

## RESEARCH ARTICLE

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## Effects of stimulus size and eccentricity on horizontal and vertical vergence

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**Abstract** We measured the gain and phase of horizontal and vertical vergences of five subjects as a function of stimulus area and position. Vergence eye movements were recorded by the scleral search coil method as subjects observed dichoptic displays oscillating in antiphase either from side to side or up and down with a peak-to-peak magnitude of  $0.5^\circ$  at either 0.1 Hz or 1.0 Hz. The stimulus was a central textured disc with diameter ranging from  $0.75^\circ$  to  $65^\circ$ , or a peripheral annulus with outer diameter  $65^\circ$  and inner diameter ranging from  $5^\circ$  to  $45^\circ$ . The remaining field was black. For horizontal vergence at both stimulus frequencies, gain and the phase lag were about the same for a  $0.75^\circ$  stimulus as for a  $65^\circ$  central stimulus. For vertical vergence, mean gain increased and mean phase lag decreased with increasing diameter of the central stimulus up to approximately  $20^\circ$ . Thus, the stimulus integration area is much smaller for horizontal vergence than for vertical vergence. The integration area for vertical vergence is similar to that for cyclovergence, as revealed in a previous study. For both types of vergence, response gains were higher and phase lags smaller at 0.1 Hz than at 1.0 Hz. Also, gain decreased and phase lag increased with increasing occlusion of the central region of the stimulus. Vergence gain was significantly higher for a  $45^\circ$  central disc than for a peripheral annulus with the same area. Thus, the central retina has more power to evoke horizontal or vertical vergence than the same area in the periphery. We compare the results with similar data for cyclovergence and discuss their ecological implications.

**Key words** Vergence · Binocular disparity · Binocular vision · Stereoscopic vision

### Introduction

Disparity vergence is a disjunctive movement of the two eyes in response to binocular disparity. Horizontal vergence occurs about vertical axes, vertical vergence about horizontal axes, and cyclovergence about the visual axes. Horizontal vergence is evoked in animals with frontal vision when fixation is changed from one depth plane to another or when a visual target is pursued as it moves in depth. Vertical vergence compensates for vertical disparities that occur in oblique gaze and for hyperphoria. Cyclovergence compensates for cyclophoria. In this study we investigated the stimulus area over which disparity signals controlling horizontal and vertical vergence are integrated. We also investigated the relative effectiveness of central and peripheral retinal stimuli in evoking vergence.

There are three aspects of vergence about which one can enquire about the effects of stimulus area: the maximum amplitude of maintained vergence, the initial response to a step change in disparity and, thirdly, the response to a continuous change in vergence.

With regard to the range of maintained vergence, the range of horizontal disparities over which the images of a central object can be fused is increased by the addition of peripheral stimuli with similar disparity (Jones and Stephens 1989). Kertesz (1981) found that, for one subject, maximum horizontal convergence was  $8.3^\circ$  for a vertical line subtending  $5^\circ$ ,  $15.4^\circ$  for a line subtending  $30^\circ$ , and  $25.9^\circ$  for a line subtending  $57.6^\circ$ . For the same subject, the maximum vertical vergence in one direction was  $1.9^\circ$  for a textured disc subtending  $5^\circ$ ,  $4.2^\circ$  for a  $30^\circ$  stimulus, and  $5.2^\circ$  for a  $57.6^\circ$  stimulus. Therefore, it seems that disparity signals for maintained horizontal or vertical vergence are integrated over an area subtending at least  $30^\circ$  to  $57.6^\circ$ .

With regard to vergence to step changes in disparity, Popple et al. (1997) measured the initial horizontal vergence response to a 12.5-arcmin step change in disparity of the centre of a random-dot stereogram relative to a fixed background. Vergence was measured by the align-

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ment of nonius lines following the brief stimulus presentation. The magnitude of the initial vergence response reached a maximum at a disc diameter of about  $6^\circ$ . Thus, for this response, the disparity signal for horizontal vergence is integrated over an area subtending  $6^\circ$ . Horizontally disparate images presented suddenly in the parafoveal region induce temporary diplopia in a small centrally fixated object (Winkelman 1951, 1953). The initial response to a step of disparity is in open-loop mode since it is not controlled by visual feedback. According to the dual-mode theory of Semmlow et al. (1986), the dynamics of the initial phase of a vergence response differ from those of the subsequent phase controlled by visual feedback.

Vertical disparity in a large peripheral stimulus induces persisting vertical disparity and diplopia into the images of a centrally placed visual object that a person is trying to fuse (Burian 1939; Houtman and van der Pol 1982). Stevenson et al. (1997) found that subjects could not hold horizontal or vertical vergence on a fixation target when the vertical and horizontal disparities of a  $7.5^\circ$  textured surround were simultaneously modulated through amplitudes of up to 40 arcmin at 0.125 Hz. Induced vertical vergence was large and the same whether subjects attended to the stationary target or to the modulated surround. Induced horizontal vergence was only small when subjects tried to fixate the stationary spot but had a gain of about 0.85 when they attended to the surround. This demonstrates that both horizontal and vertical vergence are driven by a weighted mean of competing signals from a certain area. However, people have some control over which of two competing stimuli is used to drive horizontal vergence but no control over which stimulus drives vertical vergence. This difference is presumably related to the fact that vertical disparities do not change as abruptly over the visual field as horizontal disparities. Stevenson et al. (1999) found that induced horizontal and vertical vergence in subjects trying to fixate a stationary point decreased with decreasing area or increasing eccentricity of a textured surround modulated in horizontal and vertical disparity through  $0.25^\circ$  at 0.5 Hz. The decrease in the effectiveness of the stimuli for vergence with increasing eccentricity was similar to the decreased effectiveness of the same stimuli in detection tasks. They concluded that both functions were consistent with the change in cortical magnification with increasing eccentricity.

We measured stimulus integration areas for the third aspect of vergence, namely the area beyond which there is no further increase in the gain of vergence tracking evoked by sinusoidal modulation of disparity of an isolated stimulus. In a previous study, the integration area for cyclovergence to sinusoidal changes in cyclodisparity of an isolated stimulus was found to be about  $20^\circ$  in diameter (Howard et al. 1994). In the present study we measured the gain and phase lag of horizontal vergence and vertical vergence in response to sinusoidal oscillation of horizontal and vertical disparity of isolated textured stimuli of various areas. For reasons provided in

the "Discussion", we hypothesized that the stimulus integration area for vertical disparity is much larger than that for horizontal disparity.

The second question we addressed was the effect of stimulus position on the gain and phase lag of vergence. Disparity in a foveal stimulus evokes horizontal vergence (Ludvig et al. 1965, 1966; Kertesz and Hampton 1981; Hampton and Kertesz 1983; Hung et al. 1991) and vertical vergence (Ellerbrock 1949a, 1949b; Kertesz and Hampton 1981; Houtman and van der Pol 1982). However, the gain of cyclovergence is very low, even for a stimulus  $5^\circ$  in diameter (Howard et al. 1994). Peripheral stimuli evoke all types of vergence, and are particularly effective for cyclovergence.

A stimulus of a given area becomes less effective in maintaining accurate horizontal vergence as it is moved into the peripheral visual field (Francis and Owen 1983; Hampton and Kertesz 1983). The velocity and magnitude of horizontal vergence induced by disparity steps or ramps have been found to be greater for stimuli in the centre of the visual field than for those  $3^\circ$  into the periphery (Hung et al. 1991). However, the amplitude of cyclovergence is greater with peripheral stimuli than with central stimuli of the same area (Howard et al. 1994).

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## Materials and methods

### Subjects

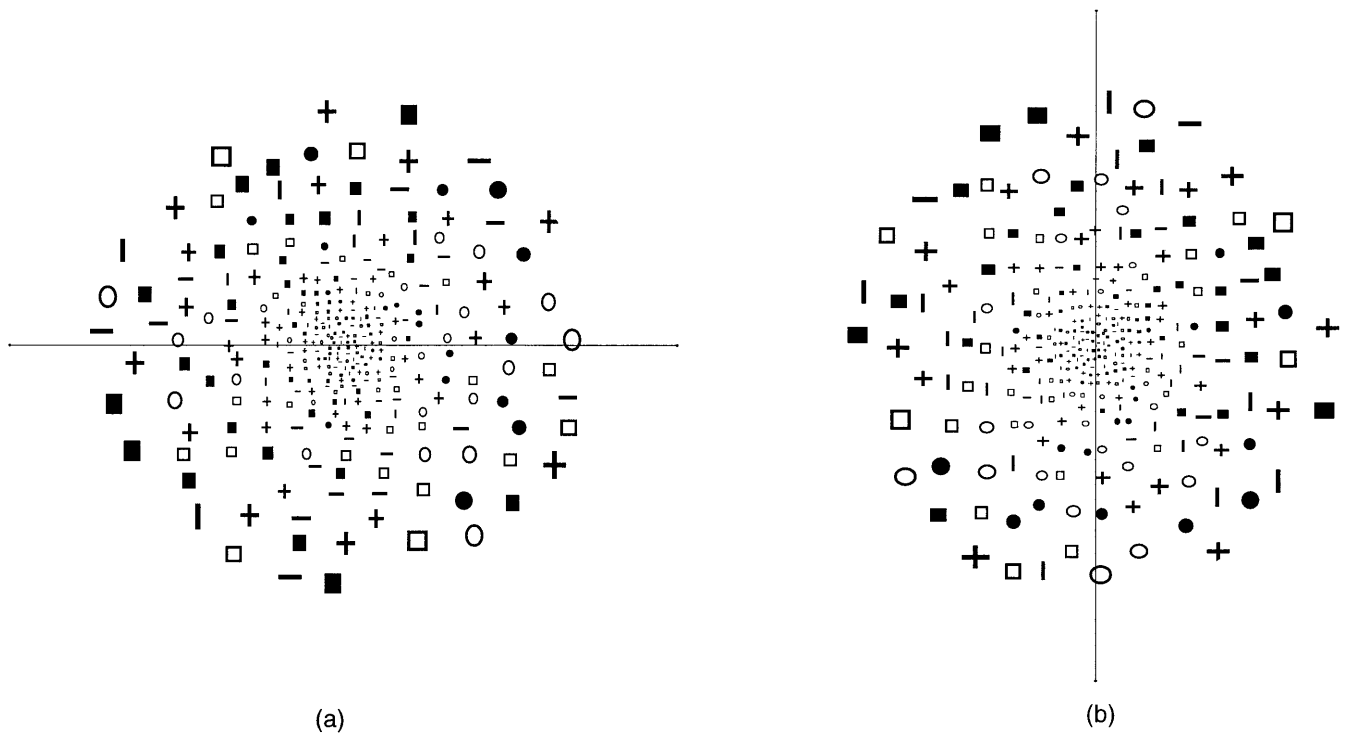
Five subjects, ranging in age from 25 to 33 years, participated in the study. Three subjects were naive as to the purpose of the studies. All subjects had normal stereoscopic vision. Three of the subjects were myopes. Two subjects wore their glasses during the experiments and one subject did not wear his glasses but reported that he could see the stimulus clearly. This study was approved by York University Ethics Committee in accordance with standards laid down in the 1964 Helsinki Declaration. All subjects gave their informed consent.

### Eye movement monitoring

Movements of the subject's eyes were measured by a Robinson scleral-coil system (Robinson 1963) using equipment made by CNC Engineering, Seattle. A search coil (Skalar Medical, Delft, Holland) was placed on each eye after application of a drop of anaesthetic. The subject sat with the head supported on a bite at the centre of the magnetic field coils contained in a cubic frame 1 m along each side. The noise in the eye monitoring system was of the order of  $0.01^\circ$  while the smallest amplitude of eye movement measured was at least  $0.1^\circ$ .

### Visual display

The stimulus consisted of a variety of randomly distributed white texture elements displayed on a black background (squares, plus signs, lines and circles). The diameter of the stimulus elements increased linearly from  $0.4^\circ$  at the centre to  $3^\circ$  at an eccentricity of  $32.5^\circ$ . Their density decreased proportionately. This scaling compensated for the decrease in visual acuity with increasing eccentricity (Anstis 1974). When horizontal vergence was measured, a horizontal line was added across the centre of the stimulus. It provided no horizontal disparity and helped subjects maintain zero



**Fig. 1** Examples of stimuli used to evoke (a) horizontal and (b) vertical vergence. The diameter of the stimulus elements increased linearly with increasing eccentricity. The actual display consisted of white texture elements on a dark ground. *Horizontal lines* stabilized vertical vergence when horizontal vergence was measured and *vertical lines* stabilized horizontal vergence when vertical vergence was measured

vertical vergence and cyclovergence. When vertical vergence was measured, a vertical line was added across the centre of the stimulus (Fig. 1). It provided no vertical disparity and helped subjects converge on the stimulus. The average luminance of the stimulus after reflection off the mirror was about 0.5 cd/m<sup>2</sup>. The area surrounding the stimulus was matte black so that only the fused textured stimulus was visible. The stimuli were computer generated and prepared as slides. Identical stimuli were projected onto rear projection screens mounted on the two sides of the cube containing the field coils. The subject viewed the displays through mirrors set at  $\pm 45^\circ$  to the frontal plane so that the fused image appeared in the frontal plane 57 cm directly ahead of the subject. Each slide was mounted on a horizontal or vertical track. A servo motor oscillated the two slides in antiphase through a peak-to-peak amplitude of  $0.5^\circ$  at each of two frequencies, either from side to side or up and down.

#### Procedure

The subjects were seated with their heads supported on a bite at the centre of the alternating magnetic fields. The eye movement system was calibrated by having subjects fixate targets at defined eccentricities.

The images to the two eyes were oscillated sinusoidally in antiphase from side to side or up and down through a peak-to-peak amplitude of  $0.5^\circ$ . The stimulus was presented for 60 s at 0.1 Hz and for 10 s at 1.0 Hz. For each oscillation frequency, each condition was repeated twice for each subject over two sessions. In one set of conditions, central stimuli with diameters of  $0.75^\circ$ ,  $5^\circ$ ,  $10^\circ$ ,  $20^\circ$ ,  $45^\circ$ , or  $65^\circ$  were used. In another set of conditions, the centre of a  $65^\circ$  stimulus was occluded by a black disc with a diameter of  $5^\circ$ ,  $10^\circ$ ,  $20^\circ$ , or  $45^\circ$ . The order of stimulus presentations was ran-

domized for each session and counterbalanced across sessions. In all conditions, subjects were asked to attend to the stimulus and keep it in clear view.

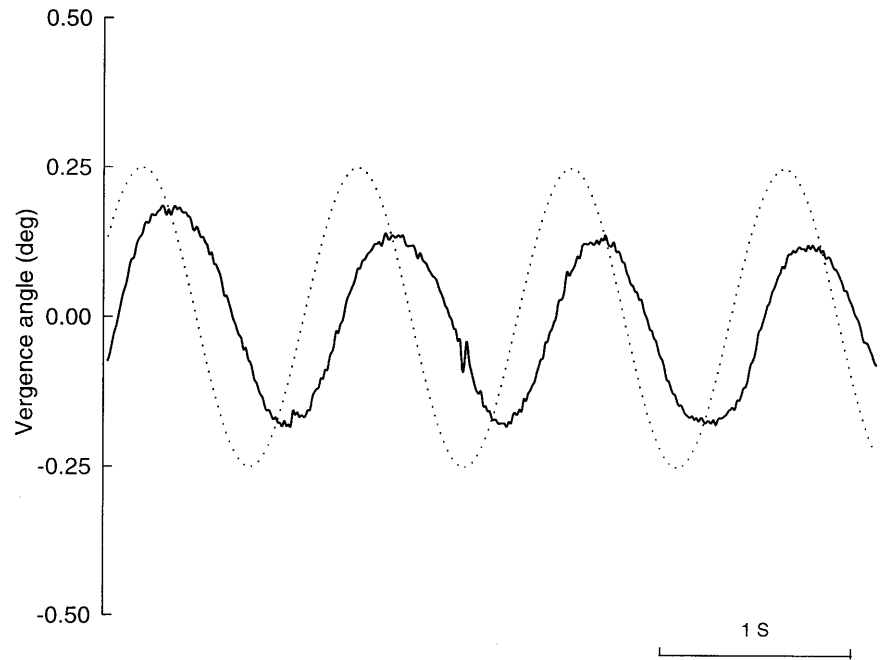
The eye-position signal and a reference signal that indicated the peak of each stimulus oscillation were recorded on digital tape and later sampled by computer at 20-ms intervals digitized with 12-bit precision. In the offline analysis, raw eye position data were first calibrated and the signed left eye signal was subtracted from the signed right eye signal. The resulting vergence record was fitted to a sinusoid using the method of least squares. The curve fitting was performed on sections of the data record on a cycle by cycle basis. Satisfactory performance of the fitting procedure was monitored by visual inspection and by objective goodness of fit measures. For horizontal and vertical vergence, the peak-to-peak amplitude of response for each sinusoidal oscillation of the stimulus was measured and the set of peak-to-peak responses within each condition was averaged. The gain of vergence was derived by dividing the peak-to-peak amplitude of vergence by the peak-to-peak amplitude of stimulus oscillation. The phase lag was measured by the average of the lags between the peaks of the responses relative to those of the stimulus.

## Results

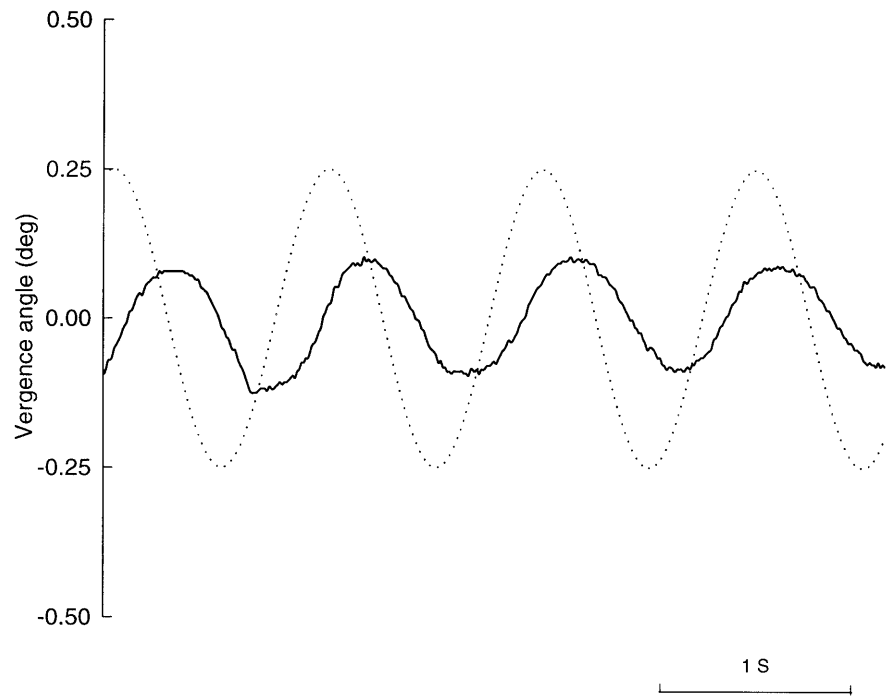
### Horizontal vergence

A sample record of horizontal vergence for one subject is shown in Fig. 2a. The mean gain of horizontal vergence for the five subjects as a function of the area of the central stimulus for the two stimulus frequencies is shown in Fig. 3. At 0.1 Hz, the mean gain was just below unity for all stimulus sizes. It can be seen that the gain of horizontal vergence evoked by a small central stimulus was almost as high as that evoked by a  $65^\circ$  stimulus for both stimulus frequencies. Repeated measures analysis of variance (diameter of stimulus  $\times$  frequency) indicated that there was no significant effect of size of the central

**Fig. 2** Sample record of (a) horizontal vergence and (b) vertical vergence produced by a  $0.5^\circ$  peak-to-peak modulation of disparity of a  $20^\circ$ -diameter central stimulus at 1.0 Hz. Each record was obtained by subtracting the position of the right eye from that of the left eye at each instant. The dotted line shows the sinusoidal modulation of stimulus disparity relative to a zero value at the viewing distance of 57 cm



(a)

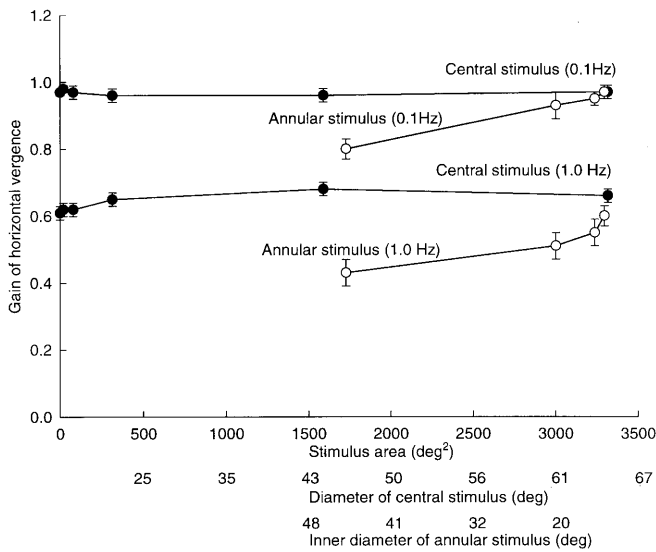


(b)

stimulus on the gain of horizontal vergence ( $F_{(5,20)}=2.229$ ,  $P>0.05$ ).

The mean phase lag of horizontal vergence for the five subjects as a function of the area of the central stimulus for the two stimulus frequencies is shown in Fig. 4. Repeated measures analysis of variance indicated no significant effect of size of the central stimulus on the phase lag of horizontal vergence ( $F_{(5,20)}=1.298$ ,  $P>0.05$ ).

The mean gain of horizontal vergence for the five subjects as a function of the area of the annular display for the two stimulus frequencies is shown in Fig. 3. For all subjects at both frequencies, gain fell as the diameter of central occlusion increased, that is, as the area of the display decreased. Repeated measures analysis of variance indicated a significant effect of central occlusion on the gain of horizontal vergence ( $F_{(3,12)}=57.26$ ,  $P<0.001$ ).



**Fig. 3** Mean gain of horizontal vergence for five subjects for frequencies of disparity modulation of 0.1 and 1.0 Hz. *Solid symbols* indicate gain as a function of the area of a central stimulus. *Hollow symbols* represent gain as a function of the area of an annular display 65° in outer diameter and of variable inner diameter. *Error bars* indicate standard errors of the mean

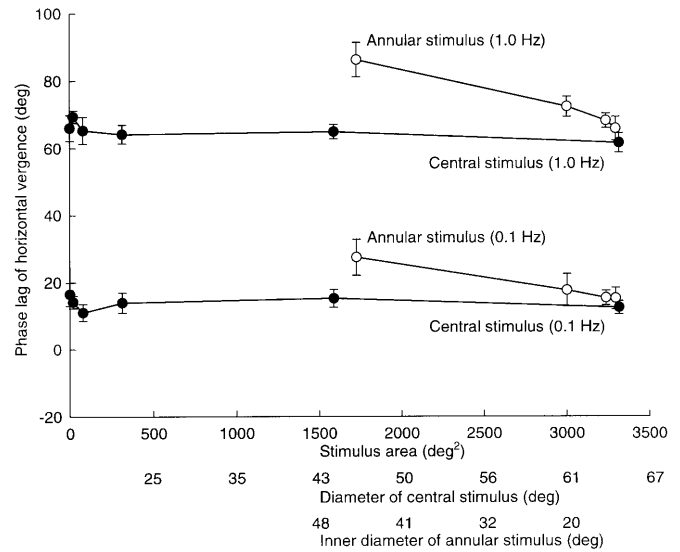
The mean phase lag of horizontal vergence for the five subjects as a function of the area of the annular display for the two stimulus frequencies is shown in Fig. 4. Repeated measures analysis of variance indicated a significant effect of central occlusion on the phase lag of horizontal vergence ( $F_{(3,12)}=16.33$ ,  $P<0.001$ ).

Comparison of the graphs for central and annular stimuli in Fig. 3 reveals the relative power of central and peripheral stimuli to evoke horizontal vergence. A 45° central disc and an annulus with 45° of central occlusion had approximately the same area. However, the central 45° stimulus evoked horizontal vergence with significantly higher gain than a stimulus with 45° of central occlusion (Tukey's HSD test,  $P<0.001$ ). This demonstrates that the central retina has more power to evoke horizontal vergence than the same area in the periphery.

The gain of horizontal vergence decreased and phase lag increased as the frequency of stimulus oscillation increased from 0.1 Hz to 1.0 Hz (Figs. 3, 4). At a stimulus frequency of 0.1 Hz, mean vergence gain was 0.97 and phase lag was 12.44°. This response cancelled most of the horizontal disparity in the stimulus. At a stimulus frequency of 1.0 Hz, mean vergence gain was only 0.66 and phase lag increased to 61.59°. Repeated measures analysis of variance indicated a significant effect of stimulus frequency on gain ( $F_{(1,4)}=1259.56$ ,  $P<0.001$ ) and phase lag ( $F_{(1,4)}=346.79$ ,  $P<0.001$ ).

### Vertical vergence

A sample record of vertical vergence of one subject is shown in Fig. 2b. Multivariate analysis of variance with



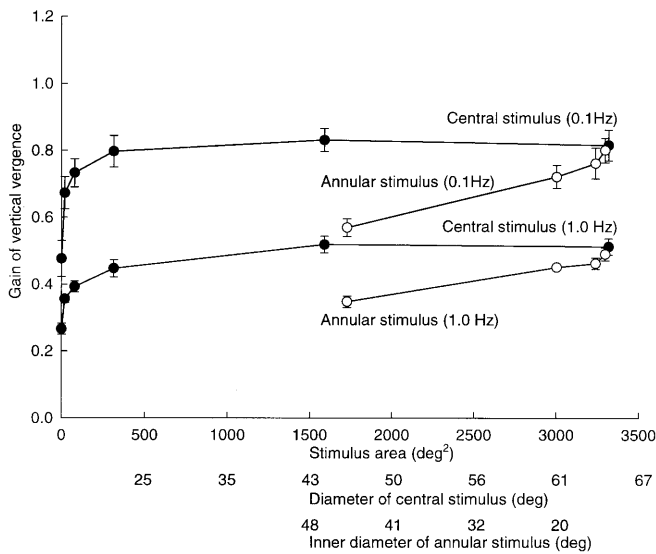
**Fig. 4** Mean phase lag of horizontal vergence for five subjects for frequencies of disparity modulation of 0.1 and 1.0 Hz. *Solid symbols* indicate phase lag as a function of the area of a central stimulus. *Hollow symbols* represent phase lag as a function of the area of an annular display 65° in outer diameter and of variable inner diameter. *Error bars* indicate standard errors of the mean

repeated measures indicated a significant effect of stimulus size ( $F_{(9,36)}=29.04$ ,  $P<0.001$ ) and stimulus frequency ( $F_{(1,4)}=82.85$ ,  $P<0.01$ ) on the gain of vertical vergence, and a significant effect of stimulus size ( $F_{(9,36)}=5.80$ ,  $P<0.001$ ) and stimulus frequency ( $F_{(1,4)}=393.04$ ,  $P<0.001$ ) on the phase lag of vertical vergence. No significant interaction between stimulus size and frequency existed for phase lag ( $F_{(9,36)}=0.69$ ,  $P>0.05$ ). A small but significant interaction between stimulus size and frequency existed for vergence gain ( $F_{(9,36)}=3.92$ ,  $P<0.01$ ). Although statistically significant, this interaction accounted for only 1% of the variance in the model.

The mean gain of vertical vergence for the five subjects as a function of the area of the central stimulus for the two stimulus frequencies is shown in Fig. 5. It is evident that the gain of vertical vergence increased as the area of the central stimulus increased to approximately 314 deg<sup>2</sup> (20° diameter).

Tukey's HSD test revealed a significant difference in gain between stimulus areas of 0.44 and 20 deg<sup>2</sup> (diameters 0.75° and 5°) ( $P<0.001$ ) and areas of 20 and 314 deg<sup>2</sup> (diameters 5° and 20°) ( $P<0.01$ ), but no significant change in gain above a stimulus area of 314 deg<sup>2</sup> ( $P>0.05$ ).

The mean phase lag of vertical vergence for the five subjects as a function of the area of the central stimulus for two stimulus frequencies is shown in Fig. 6. Phase lag decreased with the increasing area of the central stimulus for both stimulus frequencies. Tukey's HSD test revealed a significant difference in phase lag between stimulus areas of 0.44 and 20 deg<sup>2</sup> (diameters 0.75° and 5°) ( $P<0.05$ ) and areas of 0.44 and 314 deg<sup>2</sup> (diameters 0.75° and 20°) ( $P<0.001$ ), but no significant change in phase lag above a stimulus area of 314 deg<sup>2</sup> ( $P>0.05$ ).



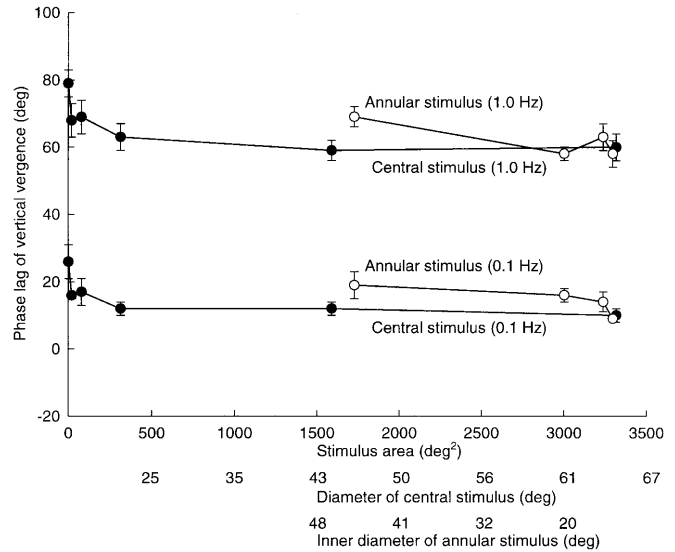
**Fig. 5** Mean gain of vertical vergence for five subjects for frequencies of disparity modulation of 0.1 and 1.0 Hz. *Solid symbols* indicate gain as a function of the area of a central stimulus. *Hollow symbols* represent gain as a function of the area of an annular display 65° in outer diameter and of variable inner diameter. *Error bars* indicate standard errors of the mean

The mean gain of vertical vergence for the five subjects as a function of the area of the annular display for two stimulus frequencies is shown in Fig. 5. Gain of vertical vergence increased with increasing area (decreasing diameter of central occlusion). Repeated measures analysis of variance indicated a significant effect of area on the gain of vertical vergence ( $F_{(3,12)}=24.60, P<0.001$ ).

The mean phase lag of vertical vergence for the five subjects as a function of the area of the annular display for two stimulus frequencies is shown in Fig. 6. Phase lag decreased with increasing area (decreasing diameter of central occlusion). Repeated measures analysis of variance indicated a significant effect of stimulus area on the phase lag of vertical vergence ( $F_{(3,12)}=6.25, P<0.01$ ).

Inspection of Fig. 5 reveals the relative power of central and peripheral stimuli to evoke vertical vergence. It is evident that the gain of vertical vergence evoked by a 45° central stimulus was significantly higher than that evoked by the stimulus with 45° of central occlusion, even though the two stimuli had approximately the same area (Tukey's HSD test,  $P<0.001$ ).

The gain of vertical vergence decreased and its phase lag increased as the frequency of stimulus oscillation increased from 0.1 to 1.0 Hz (Figs. 5, 6). For a 65° central stimulus oscillating at a frequency of 0.1 Hz, the mean gain of vertical vergence was 0.82 and phase lag was 10°. At a frequency of 1.0 Hz, vergence gain was only 0.52 and phase lag reached 60°. Repeated measures analysis of variance indicated a significant effect of stimulus frequency on the gain ( $F_{(1,4)}=82.85, P<0.01$ ) and phase lag ( $F_{(1,4)}=393.04, P<0.001$ ) of vertical vergence.



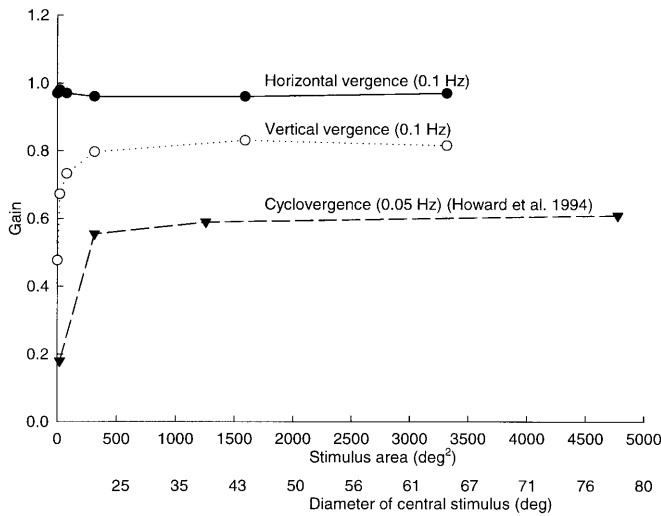
**Fig. 6** Mean phase lag of vertical vergence for five subjects for frequencies of disparity modulation of 0.1 and 1.0 Hz. *Solid symbols* indicate phase lag as a function of the area of a central stimulus. *Hollow symbols* represent phase lag as a function of the area of an annular display 65° in outer diameter and of variable inner diameter. *Error bars* indicate standard errors of the mean

## Discussion

### Stimulus integration areas

The gain of horizontal vergence evoked by a central stimulus 0.75° in diameter was nearly as large as that evoked by a stimulus 65° in diameter. Thus, the integration area for horizontal vergence in response to continuously varying disparity has a diameter less than 1°. The gain of vertical vergence increased with increasing area of the central stimulus up to approximately 314 deg<sup>2</sup> (diameter 20°). Thus, the integration area for vertical vergence tracking is much larger than that for horizontal vergence tracking. The gain of cyclovergence in response to a continuous change in cyclodisparity, obtained in an earlier study (Howard et al. 1994), showed a similar dependency on stimulus diameter to that shown for vertical vergence (see Fig. 7).

The smaller stimulus integration area for horizontal vergence compared with vertical vergence and cyclovergence can be explained in terms of the functions of the different types of vergence. Horizontal disparities vary over a range of about 14° as an object is moved from the near point to infinity. The largest disparity for the perception of depth has been found to be 7° for most observers (Westheimer and Tanzman 1956). For large disparities, monocular cues to depth probably evoke the initial vergence response. This response brings horizontal disparities in the region of interest to within the range of disparity detectors for both fine vergence control and registration of relative depth. Since horizontal disparity can change rapidly from one location to another, the visual system should be very sensitive to the horizontal



**Fig. 7** Mean gain of horizontal, vertical, and cyclovergence as a function of the area of a central stimulus. The cyclovergence record is from Howard et al. (1994)

disparity of a particular object in a particular location. Thus, the integration area for horizontal vergence should be very small and vergence tracking should be as precise for a dot as for a large stimulus. Our experimental results support this conclusion.

A vertical misalignment of the images in the two eyes is corrected by vertical vergence. A disparity signal derived from a large area is the best signal for this response. When the eyes are vertically aligned, vertical disparity does not change within the median or the horizon planes. In each quadrant of the visual field, vertical disparity increases with eccentricity and decreases with absolute distance (Howard and Rogers 1995), so that the eyes must change their vertical vergence as the gaze moves into an eccentric position. According to one estimate, a vertical vergence of about  $1.5^\circ$  is required to fixate a point  $24^\circ$  up and  $24^\circ$  to one side on a frontal plane at a distance of 33 cm (Ogle and Prangen 1953). However, the size of vertical disparities depends on the axis system used to measure them. Schor et al. (1994) found that when the gaze is directed to a target without error feedback, the visual axes intersect with an error of no more than  $0.25^\circ$  for any direction or distance of the target. This suggests that vergence movements are preprogrammed to take account of distance- and direction-dependent variations in horizontal and vertical disparity. However, a disparity signal derived from a fairly large area could be used for the parametric adjustment of vertical vergence over time. The range of vertical disparities over the visual field is only about  $\pm 1.5^\circ$ , which is probably within the range of disparity detectors. Local changes in vertical disparity produced by adjacent objects at different distances are not required for the perception of relative depth because they are necessarily accompanied by changes in horizontal disparity that adequately code relative depth. In other words, there is no necessity to respond to local changes in vertical disparity.

The gradient of vertical size disparity over a surface is used to indicate the orientation (Rogers and Bradshaw 1995) and absolute distance (Rogers and Bradshaw 1993) of surfaces. Local control of vertical vergence is not required for these purposes. One might expect that abrupt changes in vertical disparity arising from a surface seen through another surface would disturb the detection of gradients of vertical disparity in the surface upon which the eyes are horizontally converged. However, they would tend to fall outside the range of disparity detectors because they are necessarily accompanied by much larger changes in horizontal disparity.

Popple et al. (1997) found that magnitude of the initial vergence response reached a maximum at a disc diameter of about  $6^\circ$ . Thus, the integration area for the open-loop phase of disparity to a sudden change in disparity of a stimulus presented in an unchanging surround is about  $6^\circ$ . The integration area that we measured is for an isolated visual stimulus changing continuously in disparity. Further experiments are needed to determine whether the crucial difference between these two results is due to the continuous versus step change in disparity or to the presence of the stationary surround.

In our experiment, the gain and phase lag of horizontal vergence under feedback control were not affected by changes in the size of the central stimulus, at least for a vergence amplitude of  $0.5^\circ$ . For vertical vergence, mean gain increased and mean phase lag decreased as the size of the central stimulus increased to approximately  $20^\circ$ . For both horizontal and vertical vergences, gain decreased and phase lag increased with increasing occlusion of the central region of the stimulus. The gain of both horizontal and vertical vergence was significantly higher for a  $45^\circ$  central stimulus than for a peripheral stimulus of the same area. At a frequency of 0.1 Hz, vergence gains were higher and phase lags smaller than at 1.0 Hz, which is consistent with previous results (Howard et al. 1997).

#### The effects of stimulus position

The second issue we addressed is whether horizontal and vertical vergences are evoked more effectively by a central stimulus than by a peripheral stimulus. The results indicate that disparities in the central region of the retina are more effective in evoking horizontal and vertical vergences than are disparities in the periphery. The evidence provided by Stevenson et al. (1999) suggests that the decrease in the effectiveness of stimuli for vergence with increasing eccentricity can be explained by the increase in the mean size of the receptive fields of cortical cells (the cortical magnification factor) (Levi et al. 1985). Our stimulus was M-scaled but central stimuli still produced vergence with greater gain. Stevenson et al. varied the size of the random-dot display. However, the crucial factor may not be the mean size and spacing of texture elements or the size of the display but rather the presence of high-spatial frequency components at the border of each

texture element. The increase in receptive-field size with increasing eccentricity entails a progressive loss of sensitivity to high spatial frequencies. This loss is accompanied by an increase in the size of Panum's fusional area (Palmer 1961; Mitchell 1966). It is reasonable to assume that vergence is initiated when disparity reaches a fixed fraction of the mean size of Panum's fusion area in the region of the stimulus. If this is so, the peripheral retina should tolerate larger disparities within Panum's fusional area without triggering vergence than does the central retina (Howard and Rogers 1995). According to this view, the peripheral retina should be as effective as the fovea in driving vergence for stimuli totally lacking high spatial-frequency components, but the relevant experiment has not been done.

The higher gain of horizontal and vertical vergence for stimuli presented in the central retina is functionally advantageous. One of the purposes of vergence is to place the images of objects of interest on corresponding regions of the retinas. Since the central region of the retina is the one most involved in object recognition, information striking the central retina should be processed preferentially and images of objects falling on this region should be kept in correspondence. The advantage of the central retina is that it allows the eyes to locate an object of interest in the visual field more precisely and to keep vergence errors as small as possible. Therefore, one would expect that the horizontal and vertical vergence systems would be most effectively evoked by central stimuli. Inspection of Figs. 3 and 5 shows that the gains of horizontal and vertical vergence decline in a similar way as the diameter of the centrally occluded region is increased.

The information provided by horizontal disparities differs from that provided by vertical disparities (Howard and Rogers 1995). Vertical-displacement disparity evokes vertical vergence but has no effect on perceived depth. The ratio of overall vertical-size disparity to horizontal-size disparity can be used to compensate for the effects of magnification of the image in one eye (aniseikonia). Horizontal gradients of vertical-size disparity (vertical-shear disparity) can be used for judgments of the absolute distance and curvature of large frontal surfaces (Rogers and Bradshaw 1993, 1995). The ratio of vertical-shear disparity to horizontal-shear disparity could be used to compensate for misperception of inclination due to rotational misalignment of the eyes. All these uses require vertical disparities derived from a relatively large area. Therefore, there is no need for the visual system to detect local variations in vertical disparity. The integration area for vertical disparity should be much larger than that for horizontal disparity, both for the control of vergence and for stereopsis.

Psychophysical evidence supports the idea that vertical disparities used for stereopsis are processed over a larger area than horizontal disparities. Horizontal-size disparity causes both large and small textured surfaces to appear slanted about a vertical axis and horizontal-shear disparity causes them to appear inclined about a horizon-

tal axis (Ogle 1938; Westheimer 1978; Kaneko and Howard 1996). However, vertical-size disparity creates slant (the induced effect) only for surfaces more than about  $10^\circ$  in diameter (Westheimer 1978; Kaneko and Howard 1996) and vertical-shear disparity creates inclination only in large stimuli (Gillam and Rogers 1991; Howard and Kaneko 1994). For large stimuli, vertical disparities induce less slant or inclination than horizontal disparities. Differential effects of vergence and perspective seem to be responsible for these differences in large stimuli (Banks and Backus 1998).

Cyclovergence is evoked just as effectively by a far peripheral stimulus as by a large central stimulus. Unlike horizontal and vertical vergences, the gain of cyclovergence was not reduced when the central  $40^\circ$  of a  $75^\circ$  stimulus was occluded. Like vertical vergence, cyclovergence requires a large stimulus but it does not have to be in the centre of the visual field to give the highest gain (Howard et al. 1994). For a cyclodisparity of a given size, linear disparity increases linearly with increasing distance from the fovea. Thus the disparity signal is stronger in the periphery than in the centre, which presumably explains why the gain of cyclovergence was not reduced when the central  $40^\circ$  of a  $75^\circ$  display was occluded. Cyclodisparity occurs when the image in one eye is rotated with respect to the image in the other eye. Normally, this occurs only as a result of cyclophoria. The response is evoked by the component of vertical-shear disparity rather than that of horizontal-shear disparity because only the former component is uniquely produced by cyclophoria (Rogers and Howard 1991). Cyclodisparity evokes compensatory cyclovergence, which in turn tends to eliminate the cyclodisparity. Since local cyclodisparities do not occur, the integration area for cyclodisparity should be large (Howard et al. 1994).

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