



## Depth selectivity of vertical fusional mechanisms

R.S. Allison \*, I.P. Howard, X. Fang

*Centre for Vision Research, York University, 103 Farquharson, Toronto, Ontario, Canada M3J 1P3*

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### Abstract

We measured the ability to fuse dichoptic images of a horizontal line alone or in the presence of a textured background with different vertical disparity. Nonius-line measurements of vertical vergence were also obtained. Diplopia thresholds and vertical vergence gains were much higher in response to an isolated vertically disparate line than to one with a zero vertical-disparity background. The effect of the background was maximum when it was coplanar with the target and decreased with increasing relative horizontal disparity. We conclude that vertical disparities are integrated over a restricted range of horizontal disparities to drive vertical vergence. © 2000 Elsevier Science Ltd. All rights reserved.

*Keywords:* Vertical vergence; Fusion; Integration; Diplopia

### 1. Introduction

For any posture of the eyes, only a subset of points on an extended surface fall on corresponding points in the two retinae — those that lie on the point horopter. Binocular single vision is attained by a combination of vergence and sensory fusion. Sensory fusion creates a percept of a single object from binocularly disparate images and occurs within a limited disparity range known as Panum's fusional area. Larger disparities require vergence eye movement to achieve fusion. Disparity vergence is a disjunctive movement of the eyes in response to an imposed disparity. Horizontal vergence compensates for horizontal disparity; vertical vergence for vertical disparity; and cyclovergence for cyclo-disparity. At least three related roles can be postulated for vertical disparity vergence: the maintenance of eye alignment; bifoveation of local targets and the calibration of open-loop vertical vergence.

When we view a natural scene, a constant vertical disparity over the entire visual field can be due only to vertical eye misalignment. Whole-field vertical disparity is an adequate stimulus for vertical vergence, which can

correct up to about  $1.5^\circ$  of disparity (e.g. Ogle, 1964; Howard, Allison & Zacher, 1997). Furthermore, vertical disparity in a central fixation point can exist only when the two eyes are misaligned. The gain of vertical vergence increases with stimulus area for displays up to  $20^\circ$  in diameter (Stevenson, Lott & Yang, 1997; Howard, Fang, Allison & Zacher, 2000). For a given area, gain is highest for displays centred on the fovea. These results suggest that the vertical vergence system responds to vertical disparity over a fairly large integration area surrounding the fovea. These findings support the hypothesis that vertical vergence is designed to deal with the whole field parameter of vertical eye alignment. In contrast, horizontal vergence responds with high gain to disparities in small foveal targets (Howard et al., 2000).

If vertical vergence were driven solely by mean vertical disparity over the whole visual field (simply to keep the eyes in register) then local vertical disparities could not be brought into the range of efficient stereopsis. For example, fixation of a point  $24^\circ$  above and  $24^\circ$  to one side of the straight ahead at a distance of 33 cm requires  $1.5^\circ$  of vertical vergence in Fick co-ordinates (Ogle & Prangen, 1953; see Section 4 for effects of the choice of co-ordinate system). This exceeds the fusional range, and would at least degrade stereopsis (see Ogle, 1955; Mitchell, 1970). If vertical vergence were driven by local vertical disparity then vergence could sequen-

\* Corresponding author. Fax: +1-416-7365857.

E-mail addresses: allison@hpl.crestech.ca (R.S. Allison), ihoward@hpl.crestech.ca (I.P. Howard), xfang@hpl.crestech.ca (X. Fang).

tially compensate for vertical disparities as the eyes scan the visual field. In fact, an eye movement to an oblique, or tertiary, point it is accomplished through unequal sized saccades in the two eyes (Ygge & Zee, 1995). Relatively slow vertical vergence movements compensate for any remaining vertical disparity in order to achieve bifoveal fixation and may play a role in calibrating disjunctive saccades (see Section 4).

How does the relatively coarse spatial integration area for vertical vergence affect the ability of the system to achieve bifoveal fixation? In many respects, the large integration area and modest amplitude range for vertical disparity vergence are compatible with vertical disparity in natural scenes. Vertical disparity changes in a natural scene are smaller than horizontal disparity changes (Howard & Rogers, 1995). In many natural environments smooth surfaces are present and vertical disparity changes slowly. Furthermore, vertical disparities in a surface are relatively unaffected by local surface structure and instead vary systematically with changes in distance and eccentricity (Mayhew & Longuet-Higgins, 1982). Disparity averaging over a fairly large area of a surface results in a low noise estimate of vertical disparity to drive vertical vergence. However, depth discontinuities and transparency can create steep changes in vertical disparity. Averaging disparity in these cases would lead to an intermediate estimate of disparity rather than the disparity of the fixated surface.

With large depth separation between two transparent surfaces, the vertical disparities in elements comprising the surface that is not fixated may exceed the range that can be detected and processed as a vergence stimulus. Horizontal fusional range for a central target is increased in the presence of peripheral stimuli, but only when the relative disparity between the target and peripheral lines is less than about  $0.5^\circ$  (Jones & Stephens, 1989). This suggests a rather narrow range of disparity integration for sustained, horizontal vergence. Analogously, vertical disparities could be integrated over space to drive vergence without averaging across elements with vertical disparities that exceed the range of disparity detectors. The maximum vertical disparity limit beyond which the stimulus no longer elicits vergence is about  $2\text{--}4^\circ$  under static conditions with isolated stimuli (Ogle & Prangen, 1953; Ellerbrock, 1949).

However, another consideration may prevent disparity averaging over even modest discontinuities of vertical disparity. In a natural scene, differences in vertical disparity between adjacent elements in distinct depth planes are accompanied by larger differences in horizontal disparity. Within a limited range of horizontal disparities, say within Panum's area, vertical disparity changes relatively slowly over the visual field, making averaging for vertical vergence attractive. We propose that vertical disparity is averaged over a large retinal

area but only over a limited range of horizontal disparities (i.e. over an integration volume). This selectivity for horizontal disparity would provide averaging for low-noise vertical disparity estimates combined with insensitivity to vertical disparity in targets located at different depths. This is also physiologically plausible since disparity detectors respond only to a limited range of disparity (Poggio & Fischer, 1977). Thus, vertical disparities of targets with large horizontal disparity cannot be registered. In the present study we investigate the horizontal disparity selectivity of vertical fusional mechanisms. Specifically, we measured vertical diplopia thresholds and vertical vergence as a function of the horizontal disparity between a target and a surround with different vertical disparity.

## 2. Materials and methods

### 2.1. Apparatus

Computer generated images were presented dichoptically in a Wheatstone stereoscope. Computer monitors (NEC C500,  $1024 \times 768$  pixels, 75 Hz) were placed one to the left and one to the right of the subject and viewed through mirrors mounted at  $\pm 45^\circ$  to the frontal plane. Viewing distance was 37 cm. Convergence angle of the stereoscope was also set for 37 cm and the monitor orientations were appropriate for this distance. Each screen subtended  $30^\circ$  in height by  $40^\circ$  in width. Stereoscopic stimuli were presented in a dark room and all surfaces were covered with matte black cloth or paint. Care was taken to ensure that each eye saw its screen only through the mirror.

### 2.2. Images

The typical test display consisted of a dichoptic fixation cross presented either alone (i.e. on a black background) or on a textured background subtending  $23^\circ$  (see Fig. 1A). The fixation cross consisted of a long vertical line subtending  $30^\circ$ , which controlled horizontal vergence, and a shorter horizontal line subtending  $57$  min arc, which acted as a vertical fusion target and diplopia test stimulus. The fixation cross also served as a zero-disparity fixation stimulus in intervals between test stimuli. Two basic textures were used for the background (Fig. 1B, C). The geometric texture consisted of randomly distributed white texture elements on a black background and was used for most of the experiments. The texture elements were various geometric shapes. The size of the texture elements increased linearly with eccentricity to compensate for reduced acuity in the peripheral retina (this m-scaling is described more completely in Howard et al., 1997). The random-dot texture consisted of white dots (diameter  $0.08^\circ$ ) randomly positioned on a black background (dot density 12.5%).

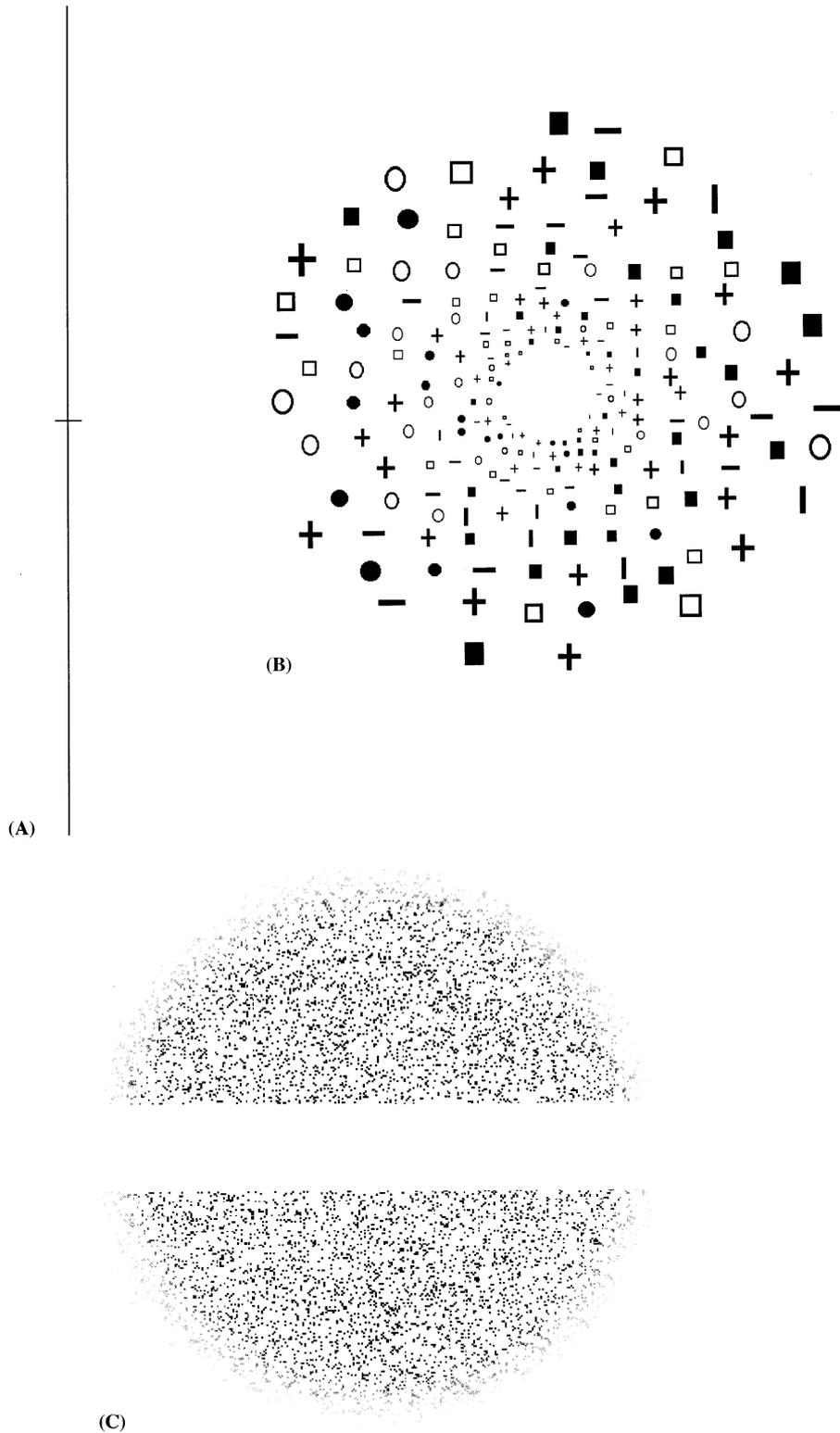


Fig. 1. Examples of stimuli used in the experiments. (A) Dichoptic fixation cross. The long vertical line stabilised horizontal vergence and the horizontal line acted as a vertical fusion target. (B) The geometrically-textured background with a 4° circular blank area for presentation of the fixation cross. (C) The random-dot display with a 4° high horizontal blank area (vertical blank areas were also used). Actual displays consisted of white texture elements or lines on a dark background.

Normally, the background pattern was identical in the two eyes except for an overall constant disparity. De-correlated background patterns were also studied. The geometric texture was de-correlated by rotating one of the half images 90° with respect to the other. The random-dot texture was de-correlated by using independent samples of dots for the left and right eyes. The peripheral edges of the random-dot background were gradually blurred with a low frequency Gaussian blur kernel for both correlated and de-correlated conditions. This blurring rendered the texture-defined boundaries of the stimulus ineffective as a stimulus for fusion.

The half images of the fixation cross and/or of the background could be moved vertically or horizontally in opposite directions to introduce horizontal or vertical disparity in integer pixel steps (1 pixel displacement in each eye equalled 0.04° of disparity). To prevent the background from interfering with the fixation cross, part of the central area of the background was blank. For the smaller disparity conditions, a 4° circular area was blank (see Fig. 1B for an example). For larger disparities, a horizontal 4° high strip across the entire display was blank (see Fig. 1C for an example).

### 2.3. Procedure

A summary of the stimulus conditions and parameters studied in these experiments can be found in Table 1. A typical trial consisted of a baseline fixation stimulus followed by a test stimulus. Between trials the display was extinguished while the subject's responses were recorded. Each trial started with 5 s fixation on an isolated, zero-disparity, fixation cross in order to start with a zero vergence posture. Following this, the test display consisting of the fixation cross with or without a background was presented. The fixation cross always had zero horizontal disparity when the eyes were converged in the plane of the screen. The horizontal disparity of the background was varied relative to that of the fixation cross. Thus, each background was presented with a variety of horizontal disparities in random order. For each condition, we studied the effect of introducing vertical disparity in the fixation cross or in the background on vertical fusion of the cross and on vertical vergence. Positive horizontal disparity indicates crossed disparity.

### 2.4. Measurement of diplopia thresholds

In each trial the stimulus was presented for 5 s and the subject attempted to fuse the horizontal elements of the fixation cross. The vertical line always appeared fused. The display then disappeared and the subject indicated with button pushes whether the horizontal line of the fixation cross appeared fused or diplopic.

Having the judgement at the end of the interval ensured that it was based on the impression following the vergence movements. We defined the diplopia threshold as the vertical disparity at which the stimulus was reported as double on 50% of trials. The method of constant stimuli was used to generate psychometric functions and the 50% point was identified with probit analysis (Finney, 1971). The stimulus levels were selected for each subject and condition in a pilot experiment. Ten repeats for each of seven levels in the vicinity of the threshold were presented for each horizontal-disparity/background condition in random order.

### 2.5. Measurement of vertical vergence

A flashed nonius line procedure was used to measure the vergence response to a given test display. As in the diplopia threshold trials, each trial consisted of 5 s fixation at zero disparity followed by 5 s viewing of the test display. After the test display disappeared a pair of horizontal nonius lines centred in the display was presented for 100 ms. The nonius lines subtended 29 min arc and were separated horizontally by 10 min arc. The subject indicated the relative vertical alignment of the lines with button pushes. The next trial commenced after the subject's response.

The objective alignment of the two nonius lines could be varied under program control in integer pixel steps. The point of subjective equality was determined by an adaptive staircase method. Multiple staircases were interlaced at random to prevent any prediction on the part of the subject. This interleaving resulted in a range of disparities being presented and precluded adaptation or phoria changes due to repeated stimulation. For each condition, both ascending and descending staircases were presented. The point of subjective equality was taken as the average of the last four of seven reversals for each staircase and averaged over the staircases for each condition. To control for any bias in the alignment procedure, estimates of vertical vergence were calculated as the nonius alignment relative to the nonius setting obtained with a zero-disparity fixation cross on a zero-disparity background. Vergence gain was calculated by dividing the nonius-line estimate of vertical vergence by the vertical disparity.

### 2.6. Subjects

Six subjects (four men and two women ranging in age from 25 to 39 years) participated in the diplopia threshold experiments — two of the authors and four subjects who were naïve with respect to the purpose of the study. Four of these subjects, including the two authors, also participated in the nonius line experiment. All had normal stereoscopic vision and gave their informed consent.

Table 1  
Summary of experimental conditions for the diplopia measurements<sup>a</sup>

Results discussed in:	Condition or subsection	Background	Vertical diplopia in fixation cross induced by vertical disparity in	Blank area	Relative horizontal disparity	Figure	Nonius measurements (Section 3.3)
Sections 3.1 and 3.2	Baseline	None	Fixation cross	n/a	n/a	Figs. 3–5	Yes
Section 3.1	3.1.1	Geometric	Background	Circular	–3.0 to 3.0	Figs. 2 and 3	No
	3.1.2	Geometric	Fixation cross	Circular	–3.0 to 3.0	Fig. 3	Yes
Section 3.2	Conditions 1, 2	Geometric	Fixation cross	Horizontal	–6.0 to 6.0 or de-correlated	Fig. 4	Yes
							No
Conditions 3, 4	Random-dot	Fixation cross	Horizontal	Horizontal	–6.0 to 6.0 or de-correlated	Fig. 5	No
							No
Condition 5	Random-dot	Fixation cross	Vertical	Vertical	De-correlated	Fig. 5	No
							No
Condition 6	Horizontal lines	Fixation cross	n/a	n/a	n/a	Fig. 6	No
							No

<sup>a</sup> The last column indicates whether nonius alignment measurements were also obtained for the condition. The baseline condition, which was the fixation cross in isolation, was tested in each experiment.

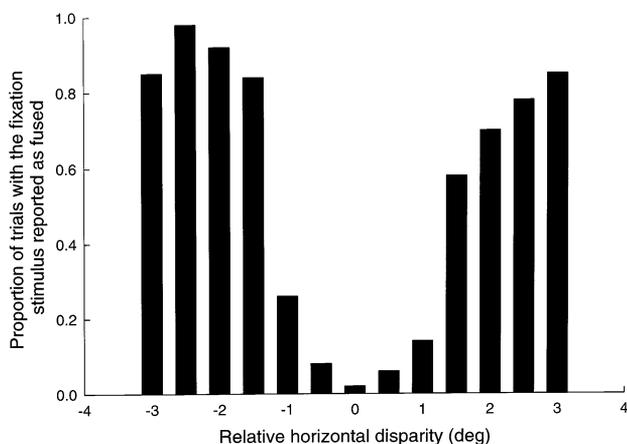


Fig. 2. Proportion of trials in which a zero-disparity fixation cross was reported as fused as a function of horizontal disparity between the target and background. The geometrically textured background had 28.8 min arc vertical disparity.

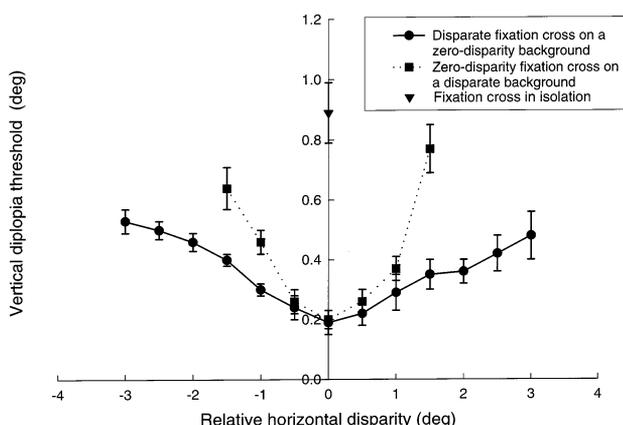


Fig. 3. Mean diplopia threshold as a function of horizontal disparity between the target and the geometrically-textured background ( $n = 6$ , error bars indicate  $\pm 1$  S.E.M.). Diplopia thresholds are shown for: vertical disparity in an isolated fixation cross; vertical disparity in the background with a zero-vertical-disparity fixation cross; and vertical disparity in the fixation cross with a zero-vertical-disparity background. The target was presented in a circular blank area in the background.

### 3. Results

#### 3.1. Diplopia thresholds with modest horizontal disparities

In this experiment we studied two separate cases. In the first case, we measured how a vertically disparate background disturbs the ability to maintain vertical vergence on a central target. Specifically, we measured the threshold level of vertical disparity in the background that caused vertical diplopia in the horizontal line of a zero-vertical-disparity fixation cross. In the second case, we examined how a zero-vertical disparity background restrained the eyes from fusing a disparate target line. Specifically, we measured the threshold level

of vertical disparity in the fixation cross that caused vertical diplopia in the horizontal line of the fixation cross on a zero-vertical-disparity background.

For each case, we presented the geometrically textured background with various degrees of horizontal disparity ( $0$ ,  $\pm 0.5^\circ$ ,  $\pm 1.0^\circ$ ,  $\pm 1.5^\circ$ ,  $\pm 2.0^\circ$ ,  $\pm 2.5^\circ$ , and  $\pm 3.0^\circ$ ) relative to the fixation cross. We also compared diplopia thresholds under these conditions with those for the fixation cross in isolation.

##### 3.1.1. Case 1: disparate background

When the background and fixation cross were coplanar, increasing the vertical disparity of the background eventually caused the horizontal line of the fixation cross to become diplopic. Presumably, the vertically disparate background drove the eyes away from zero vertical vergence, causing the images of the horizontal line to gradually pull apart despite the effort of the subject to maintain fixation. As the horizontal disparity of the background relative to the fixation cross increased, more vertical disparity was required in the background to cause the fusion target to appear diplopic. Fig. 2 shows the proportion of trials in which the test line was reported as fused when the background had a vertical disparity of 28.8 min arc and various horizontal disparities. It can be seen that the ability of the background to induce diplopia in the test line declined with increasing relative horizontal disparity.

This decline in the potency of a competing background stimulus with increased relative horizontal disparity was also reflected in changes in the diplopia threshold (Fig. 3). At zero relative horizontal disparity the diplopia threshold was 12 min arc. The threshold approximately doubled with the addition of  $\pm 1.0^\circ$  of relative horizontal disparity between the fixation cross and background. At relative horizontal disparities greater than  $\pm 2^\circ$ , subjects could fuse the fixation cross easily, even when the background had several degrees of vertical disparity. Thus, with large relative horizontal disparities the textured background proved ineffective in disturbing the ability to fuse a zero vertical disparity target.

##### 3.1.2. Case 2: disparate target

When the vertical disparity of the fixation target was increased it eventually became diplopic. For an isolated fixation cross the diplopia threshold averaged  $0.9^\circ$  across the six observers. This is the sum of vertical vergence and sensory fusion. When a zero vertical-disparity background was present the diplopia threshold was reduced. When the stimuli were coplanar the diplopia threshold was small and similar to that obtained when vertical disparity was introduced into the background rather than the target. This presumably represents the size of Panum's area. Diplopia thresholds increased significantly with increased relative horizontal

Table 2

Summary of the diplopia threshold data for six subjects for a disparate fixation cross on a zero-vertical-disparity background<sup>a</sup>

Subject	Diploid threshold with zero disparity background (min arc)	Increase in diplopia threshold for uncrossed disparity (min arc/deg)	Increase in diplopia threshold for crossed disparity (min arc/deg)	Adjusted $R^2$	Diplopia threshold without a background (min arc)
1	<b>21.60 ± 1.65</b>	<b>4.26 ± 1.05</b>	<b>7.57 ± 1.46</b>	0.80	69.60
2	<b>12.34 ± 0.71</b>	<b>4.15 ± 0.54</b>	<b>2.26 ± 0.75</b>	0.84	53.40
3	<b>8.06 ± 0.64</b>	<b>10.29 ± 0.40</b>	<b>6.00 ± 0.56</b>	0.98	67.20
4	<b>10.95 ± 0.94</b>	<b>5.59 ± 0.60</b>	<b>2.90 ± 0.83</b>	0.87	34.20
5	<b>7.89 ± 1.09</b>	<b>10.47 ± 0.69</b>	<b>7.87 ± 0.96</b>	0.95	52.20
6	<b>7.94 ± 1.00</b>	<b>8.44 ± 0.63</b>	<b>5.49 ± 0.88</b>	0.93	45.00
Mean	11.46 ± 2.16	7.20 ± 1.19	5.35 ± 0.95	0.89 ± 0.03	53.60 ± 5.46

<sup>a</sup> A linear regression was fitted to each subject's diplopia threshold data. The predictor variables were the magnitude and direction of relative horizontal disparity between the target and the geometrically textured background (with a central circular mask). The table shows, from left to right, estimated values ( $\pm$  S.E.M.) for: the diplopia threshold with a coplanar background, the increase in diplopia threshold with uncrossed disparity, the increase in diplopia threshold with crossed disparity, adjusted  $R^2$  of the model, and the measured diplopia threshold in the absence of a background. For the parameters determined from the regressions, bold type indicates a statistical significance at the  $P < 0.01$  level or better.

disparity (see Fig. 3). Table 2 shows the increase in diplopia threshold for each observer. Note that even at fairly large relative horizontal disparities of  $\pm 3^\circ$  the presence of a zero vertical-disparity background still had a restraining influence on sensori-motor fusion of the test line. This is reflected in the finding that diplopia thresholds still fell short of those obtained for the target in isolation.

### 3.2. Diplopia thresholds with larger horizontal disparities and de-correlated images

In the above experiment we could not completely eliminate the restraining effect of a background on vertical fusional responses to a central stimulus. One possibility is that the relative horizontal disparity in the background was simply not enough to put it out of the range of vertical disparity detectors. Another possibility is that texture-defined contours from the edges of the stimulus or the edges of the blank region acted as fusional stimuli. To investigate these possibilities we compared diplopia thresholds for vertical disparity in the fixation cross obtained under six conditions:

1. Fixation cross presented on a textured background with larger relative horizontal disparities ( $\pm 6$ ,  $\pm 3$  or  $0^\circ$ ). To prevent the images of the fixation cross overlapping the background, the cross was superimposed on a blank horizontal strip  $4^\circ$  in height and extending across the screen. Fig. 4 shows that increasing the horizontal disparity of the textured background relative to the fixation cross increased the diplopia threshold. However, diplopia thresholds still remained smaller than for an isolated fixation cross.

2. Same stimulus as in condition 1 but with one half image of the geometrical pattern rotated  $90^\circ$  (the blank region containing the fixation cross remained horizontal). This de-correlated the two images. Thus disparity

was undefined in the background and spurious disparities theoretically averaged to zero regardless of eye position. This procedure increased diplopia thresholds to near those found for the largest disparities in condition 1 (see Fig. 4) but they were still less than for an isolated test line.

3. A correlated random-dot pattern with blurred outer edges (Fig. 1C). The blank region containing the fixation cross remained a horizontal strip. Diplopia thresholds were now slightly smaller than those for the correlated, geometrically-textured background but showed a similar increase with increased horizontal disparity of the background relative to the target (see Fig. 5). The higher density of the random-dot pattern may have made it a stronger vertical vergence stimulus than the geometric texture.

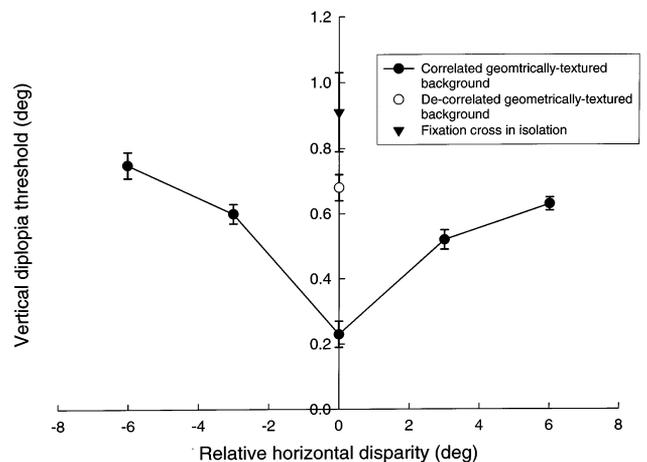


Fig. 4. Mean diplopia threshold for vertical disparity in the target as a function of horizontal disparity between the target and the geometrically-textured background ( $n = 5$ , error bars indicate  $\pm 1$  S.E.M.). Diplopia thresholds are shown for: the fixation cross in isolation; a larger range of horizontal disparity between the target and textured background than in Fig. 3; a de-correlated background. The target was presented on the horizontal strip blank area.

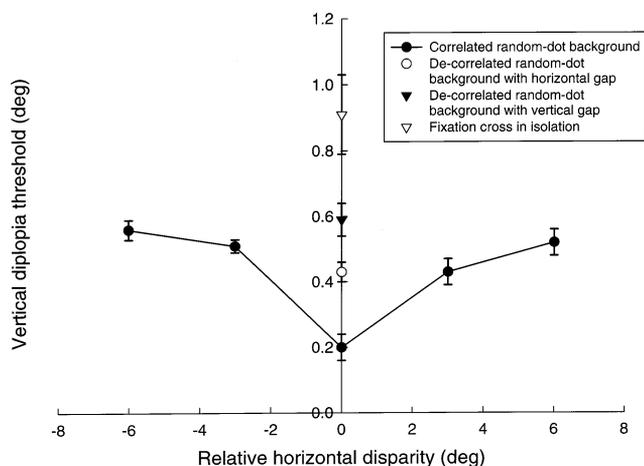


Fig. 5. Mean diplopia threshold for vertical disparity in the target as a function of horizontal disparity between the target and the random-dot background ( $n = 5$ , error bars indicate  $\pm 1$  S.E.M.). Diplopia thresholds are shown for: the target in isolation; a binocularly correlated random-dot background with a range of relative horizontal disparities; a de-correlated random-dot background with the target on a horizontal gap; and a de-correlated background with the target on a vertical gap.

4. A de-correlated random-dot pattern (independent samples of the random-dot texture in the two eyes). In condition 2, the de-correlation was only with respect to the texture elements themselves. Texture-defined edges corresponding to the edge of the textured disk and the edges of the blank region could still act as fusional stimuli. The effects of the edges of the disk were minimised in the random-dot pattern by blurring the edges. De-correlating the two images increased the diplopia threshold relative to the coplanar situation (see Fig. 5). Interestingly, diplopia thresholds with de-correlation were not as high as for the largest horizontal disparity condition with the correlated random-dot stimuli. Perhaps the lack of a clear separation in depth made the effects of the texture-defined, horizontally-oriented edges of the blank region more salient.

5. A de-correlated random-dot pattern as in condition 4 but with a vertical blank region. A vertical blank region eliminated horizontal texture-defined contours that could have acted as a fusion stimulus in conditions 1–4. This procedure increased the diplopia threshold to larger levels than found for the largest horizontal disparity random-dot stimuli in condition 3 (see Fig. 5). Thus texture-defined edges seem to be effective in driving vertical fusional mechanisms.

6. Two horizontal lines one  $11.5^\circ$  above the centre of the screen and one  $11.5^\circ$  below it. The lines subtended  $23^\circ$  in width and were 2.4 min arc thick (see Fig. 6A). We reasoned that if subjects' vertical vergence was not influenced by line contours located at this eccentricity then texture-defined edges would also be ineffective. However, the peripheral lines had a significant effect on

fusional range. When the peripheral lines had zero vertical disparity the diplopia threshold was reduced below that found for an isolated line. The presence of a competing vertical disparity signal appeared to be important, as the degree of vertical disparity in the peripheral lines affected the diplopia threshold. Specifically, the larger the difference in vertical disparity between the fixation cross and the peripheral lines the more the diplopia threshold differed from the isolated fixation

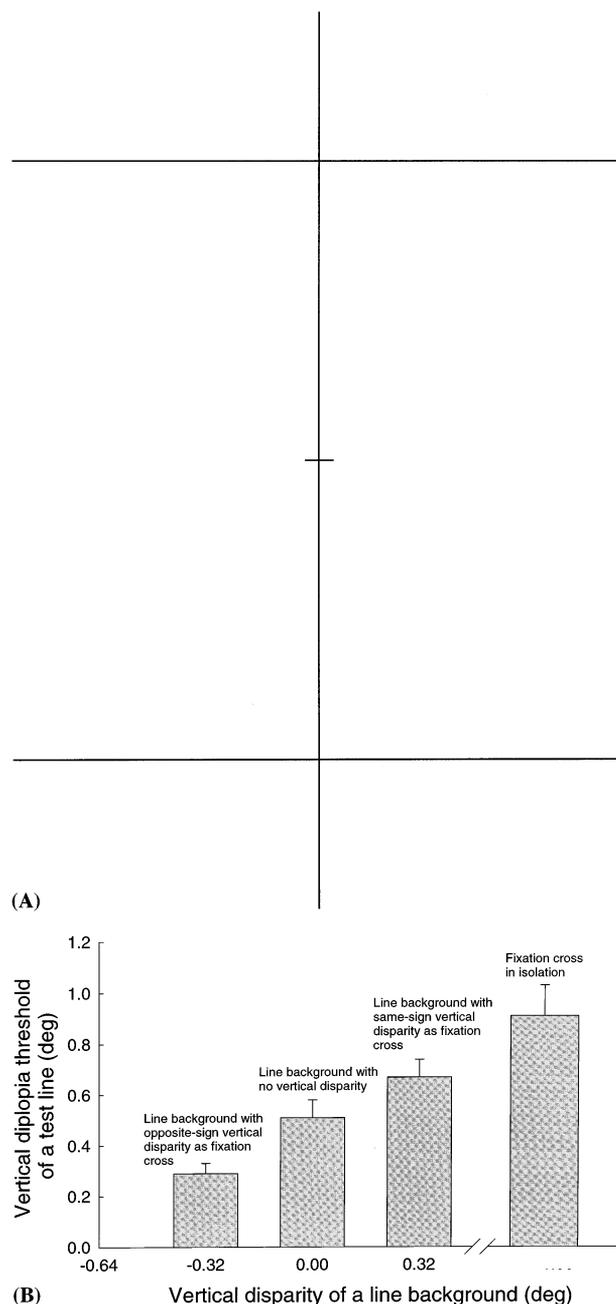


Fig. 6. (A) Schematic of the fixation cross and background stimuli for the condition with the background of eccentric lines. (B) Mean diplopia threshold for vertical disparity in the fixation cross as a function of the vertical disparity in the eccentric horizontal lines ( $n = 5$ , error bars indicate  $\pm 1$  S.E.M.).

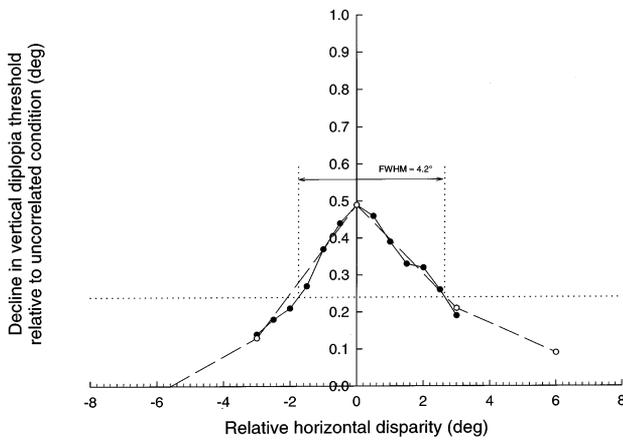


Fig. 7. Decrease in diplopia threshold as a function of relative horizontal disparity in the background ( $n = 5$ ). The magnitude of the effect of the background was defined to be the reduction in diplopia threshold relative to the de-correlated case (theoretically equivalent to an infinite horizontal disparity offset). The full-width half-maximum of the tuning curve, that is the distance between the points where the magnitude of the effect falls to half the maximum, is approximately  $4.2^\circ$  and is indicated. Data is shown for the target presented on a circular gap (from Fig. 3, closed symbols, solid line) and for the target presented on a horizontal bar gap (from Fig. 4, open symbols, dashed line) compared to the data for a de-correlated background with horizontal gap. Diplopia thresholds were on average  $0.05^\circ$  higher for the target presented on a horizontal gap but this difference has been normalised for comparative purposes.

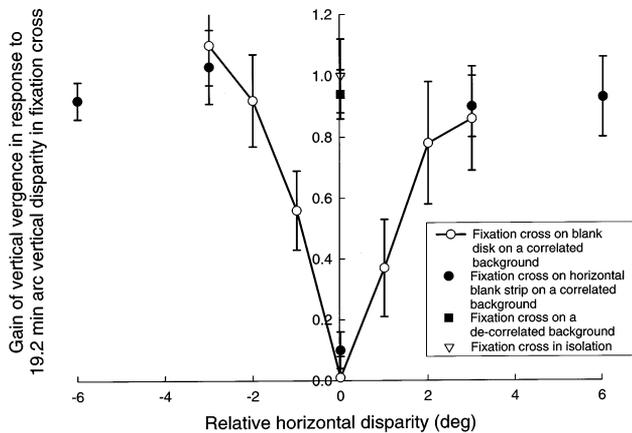


Fig. 8. Vertical vergence gain in response to disparity in a central test stimulus as a function of relative horizontal disparity in the geometrically-textured background ( $n = 4$ ). Diplopia thresholds are shown for the following background conditions: the fixation cross in isolation; a de-correlated background ( $90^\circ$  rotation between the half images); a correlated background as in Fig. 3; a correlated background as in Fig. 4.

cross case (Fig. 6B). This implies that the vertical disparity signal in the background is critical in determining the disruption effect of the background.

One measure of the selectivity of a tuned mechanism is its full-width half-maximum range. This is the distance between the points on the tuning curve where the magnitude of the effect falls to half the maximum.

Defining the magnitude of the effect to be the reduction in vertical diplopia threshold relative to the de-correlated case (theoretically equivalent to an infinite horizontal disparity offset) we see that the width of the tuning curve is approximately  $4.2^\circ$  (Fig. 7). The tuning is relatively narrower for uncrossed disparity than for crossed disparity of the background (half amplitude at  $-1.9^\circ$  versus  $+2.3^\circ$ , respectively).

### 3.3. Vertical vergence response

The presence of a competing background reduced the vertical fusional range for a disparate central target when the target and background had similar horizontal disparities. This reduction was less pronounced when the two stimuli were separated in depth. When they were well separated in depth, diplopia thresholds exceeded the classical Panum's limit. We propose that the increase in vertical diplopia thresholds with increased horizontal disparity reflects increased ability to vertically verge on the target rather than increased sensory fusional range. A significant vertical vergence response to disparity in the fixation cross, when the target and background were separated in depth, was suggested by the appearance of vertical diplopia in the background when the fixation cross was fused. To confirm this hypothesis, we estimated vergence responses to our stimuli using the flashed-nonius-line task. We measured the vertical vergence response to a fixation cross with  $19.2$  min arc of vertical disparity either in isolation or in the presence of a background with zero vertical disparity. Similar results were obtained with a target with  $9.6$  min arc of vertical disparity but, since we moved the nonius lines in integer pixels ( $2.4$  min arc), these data are too imprecise to report here. Given this step size, the reliability of the vergence measurements was relatively high with the reversals typically separated by a single step.

The responses are summarised in Fig. 8. When the fixation cross was presented in isolation, vergence gain averaged  $1.00$  across the subjects. Similar responses were obtained when the fixation cross was presented on a de-correlated background (mean gain of  $0.94$ ). When the stimulus was presented on a correlated coplanar background the background determined the response and vertical vergence was near zero. As the fixation cross and background were separated in stereo depth, by increasing relative horizontal disparity, vertical vergence gains increased and with  $\pm 3.0^\circ$  of horizontal disparity reached the levels found for an isolated stimulus.

The results for the vertical vergence gain and diplopia measures showed a similar pattern. Vertical fusional range was greatest for an isolated target, was smallest with coplanar target and background, and increased with interocular de-correlation of the back-

ground or with increasing relative horizontal disparity between target and background. However, in Fig. 8, vergence gains saturated at a separation of approximately  $3^\circ$  relative horizontal disparity while diplopia thresholds increased with increasing horizontal disparity up to at least  $6^\circ$ . Thus, at first glance, it appears that vergence responses are more tightly tuned for horizontal disparity than fusional responses. However, the vergence responses were collected for a fixed 19.2 min arc vertical disparity — not at diplopia threshold. In an additional experiment, we studied vertical vergence gains above and below diplopia threshold. We collected fusional responses while running the nonius staircases. It can be seen in Fig. 9 that as disparity was increased above the diplopia threshold the vergence tuning broadened as expected from the diplopia threshold data.

## 4. Discussion

### 4.1. Horizontal and vertical vergence interactions

Several studies have considered the effects of adding vertical disparity and horizontal disparity to the same vergence stimulus. Mitchell (1970) demonstrated that horizontal vergence movements could be elicited by short presentations of horizontally disparate stimuli even in the presence of up to  $4^\circ$  of vertical disparity. The proportion of trials in which horizontal vergence was initiated declined with increasing vertical disparity. London and Wick (1987) showed that correction of a vertical eye misalignment (tropia) increases the ability of patients to compensate for horizontal prism dispar-

ity. This implies that vertical disparity disrupts horizontal vergence. The interaction of vertical vergence and horizontal vergence was also investigated by Boman and Kertesz (1983). They found that vertical vergence latency increased and response magnitude declined when horizontal disparity was introduced into the display. Vertical disparity had no effect on horizontal vergence. However, their display contained a strong horizontal–vertical anisotropy, which may account for the anisotropy found in the results. In agreement with this hypothesis, data from Mitchell (1970) (his Figure 8) suggest that vertical disparity in vertical lines has a more detrimental effect on horizontal vergence than vertical disparity in horizontal lines. Hara, Steffen, Roberts and Zee (1998) found that the range of vertical fusion increased in eight of 12 subjects when convergence angle was increased from  $1^\circ$  to  $15^\circ$  (or to the maximum convergence attainable if the subject could not converge  $15^\circ$  of target vergence). The increase in fusional range was attributed to an increase in vertical vergence and not to changes in sensory fusional range.

These studies looked at interactions between horizontal and vertical target vergence in a single stimulus. In this situation, addition of horizontal disparity to the vertically disparate target (or vice versa) would be expected to make the task of bifoveal fixation more difficult. In the present study, the fixation target was always horizontally converged in the plane of the display. We studied the effect of changing the horizontal disparity between the target and a competing surround with a different vertical disparity. This increases the perceived separation in depth between the target and surround and, according to our hypothesis, should facilitate vertical fusion of the target.

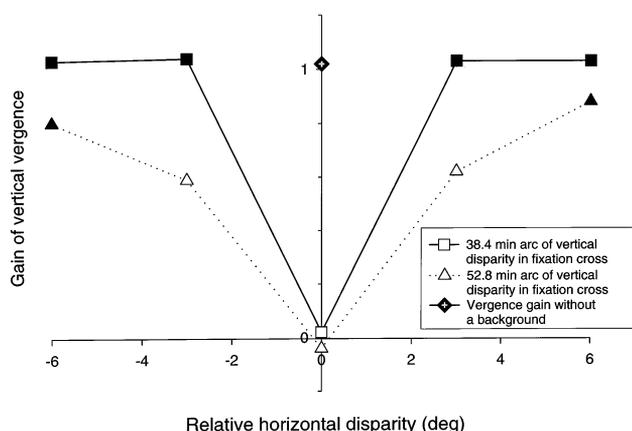


Fig. 9. The gain of vertical vergence in response to disparity in a central test stimulus as a function of relative horizontal disparity in the geometrically-textured background during simultaneous measurement of diplopia for one subject. Three other subjects showed similar results. As diplopia became apparent, vertical vergence gain tuning curves broadened. Filled circles indicate conditions where the subject reported a fused percept on more than 50% of trials; open circles indicate diplopia conditions.

### 4.2. Integration volume for vertical vergence

Howard et al. (1999) found that the gain of vertical vergence increased and phase lag decreased with increasing diameter of a central stimulus up to approximately  $20^\circ$ . Vergence gain was significantly higher for a central disc than for a peripheral annulus with the same area. This suggests that vertical disparities are pooled over a central integration area of approximately  $20^\circ$  diameter. A related finding is that vertical disparity in a large peripheral stimulus can prevent fusion of a small central target (Burian, 1939; Houtman & van der Pol, 1982). Furthermore, unlike horizontal vergence, vertical vergence gain does not depend on whether attention is focussed on the target or a peripheral stimulus (Stevenson et al., 1997). Stevenson, Reed and Yang (1998) found that induced horizontal and vertical vergence in subjects trying to fixate a stationary point decreased with decreasing area or increasing eccentricity of a competing disparate region.

In this study we have replicated the finding that a competing peripheral stimulus interferes with the ability to vertically fuse a central target. Furthermore, the maximum interference was when the target and competing surface were coplanar and diminished with introduction of a relative horizontal disparity. Tuning curves of vertical diplopia threshold versus relative horizontal disparity had a full-width half-maximum range of approximately  $\pm 2.5^\circ$  to  $\pm 3.0^\circ$ . For maintenance of fusion of a zero disparity target on a vertically disparate background the tuning curves were somewhat tighter. Vertical vergence also reached full gain at approximately this level of horizontal disparity. Thus vertical disparities appear to be integrated over a limited *volume* of stereoscopic space: over about  $20^\circ$  of retinal area and approximately  $\pm 3^\circ$  of horizontal disparity. The range of horizontal disparity vergence is difficult to determine (due to the possible involvement of vergence stimuli other than disparity) but is presumably  $10^\circ$  or more, based on studies of vergence eye movements elicited by disparity alone (Westheimer & Mitchell, 1969; Jones & Stephens, 1989; Hung, Zhu & Ciuffreda, 1997). Thus, we have found that competing stimuli with relative horizontal disparity placed within the retinal integration area of vertical vergence do not influence vertical fusional responses even when they would remain effective stimuli for horizontal disparity vergence.

An anonymous reviewer noted that sensitivity to inter-ocular correlation decreases with increasing horizontal disparity (Stevenson, Cormack, Schor & Tyler, 1992) and suggested that increasing horizontal disparity is equivalent to de-correlating the stimulus. If so horizontal disparity tuning for vertical vergence would help to tune out these noisy disparity estimates. The reviewer went further to hypothesise that the lack of an influence of a horizontally disparate background on vertical fusional range results from de-correlation noise making horizontal disparity immeasurable rather than from disparity tuning per se. While we cannot rule this out as a potential mechanism for the disparity tuning we feel it is unlikely. Inter-ocular correlation thresholds rise to 100% at about  $1.0^\circ$  of relative horizontal disparity (Stevenson et al., 1992) while we found an effect of a competing vergence stimulus at horizontal disparities of  $3.0^\circ$  or more. Also, it is unclear why horizontal vergence would not show identical range limitations under this hypothesis. Most likely, the horizontal disparity selectivity of both vertical fusion and binocular correlation detection reflect the range and tuning characteristics of the respective populations of disparity detectors that subserve these responses.

#### 4.3. Fusional range

Clinically, a vertical fusional range of  $\pm 2$ – $3$  prism dioptres is typical (Ogle, Martens & Dyer, 1967). Boltz,

Smith, Bennett and Harwerth (1980) found a range of static vertical fusion of  $\pm 3$  prism dioptres in a human subject and of  $\pm 2.5$  prism dioptres in the Rhesus monkey. Vertical fusional ranges of up to several degrees have been reported for slowly introduced vertical disparity (Ellerbrock, 1949; Ogle & Prangen, 1953). Our subjects could typically fuse an isolated fixation cross with about  $0.9^\circ$  of vertical disparity. Fusional range would presumably be larger with a larger target and slow approach. We found that this range is reduced in the presence of a background with zero vertical disparity. This reduction diminishes with increasing relative horizontal disparity up to at least  $\pm 6^\circ$ . In contrast, the reduction in the gain of vertical vergence in the presence of a background with zero vertical disparity appears to be more tightly tuned to horizontal disparity. Gain for modest vertical disparities saturates at approximately  $\pm 3^\circ$  of relative horizontal disparity.

Does this imply that the increase in fusional limit at larger disparities results from a vertical increase in Panum's limit with increased horizontal disparity pedestal? Diplopia and nonius line measurements collected simultaneously indicate that this is unlikely. As vertical disparity increased beyond the diplopia threshold the vertical vergence tuning curve flattened out. One interpretation is that vergence gain for small vertical disparities is similar for an isolated fixation cross and a fixation cross on a background but the range of vertical disparity vergence is reduced in the presence of a competing stimulus. In order to explain the data, this limit on range should increase with increasing horizontal disparity (separation in stereo depth). Thus, diplopia in the presence of a competing background stimulus can be a manifestation of the limitations on vertical vergence range as well as gain.

#### 4.4. Detection and processing of vertical disparity

Disparity detectors in the visual cortex of the anaesthetised cat and monkey have been found to be as responsive to vertical as to horizontal positional disparities and many cells respond to both types of disparity (Von der Heydt, Adorjani, Hännny & Baumgartner, 1978; Maunsell & Van Essen, 1983b). In cat striate cortex, Von der Heydt et al. (1978) reported that these cells have a range of preferred disparity with a mean of zero and a standard deviation of about  $0.5^\circ$  for both vertical and horizontal disparity. This implies they can sense vertical disparities of at least  $\pm 1.5^\circ$ , which make them a potential substrate for vertical vergence movements.

Disparity detectors in striate cortex are sensitive to image correlation (Poggio, Gonzalez & Krause, 1988) and binocular de-correlation should disrupt a vergence signal based on these detectors. De-correlating the random-dot image pair is equivalent to introducing an

infinite disparity. Chance matches have random sign and tend to cancel regardless of eye position. Thus, they do not provide a unique vergence signal. Nevertheless, de-correlation of the background stimulus did not eliminate the interference effect.

More globally, disparity signals for the de-correlated background could be based on texture-defined edges, monocular-occlusion regions, or the low-frequency and second-order features of the background. The use of a vertically oriented blank area for presenting the fixation cross and heavy blurring of the edge of the background pattern should have made horizontally oriented monocular occlusion zones and texture defined edges unusable as a vergence stimulus.

The fact that an interference effect remained with de-correlated textured backgrounds implies that vertical vergence can be evoked by the gross features of a stimulus. Horizontal vergence can be initiated, but not maintained, by mechanisms that are not form selective. This transient vergence responds to disparity in dissimilar images in the two eyes presumably to align their centroids (Jones & Kerr, 1972; Westheimer & Mitchell, 1969). We propose that the vertical vergence system is also sensitive to gross characteristics of the textured region and operates to align these regions dichoptically. Our background stimulus had both texture- and luminance-defined boundaries and vertical vergence could be driven by disparities at these boundaries. Since the texture is light elements on a dark background a low-frequency disparity signal exists even with de-correlation and blurring of the edges. One possibility is that the residual restraining effect of the de-correlated, blurred-edge background is due to the activity of a low spatial-frequency mechanism in vertical vergence similar to that proposed to subserve transient horizontal vergence (Edwards, Pope & Schor, 1998). This type of mechanism would respond to the overall alignment of the textured (brighter) region without being sensitive to the alignment of the texture elements. With a spatial scale to match our 23° background it is questionable whether such mechanisms would have sufficient precision to influence our results. It is possible that the envelope of the textured region could be used as a second-order vertical disparity stimulus (Wilcox & Hess, 1997). Without sharp texture-defined boundaries such a mechanism would be similar to the low spatial-frequency mechanism discussed above but could operate without a change in mean luminance at the edges of the textured regions.

#### 4.5. Behavioural significance

The extent of vergence required to fixate a target depends on its eccentricity and distance and on the co-ordinate system used for defining eye movements (see Howard & Rogers, 1995 for review). For example,

in the Helmholtz system, lines of constant elevation correspond to epipolar lines. Thus, binocular fixation on any point in space requires equal elevation in both eyes and target vergence is mapped completely into the horizontal dimension. Points on a surface to the right of the midline are closer to the right eye than to the left eye. Thus, even in the Helmholtz system, where target vertical vergence is always zero, the retinal projection of objects in similar visual directions as the fixation point will have a vertical disparity that decreases with egocentric distance when the eyes are in tertiary positions. In Fick's system, the locus of iso-vergent points approximates the theoretical point horopter with central fixation and symmetrical vergence (the deviation is due to non-coincidence of the centre of rotation and nodal point of the eye). Hence, a movement to any tertiary point requires a vertical vergence. The amount of vertical vergence required for any given conjugate gaze direction increases with decreased distance but the sign and magnitude vary with horizontal and vertical gaze angle and are thus not unambiguously correlated with distance.

Schor, Maxwell and Stevenson (1994) found that the visual axes intersect with a typical error of no more than 0.25° for any direction or distance of the target. When a subject makes an eye movement to a tertiary point it is accomplished through unequal sized saccades in the two eyes when Fick co-ordinates are used (Schor et al., 1994). These disjunctive movements are much faster than classical disparity vertical vergence (e.g. as reported by Houtman, Roze & Scheper, 1977). They are open loop in that they are not driven by stimulus disparity (Ygge & Zee, 1995). They compensate for most of the required vertical disconjugacy but some slow disparity-driven vertical vergence following the saccade is evident (Lemij & Collewijn, 1991). Smooth pursuit eye movements can also exhibit disconjugacy appropriate to the demands of position-specific vertical disparity (Schor, Gleason, Maxwell & Lunn, 1993a). Thus it appears that the majority of natural vertical disconjugacy required during normal gaze changes is accomplished by pre-programmed disconjugacy in 'versional' eye movements. The relatively slow vertical vergence movements compensate for any remaining vertical disparity in order to achieve bifoveal fixation.

Vertical vergence can compensate for changes in the patterns of vertical disparities (or their neuronal correlates) in the two eyes caused by changes in the size of the globe, interocular distance, oculomotor mechanics, neuronal efficiency and retinal receptor distribution, which occur with development and ageing or with injury and disease. Regardless of the co-ordinate system used, optical instruments can always introduce vertical disparities. In man, vertical vergence is important for dealing with the optical demands of spectacles. Anisometric spectacles cause size differences in the two

eyes that require position-specific vertical vergence that increases with eccentricity. Allen (1974) has reported complete adaptation to the prism demand of anisometric spectacles. Vertical disparity can also be introduced in optical display systems. For example, heads up or augmented reality displays present visual patterns superimposed upon the image of the real world. Similarly, many teleoperation and virtual reality systems combine multiple displays (for example information from a variety of sensors) often at a variety of optical distances into a single compound display. Display dependent vertical disparity can result from binocular misalignment and other distortions in the various component displays. The horizontal disparity selectivity of vertical vergence found in the present study may help to compensate for these vertical disparities in many cases.

A related role for vertical disparity vergence is the parametric calibration of saccadic and pursuit eye movements. This calibration can be regarded as a generalisation of phoria adaptation. Schor (1979) has proposed that horizontal phoria adaptation occurs when there exists a persistent demand for vergence correction. Similarly, vertical vergence presumably acts as an error signal driving adaptive mechanisms to adjust the conjugacy of 'versional' eye movements to meet the demands of the changing optical environment (McCandless, Schor & Maxwell, 1996). Adaptive changes in disjunctive saccadic or pursuit eye movements occur only if a binocularly disparate image is visible during or following the eye movement (Schor, Gleason & Horner, 1990).

Schor, Gleason and Lunn (1993b) found that phoria adaptation spread uniformly across the test field unless there was conflicting disparity information. Adaptation to opposite vertical disparities at two points resulted in position-specific phoria changes similar to those following adaptation to aniseikonic lenses (Lemij & Collewijn, 1991). Phoria adapted differently and peaked appropriately at the two adaptation points with a gradual transition over the region of the visual field between them. If the points were placed too close together a resolution limit prevented them from being adapted independently and the peaks of adaptation were outside the stimulated adaptation points. Interestingly Schor et al.'s (1993b) model of a Gaussian spread of adaptation with a sigma of approx.  $6^\circ$  is comparable with the  $20^\circ$  diameter integration area for vertical vergence ( $\pm 2$  sigma is  $24^\circ$ ).

It would be interesting to see if the depth selectivity for vertical vergence also applies to vertical phoria adaptation. Schor and McCandless (1995a,b, 1997) demonstrated that vertical phoria can adapt differentially for different horizontal vergence postures. Differential adaptation was smaller for a  $2.5^\circ$  than for a  $10^\circ$  horizontal vergence separation of the adaptation stim-

uli, but was still remarkably robust for the  $2.5^\circ$  separation. The phoria changes presumably show the spread of the influence of vertical disparity stimulation at one horizontal disparity to other horizontal disparities. Our data show how vertical vergence response to a target at one horizontal disparity is affected by simultaneous vertical disparity stimulation at a different horizontal disparity. Thus both measures are measuring different aspects of the interaction between vertical and horizontal disparity detectors in driving vergence. Since the smallest horizontal vergence separation Schor and McCandless (1995b) used was  $2.5^\circ$ , which is similar to the horizontal disparity integration range we found for vertical vergence, it is difficult to compare the horizontal disparity selectivity of vertical vergence and vertical phoria adaptation.

The vertical alignment of the eyes is maintained by at least three mechanisms. First, when we change fixation the eyes make pre-programmed saccades appropriate to the eccentricity and distance of the visual target. Second, any residual error is corrected by disparity-driven vertical vergence. A persistent demand for correction leads to the re-calibration of the pre-programmed system and associated adaptation of phoria. Third, the vertical vergence system adapts to optical and neural changes associated with growth and ageing, and to the optical demands of spectacles or other viewing devices. In the present study we have shown that vertical vergence is evoked by vertical disparity only over a restricted range of horizontal disparities. We propose that this allows for increased flexibility in the adaptation of the vertical vergence mechanism to the demands of binocular fixation.

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### References

- Allen, D. C. (1974). Vertical prism adaptation in anisometropes. *American Journal of Optometry and Physiological Optics*, *51*, 252–259.
- Boltz, R. L., Smith, E. L., Bennett, M. J., & Harwerth, R. S. (1980). Vertical fusional vergence ranges of the rhesus monkey. *Vision Research*, *20*, 83–85.
- Boman, D. K., & Kertesz, A. E. (1983). Interaction between horizontal and vertical fusional responses. *Perception and Psychophysics*, *33*, 565–570.
- Burian, H. M. (1939). Fusional movements. Role of peripheral retinal stimuli. *Archives of Ophthalmology*, *21*, 486–491.
- Edwards, M., Pope, D. R., & Schor, C. M. (1998). Luminance contrast and spatial-frequency tuning of the transient-vergence system. *Vision Research*, *38*, 705–717.

- Ellerbrock, V. J. (1949). Experimental investigation of vertical fusional movements. Part I. *American Journal of Optometry and Archives of the American Academy of Optometry*, 26, 327–337.
- Finney, D. J. (1971). *Probit analysis*. London: Cambridge University Press.
- Hara, N., Steffen, H., Roberts, D. C., & Zee, D. S. (1998). Effect of horizontal vergence on the motor and sensory components of vertical fusion. *Investigative Ophthalmology and Visual Science*, 39, 2268–2276.
- Houtman, W. A., Roze, J. H., & Scheper, W. (1977). Vertical motor fusion. *Documenta Ophthalmologica*, 44, 179–185.
- Houtman, W. A., & van der Pol, B. A. E. (1982). Fusional movements by peripheral retinal stimulation ('peripheral motor fusion'). *Graefe's Archives Clinical Experimental Ophthalmology*, 218, 218–220.
- Howard, I. P., & Rogers, B. J. (1995). *Binocular vision and stereopsis*. New York: Oxford University Press.
- Howard, I. P., Allison, R. S., & Zacher, J. E. (1997). The dynamics of vertical vergence. *Experimental Brain Research*, 116, 153–159.
- Howard, I. P., Fang, X., Allison, R. S., & Zacher, J. E. (2000). Effects of stimulus size and eccentricity on horizontal and vertical vergence. *Experimental Brain Research*, 130, 124–132.
- Hung, G. K., Zhu, H., & Ciuffreda, K. J. (1997). Convergence and divergence exhibit different response characteristics to symmetric stimuli. *Vision Research*, 37, 1197–1205.
- Jones, R., & Kerr, K. E. (1972). Vergence eye movements to pairs of disparity stimuli with shape selection cues. *Vision Research*, 12, 1425–1430.
- Jones, R., & Stephens, G. L. (1989). Horizontal fusional amplitudes. *Investigative Ophthalmology and Visual Science*, 30, 1638–1642.
- Lemij, H. G., & Collewijn, H. (1991). Short-term nonconjugate adaptation of human saccades to anisometric spectacles. *Vision Research*, 31, 1955–1966.
- London, R. F., & Wick, B. (1987). Vertical fixation disparity correction: effect on the horizontal forced-vergence fixation disparity curve. *American Journal of Optometry and Physiological Optics*, 64, 653–656.
- Maunsell, J. H. R., & Van Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey. II. Binocular interactions and sensitivity to binocular disparity. *Journal of Neurophysiology*, 49, 1148–1167.
- Mayhew, J., & Longuet-Higgins, H. C. (1982). A computational model of binocular depth perception. *Nature*, 297, 376–378.
- McCandless, J. W., Schor, C. M., & Maxwell, J. S. (1996). A cross-coupling model of vertical vergence adaptation. *IEEE Transactions on Biomedical Engineering*, 43, 24–34.
- Mitchell, D. E. (1970). Properties of stimuli eliciting vergence eye movements and stereopsis. *Vision Research*, 10, 145–162.
- Ogle, K. N. (1955). Stereopsis and vertical disparity. *AMA Archives of Ophthalmology*, 53, 495–504.
- Ogle, K. N. (1964). *Researches in binocular vision*. New York: Hafner.
- Ogle, K. N., & Prangen, A. de H. (1953). Observations on vertical divergences and hyperphorias. *AMA Archives of Ophthalmology*, 49, 313–334.
- Ogle, K. N., Martens, T. G., & Dyer, J. A. (1967). *Oculomotor imbalance in binocular vision and fixation disparity*. Philadelphia: Lea and Febiger.
- Poggio, G. F., & Fischer, B. (1977). Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkey. *Journal of Neurophysiology*, 40, 1392–1405.
- Poggio, G. F., Gonzalez, F., & Krause, F. (1988). Stereoscopic mechanisms in monkey visual cortex: binocular correlation and disparity selectivity. *Journal of Neuroscience*, 8, 4531–4550.
- Schor, C. M. (1979). The relationship between fusional vergence eye movements and fixation disparity. *Vision Research*, 19, 1359–1367.
- Schor, C. M., & McCandless, J. W. (1995a). Distance cues for vertical vergence adaptation. *Optometry and Vision Science*, 72, 478–486.
- Schor, C. M., & McCandless, J. W. (1995b). An adaptable association between vertical and horizontal vergence. *Vision Research*, 35, 3519–3527.
- Schor, C. M., & McCandless, J. W. (1997). Context-specific adaptation of vertical vergence to correlates of eye position. *Vision Research*, 37, 1929–1937.
- Schor, C. M., Gleason, G., & Horner, D. (1990). Selective nonconjugate binocular adaptation of vertical saccades and pursuits. *Vision Research*, 30, 1827–1844.
- Schor, C. M., Gleason, G., Maxwell, J., & Lunn, R. (1993a). Spatial aspects of vertical phoria adaptation. *Vision Research*, 33, 73–84.
- Schor, C. M., Gleason, G., & Lunn, R. (1993b). Interactions between short-term vertical phoria adaptation and nonconjugate adaptation of vertical pursuits. *Vision Research*, 33, 55–64.
- Schor, C. M., Maxwell, J. S., & Stevenson, S. B. (1994). Isovergence surfaces: the conjugacy of vertical eye movements in tertiary positions of gaze. *Ophthalmic and Physiological Optics*, 14, 279–285.
- Stevenson, S. B., Cormack, L. K., Schor, C. M., & Tyler, C. W. (1992). Disparity tuning in mechanisms of human stereopsis. *Vision Research*, 32, 1685–1694.
- Stevenson, S. B., Lott, L. A., & Yang, J. (1997). The influence of subject instruction on horizontal and vertical vergence tracking. *Vision Research*, 37, 2891–2898.
- Stevenson, S. B., Reed, P. E., & Yang, J. (1998). The effect of target size and eccentricity on reflex disparity vergence. *Vision Research*, 39, 823–832.
- Von der Heydt, R., Adorjani, C. S., Hännly, P., & Baumgartner, G. (1978). Disparity sensitivity and receptive field incongruity of units in the cat striate cortex. *Experimental Brain Research*, 31, 523–545.
- Westheimer, G., & Mitchell, D. E. (1969). The sensory stimulus for disjunctive eye movements. *Vision Research*, 9, 749–755.
- Wilcox, L. M., & Hess, R. F. (1997). Scale selection for second-order (non-linear) stereopsis. *Vision Research*, 37, 2981–2992.
- Ygge, J., & Zee, D. S. (1995). Control of vertical eye alignment in three-dimensional space. *Vision Research*, 35, 3169–3181.