DISPARITY PROCESSING OF SPATIAL FREQUENCIES IN MAN

By THOMAS B. FELTON, WHITMAN RICHARDS AND
ROBERT A. SMITH, JR.

*From the Department of Psychology, Massachusetts Institute
of Technology, Cambridge, Mass. 02139, U.S.A.*

SUMMARY

1. Adaptation to a high-contrast sine-wave grating has been shown previously by Blakemore & Campbell (1969) to raise the modulation required to detect a low-contrast grating that has the same or similar spatial frequency as the adapting grating.

2. A similar adaptation effect occurs when the adaptation and test gratings are seen binocularly and are presented off the plane of fixation. When the gratings are not located on the plane of fixation, however, the greatest rise in threshold following adaptation occurs for test gratings presented in the same plane as the adapting grating. Thus, the neural mechanisms adapted to the high contrast patterns must be processing disparity information.

3. The spatial frequency response of the disparity adaptation effect has been measured by adapting to gratings of different spatial frequencies presented at a given disparity, and comparing threshold elevations for identical test gratings presented in the same (disparate) plane as the adapting grating or in the plane of fixation.

4. The unbiased adaptation effect specific to disparity is greatest for gratings whose periods are twice the disparity.

5. There is no adaptation effect specific to disparity for individuals possessing only convergent or only divergent disparity mechanisms.

6. The results suggest that disparity mechanisms make bar by bar correlations as opposed to edge by edge correlations and that narrow bar detectors feed small disparity mechanisms whereas wide bar detectors feed large disparity mechanisms.

INTRODUCTION

Recent neurophysiological studies have demonstrated the presence of selectively tuned disparity detecting neurones in the visual cortex of the cat (Barlow, Blakemore & Pettigrew, 1967; Pettigrew, Nikara & Bishop,

1968; Bishop, Henry & Smith, 1971) and the monkey (Hubel & Wiesel, 1970). In either animal, neurones may be found that respond to different degrees of horizontal disparity, with each individual neurone responding maximally to a specific disparity and little or not at all to neighbouring disparities. The presence of similar feature-specific analysers in the human brain has been inferred since Wheatstone's demonstration (1838) of the effectiveness of the disparity cue for stereopsis (Ogle, 1964). Particularly forceful arguments for disparity detecting neurones in man are made from studies of adaptation to disparity that yield after-effects of distortions in depth (Ames, 1935; Blakemore & Julesz, 1971). The primary advantage of examining the properties of after-effects is that several earlier levels of more peripheral information processing may be overreached to arrive at the more central site of the after-effect itself (Richards, 1971a). The present procedure utilizes this principle to study the interaction between the encoding of spatial frequency and disparity in the human visual system. Thus, two different after-effects are generated, one specific to spatial frequency and a second specific to disparity, and their interactions are then examined.

Viewing a high contrast sine-wave grating produces an elevation in threshold modulation which is specific to spatial frequency: test gratings of the same or neighbouring frequencies as the adaptation grating become harder to see than gratings over twice or less than half the adaptation frequency (Blakemore & Campbell, 1969). The following experiments extend this after-effect into three dimensions. Thus, rather than fixating directly upon the adapting grating, binocular parallax between each eye was introduced by adapting to a grating located behind the plane of fixation. By adapting off the plane of fixation, the bars of the grating in most cases will be seen out-of-phase in each eye and consequently should stimulate and fatigue disparity detectors. A possible outcome of this procedure is for the adaptation process to affect primarily the binocular units most responsive to the induced stimulus disparity. In this case, a threshold elevation for detecting a grating would occur maximally when the test grating is off the plane of fixation (at the same location as the adapting grating) and be greatly reduced when located in the fixation plane. That is, the grating adaptation effect would exhibit disparity specificity. It was this outcome that in fact was observed for suitably chosen grating frequencies.

METHODS

A sinusoidal vertical grating was displayed on the face of a Tektronix 535 oscilloscope using a modified television technique. The amplitude of the modulating signal sent to the Z axis of the oscilloscope could be adjusted by the subject from a remote

control potentiometer. This allowed the subject to adjust the contrast of the grating. The frequency of the modulating signal was equivalent to the frequency of the grating on the oscilloscope face, the latter being expressed in cycles per centimetre of scope screen. This frequency was convertible to cycles per degree of visual angle for a given distance between the stimulus and the eyes of the observer (for a further elaboration of this method of producing a grating, cf. Blakemore & Campbell, 1969). The stimulus was positioned one metre from the observer's eyes. At this distance the circular display screen subtended 4 deg diameter and had a mean luminance of 65 cd/m². One degree (of visual angle) above this display screen a dark wire extended out in front (see Fig. 1) with a distinctive spot appearing on its frontmost extension, thereby providing a point of fixation ($\frac{1}{8} \times \frac{1}{4}$ deg). Fixating on this point at a non-zero distance in front of the stimulus grating thus created disparate images of the grating on the observer's retinae (except, for example, when the period of the grating equalled the fixation disparity). A second point of fixation (a $\frac{1}{4} \times \frac{1}{4}$ deg cross) was
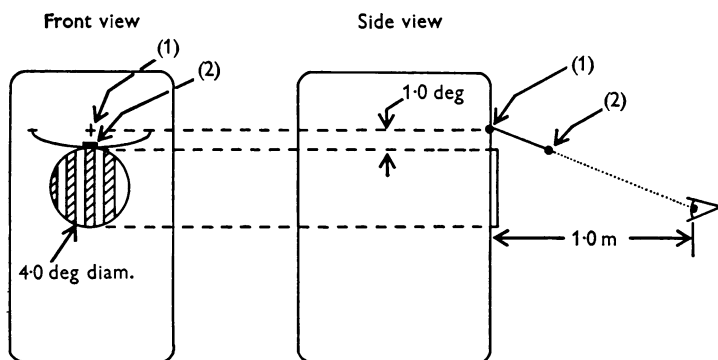

Fig. 1. Schematic portrayal of the experimental arrangement. The two points of fixation, viz. in the stimulus plane and in front of the stimulus plane, are indicated as (1) and (2).

created on the plane of the scope face. Its position lay directly behind the wire fixation point and down just enough to be visible (not be blocked by the wire, see Fig. 1). Thus there were two fixation conditions: one where the stimulus grating appears in the plane of fixation and a second where the grating appears behind the fixation plane. To avoid the formation of conventional afterimages, all gratings were modulated in time at $\frac{1}{2}$ Hz. This low rate of temporal modulation causes little effect upon the subject's sensitivity for this kind of task (Robson, 1966) and, in fact, may help to stabilize the observer's threshold criterion.

The subject's contrast threshold for a grating is a reliable measure of his contrast sensitivity (Sachs, Nachmias & Robson, 1971). The subject is asked to adjust the modulation of the grating until the bars appear at threshold. The ratio of the threshold settings taken before and after adaptation with a high contrast grid is a good measure of the adaptation effect (Blakemore & Campbell, 1969). Our procedure was a simple extension of this approach.

In the first part of the experiment the subject was asked to set the contrast of the grating to threshold, using his remote control potentiometer, for each of the two stimulus conditions: (1) grating presented in the fixation plane (no-disparity condition) and (2) with fixation in front of the grating (disparity condition). When the subject signalled that he had set his threshold, the r.m.s. value of the modulating

voltage was recorded as his threshold reading. Enough readings were taken at each fixation condition to obtain a reliable threshold estimate i.e. the number of readings taken was a direct function of the variance exhibited in the subject's successive settings (with a minimum of four). The average for each of the two sets of readings established the subject's normal (unadapted) threshold sensitivity to a grating appearing either with or without disparity relative to the fixation plane.

In the second part of the experiment, the subject was adapted to a high contrast grating (appoximately 50 % modulation) located with disparity behind the fixation plane (the subject fixated on the wire in front of the scope face). The adaptation period lasted 3 min. At the end of this period, the grating was reduced in contrast, and control of the amplitude modulating signal was returned to the subject. The subject's task now was to set his contrast threshold within 10 sec. In one case the threshold was taken for fixation in the plane of the grating (no disparity); the next trial measured the threshold when fixating in front of the grating (same disparity as adaptation). In between each setting he was given 20 sec of readaptation. Again enough recordings were taken here to establish reliable threshold estimates for each condition.

Thus, four threshold values were measured. For a given grating frequency (c/deg), two of these values were the pre-adaptation and post-adaptation thresholds for the disparity condition, while the other two values were the pre- and post-adaptation thresholds for the non-disparity condition. The adaptation effect for either condition was simply the subject's post-adaptation threshold divided by his pre-adaptation threshold. The measure of the *disparity specific* adaptation effect was then the ratio of the subject's adaptation effect with fixation disparity to his adaptation effect when the grating was seen with no disparity. This value which we called α was defined as follows:

$$\alpha = \frac{\text{Post-adapt disparity threshold}}{\text{Pre-adapt disparity threshold}} \Big/ \frac{\text{Post-adapt no-disparity threshold}}{\text{Pre-adapt no-disparity threshold}}.$$

Using this index (α) as the measure of the selective adaptation effect, the basic design of the experiment was then to obtain values of α for a given disparity, while varying the spatial frequency of the stimulus for each experimental run. That is, the binocular disparity between the fixation point (on the wire) and the screen was held constant while the spatial frequency of the adapting and test-grating was varied. The final results were therefore in the form of curves describing the adaptation effect (α) for various spatial frequencies, with each curve obtained at a given fixation disparity.

RESULTS

Fig. 2 shows the main features of the grating adaptation effect specific to a disparity of 0·65 deg. The spatial frequency of the adapting (and identical test) grating is given on the abscissa. When the period of the grating is roughly twice the fixation disparity, the disparity adaptation effect (α) is maximal. In this case the sine-wave bars of the adapting and test gratings are equal in angular width to the fixation disparity. Thus, during adaptation, geometrically corresponding retinal positions in each eye are viewing bars of opposite contrast. (As seen on the lowest abscissa scale the gratings are 180 deg out of phase in each eye here.) The ordinate on Fig. 2 shows that the rise in contrast threshold following adaptation to

antiphase gratings is about 1·7 times larger than the rise for test gratings seen binocularly in phase (i.e. when the test grating is located in the plane of fixation). A similar, but much smaller rise in threshold is also observed for gratings near 15/6 c/deg, corresponding to the first odd integer multiple of the observed centre frequency. This higher frequency, as well as all
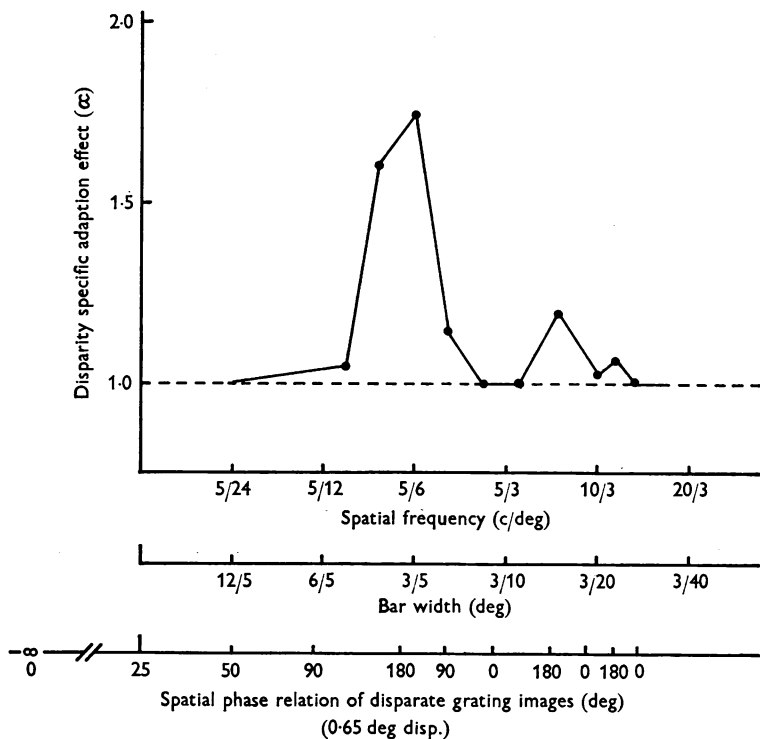

Fig. 2. The disparity specific adaptation effect function (0·65 deg disparity) is plotted for T.F. against three equivalent abscissa scales: spatial frequency, bar width, and spatial phase of disparate grating images. The bottom scale (spatial phase...) is derived through the calculation of the spatial phase difference of the disparate grating images with respect to corresponding points on the two retinae. Only relative spatial phase is of interest here, therefore the scale is periodic about 180 deg.

higher odd integer multiples are also seen 180 deg out-of-phase in each eye for a 0·65 deg fixation disparity. However, even less of an adaptation effect was observed for gratings near 25/6 c/deg ($5 \times 5/6$ c/deg) suggesting that the higher harmonics are being increasingly attenuated.

Disparity-specific adaptation also was not found for grating frequencies that were even-integer multiples of the centre frequency (i.e. near 5/3 and 10/3 c/deg). Because the period of these latter frequencies exactly matches

the binocular phase shift introduced by the fixation disparity, both test conditions are essentially identical (i.e. adaptation and test conditions are all equivalent to fixation on the grating itself).

Turning to the low frequency fall off (below the centre frequency of 5/6 c/deg), considerations of the previous kind do not completely explain this portion of the adaptation curve. More specifically, consider gratings of 5/12 c/deg. They will not be in phase during adaptation. As shown clearly by Fig. 3, a grating of 5/12 c/deg seen with a fixation disparity of nearly 0·65 deg will be approximately 90 deg out-of-phase in each eye. Not until the grating frequency reaches 0 c/deg will the binocular grating images be seen in-phase again. Nevertheless, comparing 5/12 with 10/9 c/deg (each has close to a 90 deg phase shift), the disparity-specific adaptation effect (α) has fallen to unity (null effect) for 5/12 c/deg while the effect is still one-sixth its peak value for 10/9 c/deg. Thus, although the phase difference of the gratings in each eye appears to be an important factor determining the magnitude of the disparity adaptation effect it cannot completely account for the steepness of the low frequency fall off. As will be seen later, the shape of the low frequency fall off of the primary adaptation effect suggests that the adapted disparity detectors were correlating bars, rather than edges in each eye.

Retinal eccentricity

When the eyes are converged upon a fixation point in front of the screen, slightly different eccentric retinal regions of each eye are adapted. It is possible that the threshold rise measured when fixating the screen is less because the stimulus does not fall entirely upon adapted retinae. Two observers thus adapted to a 5/6 c/deg grating with monocular fixation on the scope face at an eccentricity measured relative to point 1 (Fig. 1). Threshold rises following adaptation were then determined monocularly with post-adaptation fixation held constant at 0·0° eccentricity (point 1 for Fig. 1).

Table 1 summarizes these results. No change in threshold elevation was observed for adaptation eccentricities up to and including $\frac{1}{4}$ deg. At an eccentricity of $\frac{1}{2}$ deg, however, the monocular grating adaptation effect for our 4 deg field falls by 20%, with progressive decreases as fixation eccentricity is increased further. Monocular retinal eccentricities of $\frac{1}{2}$ deg correspond to a binocular fixation disparity of 1 deg. Our subsequent data on the disparity specific adaptation effect are limited to adaptation disparities of 1 deg or less. At this largest fixation disparity, the effects of stimulus displacements on the retina may reach 20%. For our 0·65 deg disparity condition, however, these errors due to stimulus displacements should not exceed the variance in the estimate of α from one day to the next.

Evidence for adaptation to disparity

There are two obvious interpretations of the adaptation effect shown in Fig. 2: first, the adaptation procedure might fatigue a link between neurones responding to the grating and the disparity detectors that these neurones innervate. If such a link is present, then the range of grating
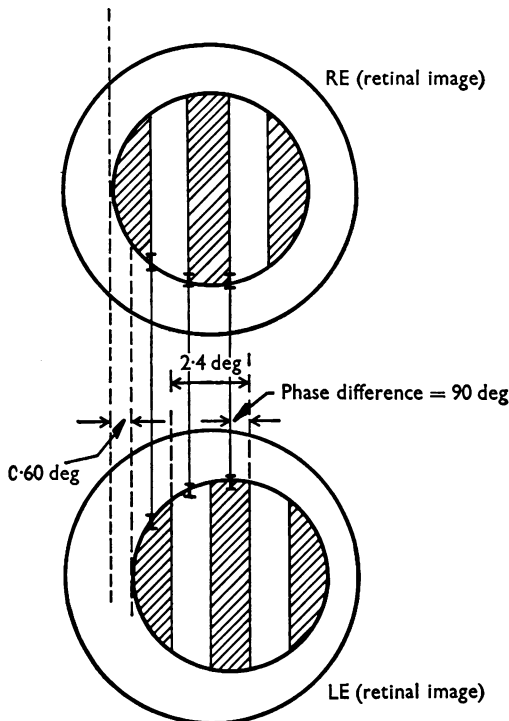

Fig. 3. The retinal images of a 5/12 c/deg grating seen with a fixation disparity of 0·60 deg are 90 deg out of phase with each other (with respect to corresponding points on the two retinae).

frequencies that yield a disparity-specific adaptation effect (α) is an indication of the breadth of the spatial frequency channels innervating a given set of disparity detectors. On the other hand, out-of-phase gratings presented to each eye might drive two different populations of neurones, each of which will fatigue independently. The fact that a grating adaptation effect is obtained to gratings seen 180 deg out-of-phase in each eye strongly suggests that a single binocular neurone encoding only spatial frequency (and not phase) has not been adapted. For if one neurone received such conflicting contrast signals from each eye, there should be no adaptation effect (i.e. one eye will be driving the unit while the other is inhibiting it,

resulting in little or no net activity). Thus, in the specific case where the gratings are 180 deg out-of-phase, any adaptation effect solely specific to grating frequency (and not to phase) should be a monocular effect. Of course, this reasoning does not exclude the possibility that frequency specific monocular and binocular effects might become unequal following adaptation to gratings seen binocularly in-phase. Of interest at present, however, is to determine whether adaptation to 180 deg out-of phase gratings leaves a residual inphase adaptation effect that is essentially a monocular one.

TABLE 1. Results of eccentricity study. Adaptation values were obtained by dividing the pre-adapt threshold value (taken at the indicated eccentricity) into the post-adapt threshold value (taken at 0·0 deg eccentricity)

Eccentricity (deg)	0	$\frac{1}{4}$	$\frac{1}{2}$	1	2
Monocular grating adaptation effect	7×	7×	5·5×	3×	2×

Two control experiments were therefore run that demonstrated: (1) adaptation specific to phase does not occur for monocular stimuli, and (2) following adaptation to a grating seen binocularly 180 deg out-of-phase (i.e. with disparity), threshold elevations for the grating seen binocularly in-phase were equal to the monocular adaptation effect.

TABLE 2. Threshold contrast (in r.m.s. V) measured on the grating plane before and after adaptation to gratings viewed with 0·65 degrees of disparity

	5/6 c/deg grating				10/6 c/deg grating			
	T.F.		W.R.		T.F.		W.R.	
	Bino-cular	Mono-cular	Bino-cular	Mono-cular	Bino-cular	Mono-cular	Bino-cular	Mono-cular
Pre-adapt threshold	1·8	2·4	2·7	3·6	1·2	1·5	1·6	1·9
Post-adapt threshold	2·5	3·6	5·1	7·4	2·2	2·6	4·3	4·4
Threshold elevation	1·4×	1·5×	1·9×	2·1×	1·8×	1·7×	2·7×	2·3×
Binocular/mono-cular ratio	0·94		0·91		1·06		1·16	

Using the same paradigm, but with monocular fixation always on the screen, contrast thresholds were measured for gratings from $\frac{1}{2}$ to 4 c/deg, with fixation point either centred in the middle of a bar (90 deg phase shift) or at the edge of a bar where there was no luminance modulation. No adaptation effect specific to phase was ever observed in extensive measurements made on T.F. nor on less detailed studies with other observers. That is, following monocular adaptation to a grating 90 deg out-of-phase

with the fixation point, equal threshold elevations were found for gratings seen either in-phase or 90 deg out-of-phase. Of course, although some future demonstration of monocular, phase-specific adaptation might occur (such as to contrast-reversal at edges), monocular adaptation specific to spatial phase appears unlikely in our paradigm.

The complementary control experiment, that examines the monocular residue following disparity adaptation, is summarized in Table 2. Both subjects adapted with fixation 0·65 deg in front of the scope face (out-of-phase gratings) but all thresholds were taken with fixation on the scope itself (in-phase gratings). In general, monocular thresholds were about 1·4 × higher than binocular thresholds suggesting that probability summation and two independent channels mediate detection in this case (see also Campbell & Green, 1965). In spite of this threshold difference, however, the adaptation effects measured by the threshold elevations were identical to within about 10 % (bottom row of Table 2). This equivalence suggests that the phase-insensitive component of adaptation measured binocularly is a monocular component.

One other series of experiments also bears on the question of whether the parameter α measures a disparity-specific adaptation effect. In addition to subjects T.F. and W.R., four other (naïve) subjects were also studied. Two of these latter subjects did not get the disparity specific adaptation effect at all. However, these two subjects had previously been diagnosed as possessing only one class of disparity analysers, using the forced-choice technique described by Richards (1970). For example, one subject had been diagnosed as having detectors responsive only to crossed disparities. This subject showed the customary monocular adaptation effect but no disparity specific effect. Even when the fixation point was reversed to appear in a mirror behind the adapting grating, the subject failed to get a differential effect. Our disparity specific adaptation effect thus seems to be quite specific to the stereoscopic abilities of the subject.

Adaptation to other disparities

In order to extend the results of Fig. 2 to other disparities, the disparity adaptation effect (α) was measured using the same grating frequencies but different fixation disparities for adaptation. Adaptation curves similar to those in Fig. 2 were obtained at four disparities for both T.F. and W.R. The half-width of these (primary) tuning curves was about one third the optimal bar width of the grating. A fifth disparity condition of 1·03 deg for T.F. failed to show precise tuning. With the exception of this condition (which yielded two primary maxima) all other curves had clear peaks that showed which gratings gave the greatest adaptation, α, for any given disparity. In Fig. 4, this optimal grating frequency has been translated

into the corresponding bar width and plotted against the adaptation disparity (two points appear for T.F. at 1·03 deg of disparity). As can be seen, the data for both observers are very similar: disparity adaptation for large disparities requires large bar widths or coarse gratings, whereas smaller disparities require smaller bar widths or finer gratings for optimal adaptation to disparity.

In Fig. 2, for a fixation disparity of 0·65 deg, the optimal bar width is approximately equal to the adaptation disparity. This correlation was explained in terms of yielding optimal out-of-phase binocular registration
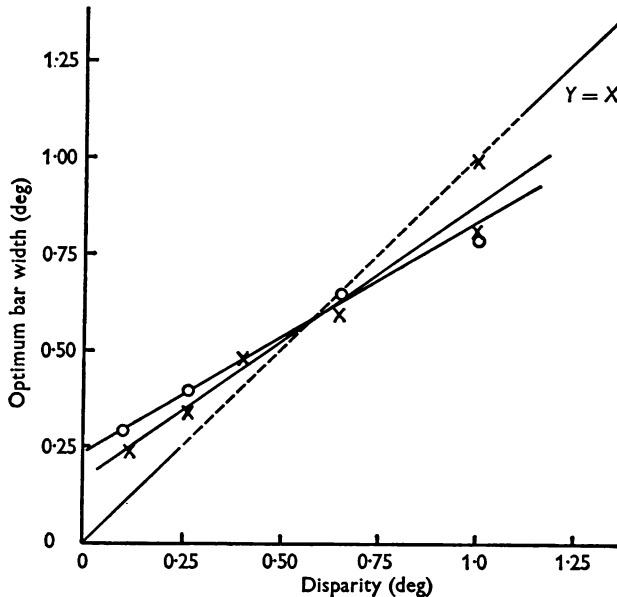

Fig. 4. The bar width which gave the greatest disparity specific adaptation effect (optimum bar width) is plotted for two subjects, W.R. (○) and T.F. (×).

for disparity detection. Following a similar argument, one might expect that the optimal bar width for disparity adaptation would in general be equal to the disparity. In this case, the points in Fig. 4 should fall along the 45 deg diagonal such that $y = x$. In fact, the derived curves are straight lines, but have shallower slopes than expected (near $\frac{1}{2}$) and higher ordinate intercepts (between 0·18 and 0·25 deg).

Two factors might be responsible for the deviation from pure equality between optimum bar width and disparity. First, the neural population distribution of disparity detectors may not be uniform over disparity. Detectors for some disparities may be more common than others or at

least less sensitive. Because of the finite width of the adaptation effect, some distortions toward the most popular or most sensitive detectors would be expected. One estimate of the population density (or sensitivity) of disparity detectors might be the maximum strength of the adaptation effect at any given disparity. Fig. 5 is such a plot. Maximal adaptation occurs for both subjects at about 0·65 deg of disparity. This result is in close agreement with Richards's (1971*b*) estimation that disparities in the neighbourhood of $\pm \frac{1}{2}$ to $\frac{3}{4}$ deg are the most effective binocular stimuli for
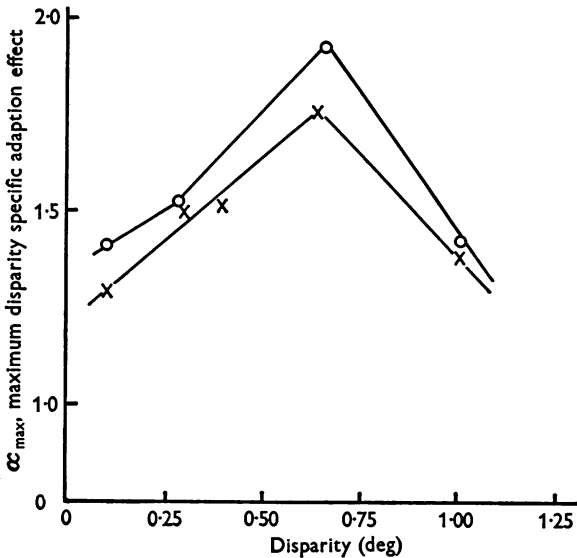

Fig. 5. The maximum disparity specific adaptation effect is shown for the disparities at which the effect was tested for subjects W.R. (○) and T.F. (×).

depth sensations. Such a bias in the neural population of disparity detectors is consistent with the rotation of the best fitting line in Fig. 4 around the 0·65 deg disparity point. Thus, points below or above this central point have their optimal bar widths pushed toward the optimal bar width (0·65 deg) for the maximally efficient disparity (0·65 deg) due to the dominating tendency of these disparity detectors.

One further point should be made with respect to the optimal bar width for disparity adaptation. It should be obvious that a disparate grating can be correlated in a number of ways to elicit depth sensations. For a given fixation disparity, d, the bars of a grating will be correlated in frontal planes whose disparity relative to the fixation point is given by $d \pm nJ$ ($n = 0, 1, 2, ...$) where J is the period of the grating and n is limited by the finite number of bars present. Blakemore & Hague (1972)

have demonstrated that disparity adaptation occurs at intervals of nJ degrees of disparity, for $d = 0$ and $n = \pm 1$. (In our paradigm, we have also observed that adaptation to a grating seen behind the fixation point yields similar tuning curves of α vs. spatial frequency for test gratings appearing either in front or behind the fixation point.) Therefore the expectation is that our adaptation effect obtained at a given grating frequency and adaptation disparity is the result of more than one specific subset of adapted disparity detectors. The most efficient bar by bar correlation is generally the fundamental ($n = 0$) as the maximum number of bars will be processed here. However, for narrow gratings and small disparities, the differences in the number of correlated bars for the various frontal planes will also be relatively small, thereby reducing the number advantage that the fundamental disparity detectors enjoy. Perhaps also the effect of disparity bias will further offset this number advantage. Our findings for larger disparities, therefore, may not apply as clearly for small disparities, which possibly can be studied best using smaller fields.

DISCUSSION

One can view the adaptation turning curves (e.g. Fig. 2) as an indication of disparity specific processing of spatial frequencies. Thus, where the adaptation ratio is high, the grating is presumably being processed by the disparity system at a high signal to noise ratio. For a given disparity then the optimum grating (Fig. 4) seemingly provided the best signal of all for the disparity subsystem active at that disparity.

What aspects of this optimum grating are detected and then analysed by the disparity selective neurons? Based upon neurophysiological evidence (Hubel & Wiesel, 1970; Bishop et $al.$ 1971), there are two likely candidates: the disparity analysis could be accomplished by correlating either edge or bar detecting neurons. Which of these possibilities then best fits our results? The key to a decision lies in the behaviour of the low-frequency fall off in the primary adaptation tuning curve (Fig. 2). If edge correlations are being made, lower grating frequencies should continue to yield disparity adaptation (assuming that edge detectors consist of a single step between an excitatory and inhibitory region). This expectation follows from the nature of the transfer function of an edge detector, which exhibits no marked attenuation at low frequencies (Bracewell, 1965). Thus, wide low-frequency gratings should still yield adaptation effects if edge detectors are mediating the disparity processing. Yet Fig. 2 shows that this is not the case. On the other hand, if bar by bar correlations are being made, then a greatly diminished adaptation effect at low frequencies would be expected (assuming that bar detectors consist of an excitatory centre with flanking

inhibitory surrounds). In particular, such detectors would be stimulated best by sine-wave gratings whose period roughly corresponded to the size of the bar detector's receptive field. Gratings both coarser or finer than that optimal will be less effective stimuli (cf. Enroth-Cugell & Robson, 1966). Because Fig. 2 indicates that the adapted neurones have narrow tuning curves, our results strongly favour the hypothesis that the disparity analysers are correlating bar by bar rather than edge by edge detecting neurones. (In its strongest form, this conclusion predicts no disparity specific adaptation to an edge. However, a slight effect ($\alpha = 1\cdot15$) was observed for two of the authors following adaptation to a 0·65 deg disparate edge. We believe this result was a consequence of the presence of Mach bands at the edge of the luminance step.)

Fig. 4 further reinforces the argument for disparity analysers making bar by bar correlations. This figure shows that the optimum signal for a small disparity is a narrow bar grating (high spatial frequency); whereas for a large disparity, the most effective stimulus is a wide bar grating (low spatial frequency). Over the 1·0 deg range of disparities examined, there is approximately a two octave range of spatial frequencies which will serve as optimum stimuli. Within this range, narrow bars innervate small disparity analysers, and wide bars innervate large disparity analysers.

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