, foveal or eccentric presentation. The simplest hypothesis to account for the observed disparity scaling of the upper disparity limit was a correlation between preferred sizes and disparities of cortical receptive fields. Binocular fusion shows a disparity scaling effect for sinusoidal variations in a vertical line, but little change for sinusoidal variations in a horizontal line or for rectangular variations in either direction. Fusion thus exhibits vertical/horizontal anisotropy but the effects are not explained by a size-disparity correlation in cortical receptive fields.

In a preliminary report (Tyler, 1973a) I have described the limits of stereoscopic depth sensation for complex disparity configurations. The purpose of this paper is to present a fuller analysis of these limits and to make suggestions concerning the type of neural organisation that could be responsible for them. These neurophysiological suggestions are of necessity based on such tenuous and incomplete information as is available, but they are hopefully intended as a guide to further possibilities for investigations, rather than as a definitive model. The results are treated in three sections. The first section describes the extent of stereoscopic sensitivity to sinusoidal disparity variations in line stimuli. The two following sections describe the effects of other configurations of disparity variations on the maximum depth limit and the fusion limit respectively.

1. STEREOSCOPIC SENSITIVITY FOR SINUSOIDAL DISPARITY VARIATIONS

The limits at which sinusoidal variations in disparity of a vertical line stimulus would elicit perceived depth differences were measured. Control conditions were used to measure the extent to which the results were affected by the number of cycles of the stimulus visible, inhomogeneity of the retina and retinal locus.

Method

Vertical line stimuli were generated on the face of an oscilloscope laid on its side. The oscilloscope time base of 1 kHz provided the vertical extension of the lines. An oscillator fed a sinusoidal voltage of variable frequency and amplitude to the horizontal axis. Images to the two eyes were selected by the conventional arrangement of crossed polarizing filters at the oscilloscope screen and at the subject's eyes. Vergence was corrected by means of prisms so as to be normal for the viewing distance used in each experiment. The stimulus configurations consisted of a static sinusoidal line viewed in one eye with a straight line to the other. Viewed at 30 cm, the lines were 15° high and 10′ thick with a luminance of 10 ft-L. The screen had a background luminance of 0·016 ft-L. The subject usually perceived this stimulus as a single line curved sinusoidally in depth, with the plane of curvature passing through one eye rather than the midline (see Fig. 1.). The stimulus was the sinusoidal version of Panum's limiting case for stereopsis, containing lateral as well as depth displacement. If antiphase sinusoids

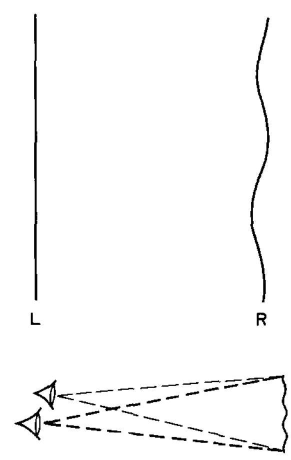

Fig. 1. Diagram of stimulus. Upper portion—left and right eye views of a sample stimulus. Readers may view this as a stereogram (with the page at 40 cm) by holding two cards at 15 cm from the eye, such that the right eye views the left-hand stimulus and vice versa. The observed sinusoidal disparity is above the fusion limit but below the depth limit, so that depth with diplopia is perceived. Lower portion—depiction of stimulus as seen by subject.

* Present address: Bell Telephone Laboratories, Murray Hill, New Jersey, U.S.A.

were presented to the two eyes so as to eliminate lateral displacement, a problem of vertical registration would arise. By a slight vertical vergence realignment the subject could bring antiphase sinusoids in phase in the fused image and thus abolish the binocular disparity. With a straight line in one eye no such realignment is possible.

For stereoscopic sensitivity the subject was asked to determine by the method of adjustment the threshold amplitude of sinusoidal disparity variations at which no part of the display appeared at a different depth from any other part. This instruction avoided confusion between lateral and depth effects. The subject was instructed to fixate at the point in the display optimal for perception of depth, but not to make depth judgements while moving the eyes. Peak-to-peak amplitude of the threshold monocular sinusoidal input was measured as a function of spatial frequency of the disparity. For each experimental condition frequencies were presented in random order. Two readings, or in some cases more (noted in figure caption), were obtained for each condition described here. Where two conditions are compared readings were obtained for both conditions concurrently so as to ensure that the differences described were immediately evident in direct comparison. All major effects described were verified by direct observation. All subjects in this study had good stereoscopic vision by the criterion of rapid perception of complex random-dot stereograms, and wore normal refractive correction during observations.

For the maximum depth limit the same procedure was used except that the maximum amplitude of disparity was determined. When the amplitude of disparity variations is increased from zero diplopia occurs at some point where depth differences are still perceived (Ogle, 1952), and then a point is reached where depth differences disappear. This latter point will be referred to as the maximum depth limit. These percepts are described fully in Tyler (1973a). The subject was instructed to maintain the same criterion of absence of depth differences, although diplopia was clearly present in the display. (The range of fusion limits under these conditions is considered in Section 3.) As a result, a bivalued function was obtained within which the subject could always see depth differences. The points of maximum frequency were obtained by adjusting the frequency for a fixed amplitude rather than the reverse.

Results

The limits of stereoscopic resolution are shown in Fig. 2 for two subjects, and as the filled circles in Fig. 3 for a third subject.

In the figures, vertical bars show one standard deviation of the settings for each mean, averaged over all means in a given condition. It was found by inspection that deviations were proportional to the absolute amplitude of the settings, so that a logarithmic transformation of the data was used prior to the standard deviation calculation. Double logarithmic coordinates are used both because the data extend over a range of several orders of magnitude and also for comparison with studies using other dimensions of sinusoidal stimulus variation (e.g. Campbell and Green, 1966; Blakemore, 1970; Tyler, 1971). The ordinate indicates the peak-to-peak disparity at the perceived depth limit, while the abscissa shows the spatial frequency of the sinusoidal disparity variations.

The scope of stereoscopic sensitivity is shown by the enclosed area marked "DEPTH" in Figs. 2–6. The boundary of this area has the interesting feature that it is strongly dependent on the spatial frequency of disparity variation. There is good agreement in the data for the three subjects on the form of the area of depth sensitivity, despite quantative differences by up to a factor of 3 in any setting. The linear relationship between

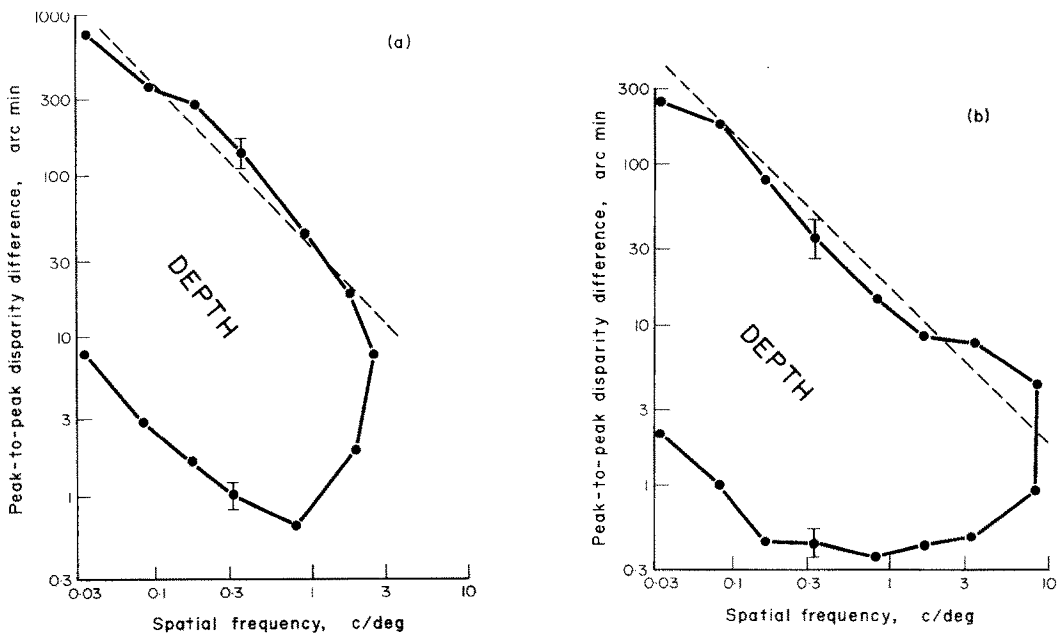

Fig. 2. Complete region of depth perception as a function of spatial frequency of vertical sinusoidal disparity variations with fixed aperture. Dashed line has slope of −1. (A)—subject JT. (B)—subject LCV.

the maximum disparity difference and the period of the sinusoid (the reciprocal of spatial frequency), will be referred to as *disparity scaling*, since the ratio of disparity to period remains constant for the depth maximum, and thus the sinusoid merely scaled up or down to reach the depth criterion.

It is possible that the form of the disparity function might result from the variation in number of cycles of sinusoidal disparity variation visible in the fixed aperture as spatial frequency was varied. The function was therefore measured with the number of cycles visible held constant at a single cosine cycle by varying the aperture. The results for one subject are shown in Fig. 3 (open circles). Although the form of the function is somewhat distorted it retains the main features of the fixed aperture functions (dashed curves). The greatest differences occur towards higher frequencies (i.e. small apertures in the 1 cycle condition).

The magnitude of the effect of reducing the number of cycles visible was confirmed at a fixed frequency of 1 c/deg in two subjects (Fig. 4). The number of cycles was varied from 1 to 15. The maximum disparity limit (open circles) shows a similar effect to Fig. 3 at 1 c/deg, namely a slight increase in the maximum disparity variation with reduction in number of cycles visible. The threshold function shows a similar decrease in sensitivity to that shown in Fig. 3 with 1 cycle visible. In addition it shows that most of the effect occurs between 1 and 2 cycles.

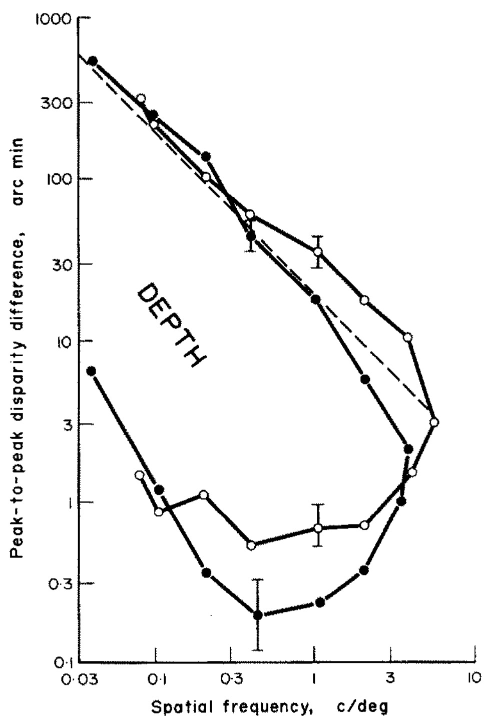

Fig. 3. Complete region of depth perception as a function of spatial frequency for subject CWT. Filled circles—fixed aperture. Open circles—variable aperture such that one cycle was visible at each frequency, with three readings per data point. Dashed line has slope of −1.

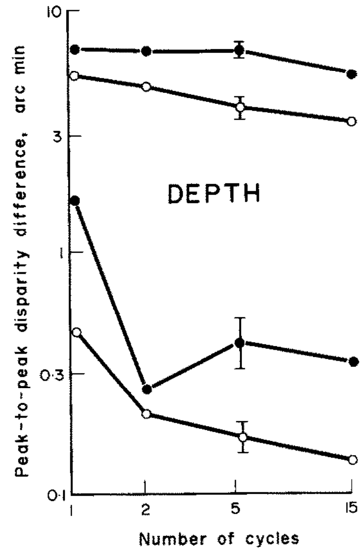

Fig. 4. Effect of varying number of cycle visible on minimum (lower portion) and maximum (upper portion) depth limits. Filled circles—CWT. Open circles—LCV.

Since the minimum disparity variation for depth detection is elevated by up to 0·5 log units with reduction in number of cycles, disparity detection improves when it is possible for the stereoscopic system to summate over more than 1 cycle. The data of Fig. 4 suggest that the major portion of summation occurs over 2 cycles. Similarly, the 1 cycle curve of Fig. 3 diverges where 2 cycles become visible in the fixed aperture curve. On the other hand the maximum depth limit is actually increased by reducing the number of cycles visible.

In order to obtain a large field of view the display described so far was viewed from the short distance of 30 cm. The retinal region from 0° to 7·5° receiving the stimulus is highly inhomogeneous. The experiment was therefore replicated viewing the display at 3 m such that the retinal images of the stimulus lines were 1′, which is as narrow as optical limitations of the ocular media allow. At this distance the stimuli subtended 1·5° and were therefore observed entirely within the fovea. The small field condition for two subjects (Fig. 5) shows a frequency dependence of the stereolimits similar to the large field condition, even though the lowest spatial frequency which can be tested usefully is 0·57 c/deg. The envelope of disparity sensitivity falls in the same region as for the large field condition, no mean values differing by more than a factor of two. The monocular limits of visibility of curvature (Tyler, 1973c) are shown under the small field condition for comparison (filled circles). It is clear that stereoscopic resolution of sinusoidal variations is still limited to considerably lower frequencies than is monocular resolution.

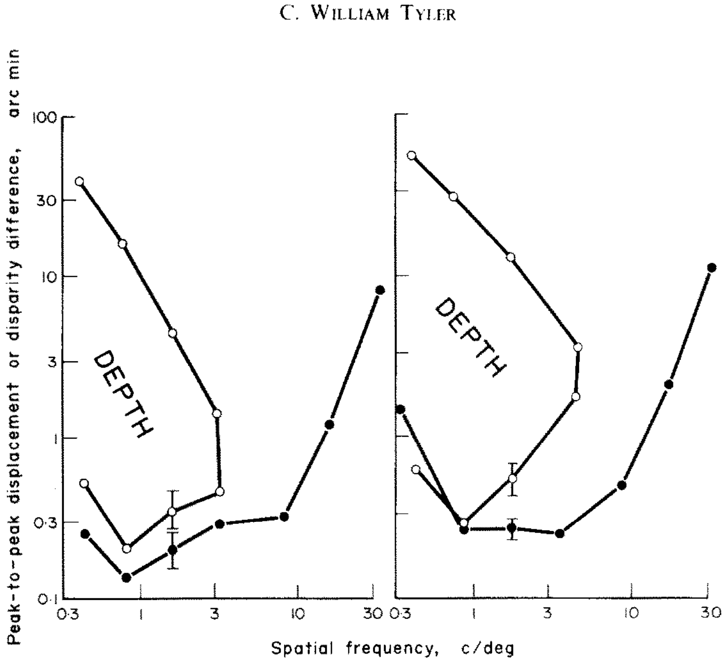

Fig. 5. Monocular (filled circles) and stereoscopic (open circles) limits for sinusoidal curvature of vertical line at resolution limit. Ordinate refers to displacement of the line which becomes the disparity when a straight line is present in the other eye. Left-hand portion—CWT. Right-hand portion—JT.

A second control for retinal inhomogeneity was performed by viewing the line stimuli with eccentric fixation. A monocular fixation line was generated at 7° horizontal eccentricity from the periodic stimulus. Thus the stimulus projected to relatively homogeneous retina between 7° and 10° eccentricity. The subject was instructed to fixate a point on the fixation line for optimal depth while making the threshold adjustments. The use of a monocular fixation allowed vergence angle to be determined optimally for the test stimuli without interference by the fixation stimulus, thus compensating for deviations of the horopter from the Vieth–Muller circle. The results for one subject show once again an envelope of stereoscopic sensitivity (solid curve and open circles in Fig. 6) of a similar form to that for central fixation. Monocular acuity for the sinusoidal line at this eccentricity (filled circles in Fig. 6) shows a similar reduction in sensitivity, so that the relationship between monocular and stereoscopic sensitivity (Tyler, 1973a) is essentially unaffected by peripheral observations.

Discussion

Stereoscopic sensitivity has been compared with monocular sensitivity for the same type of stimulus elsewhere (Tyler, 1973a). It was concluded that stereoscopic sensitivity exhibited cortical limitations that were not present in monocular vision. This limitation corresponds to the reduction in stereopsis for complex figures noted by Wheatstone (1938). There appears to be a corresponding physiological distinction between form and depth detectors. Hubel and Weisel (1970)

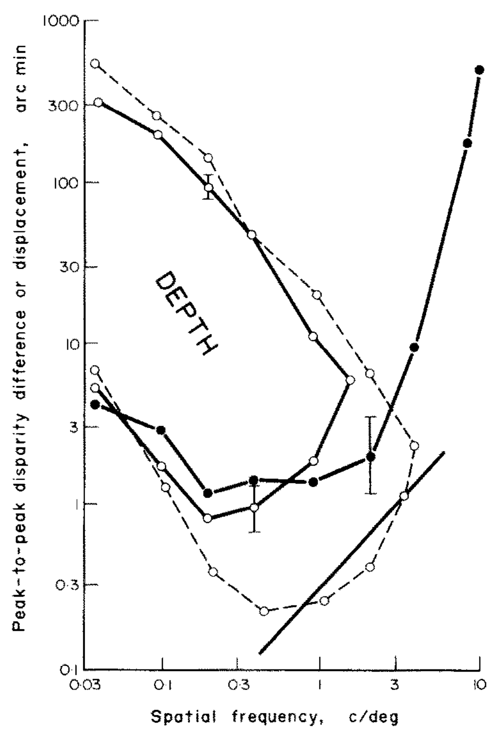

Fig. 6. Monocular (filled circles) or stereoscopic (open circles) limits for sinusoidal curvature of vertical line at 7° eccentricity for CWT. Four readings per data point. Dashed curve: stereolimits for foveal fixation from Fig. 3.

found that orientation and disparity preferences were arranged differently for cells in area 18 of the monkey. Columns or strips of cells responding to similar orientations were very narrow compared with those for depth. This suggests that cortical resolution for orientation should extend to higher spatial frequencies than for depth, since the rate of change of orientation detectors across the cortex is greater than for depth detectors.

A direct comparison of central (full line) and 7° (dashed lines) curves (Fig. 6) make it clear that at low frequencies neither minimum nor maximum disparity difference thresholds are affected by eccentric observation. High frequency sensitivity is considerably reduced so that the highest frequency which will elicit any depth sensation is about 1 c/deg. Note that in this result eccentric fixation has the opposite effect to reduction of stimulus aperture.

If the high frequency limitation were determined by disparity units with a minimum average length, then the high frequency maximum would be expected to have a slope of +1 (straight line in Fig. 6) on the assumption that near threshold, increases in disparity will compensate for the effect reduction in the area of the receptive field stimulated on the depth response. Eccentric fixation produces a change which conforms to the hypothesis that the average minimum length is increased, the increase being approximately 1 log unit. The actual length of the units cannot be determined without more information about their other characteristics. The results emphasize that the mechanism determining the high frequency limit is separate from the mechanisms determining disparity scaling and the low frequency reduction in disparity discrimination, since they are differentially affected by eccentric fixation.

Disparity scaling seems to be a general phenomenon in stereoscopic vision, for it occurs in a similar form in random-dot stereogratings (Tyler, 1974). These are random-dot displays containing sinusoidal disparity variations with negligible monocular cues. The limits of visibility of the stereogratings show similar spatial frequency dependence to sinusoidal line disparity stimuli.

Similarly Blakemore (1970) found that for perception of a fused contrast grating tilted in depth, the limiting feature was the ratio between the periods of the gratings in each eye, rather than the total cumulative disparity across the image. For a given image size, the limiting feature was the ratio of grating periods rather than bar-to-bar disparity or the maximum cumulative disparity in the display. Thus the controlling features (in this case of the fusion limit) were limited by spatial frequency rather than point to point disparity.

The non-monotonic character of the stereolimits in Figs. 2–6 deserves comment. It was implicit in the early recognition of binocular rivalry of contours (Wheatstone, 1938) that only a finite range of disparities would elicit depth sensations. Above this range disparity stimuli are perceived only as a depthless double image and below the range the disparity was undetectable. It follows that any specification of the limits of stereoscopic depths must involve a bivalued function, for example, the range of stereopsis as a function of retinal location (Ogle, 1952). An interesting analogy occurs in the observation of apparent movement, or a temporal rather than interocular separation of two stimuli. Apparent (phi) movement has both a lower limit (simultaneity) and an upper limit (succession) (Wertheimer, 1912) which both show spatio-temporal frequency dependence (Tyler, 1973b). The equivalence of interocular disparity for stereopsis and temporal disparity for phi movement in the same basic stimuli has been demonstrated by Anstis (1970), who showed that when a stereopair is alternated in time phi movement is observed and that stereopsis and phi movement were equally affected by various image degradations.

2. STIMULUS CONFIGURATION AND DISPARITY SCALING

The scaling of the limiting disparity beyond which even qualitative perception of depth is lost may be investigated by means of stimulus configurations similar to those described in Section 1. The two salient hypotheses for the neural basis of disparity scaling will be referred to as an orientation limit hypothesis and a size-disparity correlation hypothesis. The orientation limit hypothesis suggests that the maximum disparity for perceived depth is limited by the difference in orientation of stimuli or components of stimuli presented to the two eyes. This may also be described as a limit in rate of change of disparity. The results of Marlowe (1969) and Frisby and Roth (1972) suggest that the maximum difference in orientation between lines in presented to each eye for which a depth percept may be obtained is approximately 60°. However they did not use lines of different lengths, so it is possible that this orientation limit is actually determined by the maximum disparity difference between the ends of the lines rather than a specific orientation factor. The results in Figs. 2–6 conform to an orientation limit of about 45°.

An alternative hypothesis to explain disparity scaling is that there may be a correlation between the retinal size of a stimulus and the optimal disparity at which depth is perceived. The neural basis may be simply envisaged as a correlation between size and disparity for disparity-detecting neurons in the cortex, such that most neurons with small receptive fields are tuned to small disparities, and most neurons with large receptive fields are tuned to large disparities. An easy test between the orientation and correlation hypotheses is to investigate whether disparity scaling occurs for stimuli containing no orientation differences; for example, a disparity variation with a rectangular rather than sinusoidal waveform, so that the disparity alternates between two values down the line.

Results

Using the same stimulus presentation as before, minimum and maximum rectangular disparity variation eliciting perceived depth difference were measured both for a single cycle (Fig. 7) and repetitive changes with a fixed aperture of 15° (Fig. 8). The observers were instructed to fixate so as to produce the optimal depth perception. Subjective reports indicated that this occurred when the bent line in one eye straddled the straight line in the other, so that the disparity varied about zero.

Strong disparity scaling is evident in the stereomaximum under both conditions, in the absence of orientation differences in the stimuli. It follows that an orientation limit is not an adequate hypothesis for disparity scaling.

However, before adopting a size-disparity correlation explanation it is important to verify that retinal inhomogeneity is not producing the rectangular disparity scaling. Although Fig. 6 demonstrates that retinal inhomogeneity has a negligible effect on disparity scaling for sinusoidal stimuli, it is possible that it becomes a factor when rectangular variations are used. The maximum depth limit for rectangular disparity variations was therefore measured with fixation on a monocular line at 7° from the test stimulus, in a replication of the sinusoidal experiment of Fig. 6. The results (dashed line, Fig. 8) show that disparity scaling occurs at 7° and falls closer to a slope of unity than with foveal fixation.

The constant ratio between the sinusoidal and rectangular limits is not due to the presence of curved versus straight segments since the stereolimit for a triangular change in disparity (triangles, Fig. 8) occurs at even greater disparities than for the sinusoid. The ratios between these three waveforms are not proportional to the ratios of their fundamental Fourier components, which are indicated in the inset (Fig. 8).

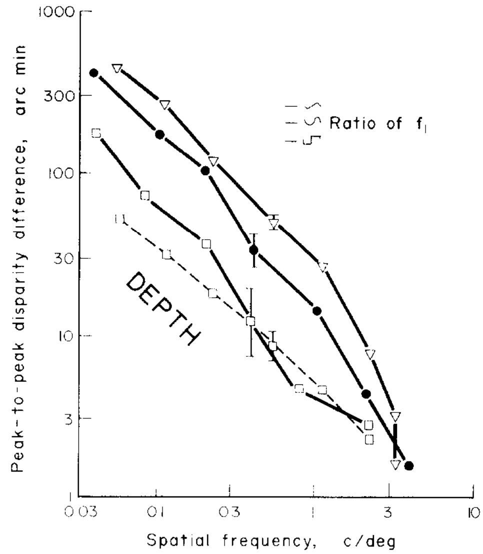

Fig. 8. Upper depth limit for CWT with various disparity configurations: Filled circles—sinusoidal, open square—rectangular, open triangles—triangular. Dashed curve—rectangular configuration viewed at 7° eccentricity. Inset—ratio of fundamental Fourier components (f_1) for the three waveforms.

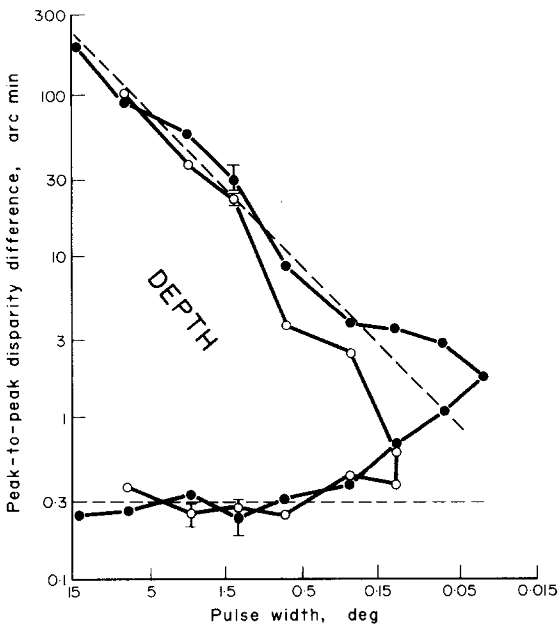

Fig. 7. Stereolimits for single-cycle square pulse as a function of pulse width for LCV (filled circles) and CWT (open circles). Abscissa is inverted to correspond with previous figures.

In contrast to the frequency dependence of the stereomaximum, threshold stereosensitivity was unaffected by the extent of the single square pulse down to 0.1° (Fig. 7). This difference in behaviour of the two types of threshold is considered below.

Discussion

The presence of disparity scaling at 7° eccentricity is sufficient to exclude retinal inhomogeneity as a major factor. The simplest explanation for disparity scaling therefore seems to be the size-disparity correlation. In terms of cortical disparity-sensitive neurons (Barlow, Blakemore and Pettigrew, 1967; Hubel and Weisel, 1970) the implication is that neurons sensitive to long vertical stimuli are tuned to large disparities, while those for short stimuli prefer small disparities, etc. At present the neurophysiological evidence suggests that disparity cells may have a range of preferred sizes of stimulus, a correlation between preferred horizontal sizes and preferred disparities. For example, analysis of data of Pettigrew, Nikara and Bishop (1968, Fig. 11) shows a correlation of 0.81 between log size and log disparity of receptive fields. This is likely to be reflected in a similar correlation for vertical size and disparity, and suggests the neural basis for disparity scaling.

A comparison of the effects of stimulus configuration on threshold and maximum depth limits makes it clear that these two limits must be governed by different processes. Just as with sinusoidal disparity variation, the stereothreshold for rectangular variations shows only the frequency dependence which can be attributed to the visibility of the monocular stimulus (Tyler, 1973c), whereas disparity scaling at the stereomaximum occurs where there is no corresponding limit in monocularly perceived amplitude (unpublished data). Thus frequency dependence of stereothreshold is abolished by rectangular variations (as it is for monocular threshold) whereas disparity scaling occurs to the same extent as with sinusoidal variations.

The proposed size-disparity correlation can nevertheless account for the major differences between threshold and maximum functions. While the size-disparity correlation accounts for disparity scaling at the stereomaximum, the size of the stimulus elements does not influence stereothreshold relative to monocular threshold up to about 1 c/deg. This relationship could conveniently be explained if stereothreshold were determined by minimal stimulation of detectors sensitive to the smallest disparities, which would exhypothesi have the smallest field size. Hence the use of longer elements in the lower spatial frequency conditions will not add any fine disparity information and stereothreshold should remain constant.

On the other hand for the maximum limits the rectangular stereomaximum occurs at approx 0·5 log unit smaller disparity than the sinusoidal stereomaximum (Fig. 8). A possible reason for this result is suggested by an experiment of Richards (1973). He found evidence of inhibition in detection of disparities of vertically adjacent stimuli measured by a reduction in perceived depth. The inhibition occurred reciprocally between detectors crossed and uncrossed disparities. It was reduced to negligible proportions as the absolute disparity was reduced, in agreement with the results of Tyler (1973a) that disparity inhibition is absent at stereothreshold [although monocular contour inhibition is probably present (Tyler, 1973c)]. Richards' results appear to show that inhibition between disparity detectors could reduce perceived depth by up to half the depth difference between the two stimuli. If it is assumed the inhibition requires the crossed and uncrossed stimuli to be vertically adjacent, such inhibition would reduce sensitivity to rectangular stimuli, while sinusoidal stimuli would be unaffected, since the crossed and uncrossed elements at large disparities are not spatially adjacent. Thus all major results are accounted for by a size-disparity correlation with reciprocal inhibition between crossed and uncrossed disparity detectors.

3. STIMULUS CONFIGURATION AND THE LIMITS OF FUSION

The final criterion for which the effects of stimulus configuration were investigated was the threshold for binocular fusion or absence of diplopia. I have reported that for sinusoidal disparity variations in a vertical line, disparity scaling occurs in a similar manner to the stereomaximum (Tyler, 1973a). A question that arises is whether the fusion and stereomaximum limits are governed by the same or different types of mechanisms. The presence of fusion in stereoblind subjects makes it clear that separate mechanisms are involved (Richards, 1970) but to what extent the two mechanisms operate differently has not been investigated. Using the same technique as before, the effect of changing stimulus configuration to a rectangular wave on the limit of fusion was investigated.

Results

The data previously reported for fusion limits of sinusoidal disparity variations [replotted as filled circles in Fig. 9(a) from Tyler (1973a)] may be compared with the fusion limits for rectangular disparity variations [open squares in Fig. 9(a)]. Clearly, much of the frequency dependence is abolished on observation of rectangular variations, although an effect of about a factor of 3 remains between 2·0 and 20 c/deg.

One difference that is immediately evident between the fusion and depth limits is that fusion can occur in both horizontal and vertical dimensions whereas retinal disparity only indicates depth in the plane of separation of the eyes, i.e. the horizontal dimension if the observer is upright. Additional information about the fusion limit can therefore be obtained by measuring the function of Fig. 9(a) with vertical disparities.

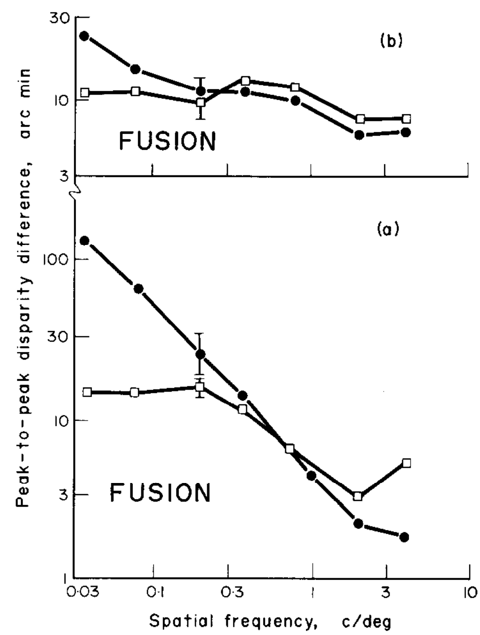

Fig. 9. Fusion limits with vertical (a) and horizontal (b) lines [horizontal (a) and vertical (b) disparities] for CWT using sinusoidal (filled circles) or rectangular (open circles) variations in disparity. Four readings per data point.

Figure 9(b) shows that the fusion ranges for both sinusoidal (circles) and rectangular (squares) vertical disparity variations are little affected by spatial frequency of disparity variation. Rectangular disparity sensitivity is constant within experimental error while sinusoidal sensitivity shows 0·5 log units decrease in range with 2 log units increase in spatial frequency. In both horizontal and vertical directions the fusion limit spans the classical value of around 6′.

Discussion

Comparison of horizontal and vertical data suggest that in the horizontal dimension fusion sensitivity approaches depth sensitivity whereas vertical disparities have a roughly constant fusion limit. This arrangement is clearly advantageous since vertical diplopia can be corrected by eye movements whereas horizontal diplopia is unavoidable with a horizontal eye separation.

The reduction in frequency sensitivity of fusion but not maximum depth for rectangular variations of horizontal disparity suggests that binocular fusion operates much more effectively on gradual spatial changes in disparity than abrupt ones. Although the effects are smaller, the same generalization is true of vertical disparities. These relationships do not immediately suggest a physiological mechanism, but neither a size-disparity correlation nor a fixed orientation limit will suffice to account for fusion limitations.

Acknowledgements—Supported by the Foundations Fund for Research in Psychiatry, grant 70-481. My thanks to Jean Torres and Carl Volpe for their assistance.

REFERENCES

Anstis S. M. (1970) Phi movement as a subtraction process. *Vision Res.* **10,** 1411–1430.

Barlow H. B., Blakemore C. and Pettigrew J. D. (1967) The neural mechanism of binocular depth discrimination. *J. Physiol., Lond.* **193,** 327–342.

Blakemore C. (1970) A new kind of stereoscopic vision. *Vision Res.* **10,** 1181–1190.

Campbell F. W. and Green D. G. (1966). Optical and retinal factors affecting visual resolution. *J. Physiol., Lond.* **181,** 576–593.

Frisby J. P. and Roth B. (1972) Orientation of stimuli and binocular disparity coding. *Q. Jl exp. Psychol.* **23,** 367–372.

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

Marlowe L. H. (1969) Orientation of contours and binocular depth perception. Ph.D. thesis, Brown University.

Ogle K. N. (1952) On the limits of stereoscopic vision. *J. exp. Psychol.* **44,** 253–259.

Pettigrew J. D., Nikara T. and Bishop P. O. (1968). Binocular interaction on single units in cat striate cortex. *Expl Brain Res.* **6,** 391–410.

Richards W. (1970) Stereopsis and stereoblindness. *Expl Brain Res.* **10,** 380–388.

Richards W. (1973) Disparity masking. *Vision Res.* **12,** 1113–1124.

Tyler C. W. (1971) Stereoscopic depth movement: Two eyes less sensitive than one. *Science, N.Y.* **174,** 958–961.

Tyler C. W. (1973a) Stereoscopic vision: Cortical limitations and a disparity scaling effect. *Science, N.Y.* **181,** 276–278.

Tyler C. W. (1973b) Temporal characteristics of apparent movement: Omega movement vs phi movement. *Q. Jl exp. Psychol.* **25,** 182–192.

Tyler C. W. (1973c) Periodic vernier acuity. *J. Physiol., Lond.* **228,** 637–647.

Tyler C. W. (1974) Depth perception in disparity gratings. *Nature, Lond.* **251,** 140–142.

Wertheimer M. (1972) Experimentelle Studien uber das Sehen Bewegungungen. *Z. Psychol.* **61,** 161–265.

Wheatstone C. (1938) Some remarkable phenomena of binocular vision. *Phil. Trans. R. Soc.* **128,** 371–394.