Exp Brain Res (2004) 156: 305–313
DOI 10.1007/s00221-003-1790-0

RESEARCH ARTICLES

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The stimulus integration area for horizontal vergence

Received: 24 May 2003 / Accepted: 17 November 2003 / Published online: 18 February 2004

Abstract Over what region of space are horizontal disparities integrated to form the stimulus for vergence? The vergence system might be expected to respond to disparities within a small area of interest to bring them into the range of precise stereoscopic processing. However, the literature suggests that disparities are integrated over a fairly large parafoveal area. We report the results of six experiments designed to explore the spatial characteristics of the stimulus for vergence. Binocular eye movements were recorded using magnetic search coils. Each dichoptic display consisted of a central target stimulus that the subject attempted to fuse, and a competing stimulus with conflicting disparity. In some conditions the target was stationary, providing a fixation stimulus. In other conditions, the disparity of the target changed to provide a vergence-tracking stimulus. The target and competing stimulus were combined in a variety of conditions including those in which (1) a transparent textured-disc target was superimposed on a competing textured background, (2) a textured-disc target filled the centre of a competing annular background, and (3) a small target was presented within the centre of a competing annular background of various inner diameters. In some conditions the target and competing stimulus were separated in stereoscopic depth. The results are consistent with a disparity integration area with a diameter of about 5°. Stimuli beyond this integration area can drive vergence in their own right, but they do not appear to be summed or averaged with a central stimulus to form a combined disparity signal. A competing stimulus had less effect on vergence when separated from the target by a disparity pedestal. As a result, we propose that it may be more useful to think in terms of an integration *volume* for vergence rather than a two-dimensional retinal integration *area*.

Keywords Vergence · Binocular disparity · Binocular vision · Stereoscopic vision

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Introduction

In vision, as an object is moved from the near point to infinity, horizontal disparities vary over a range of about 14° (Howard and Rogers 2002). Local horizontal disparities are used to code relative depth. Since horizontal disparity can change rapidly from one location to another, the visual system should be very sensitive to local variations in disparity in the area of interest. Locally evoked horizontal vergence is therefore required to fuse the images of an object of interest and bring local disparities into the range of precise stereopsis. Horizontal vergence must respond to disparity in a selected object even in the presence of neighbouring objects with different disparities. By this reasoning, the integration area for disparity signals driving horizontal vergence should be very small, which means that vergence should be as precise for a dot as for a large stimulus. However, other factors suggest that, under some conditions, disparities driving horizontal vergence are integrated over a certain area. Mallot et al. (1996) have shown that the vergence system responds preferentially to stronger signals when signal strength is defined by stimulus density or contrast. The strength of a visual signal could also be affected by its spatial extent. Pooling disparity over an extended retinal area would provide a more robust vergence signal relative to disparity noise.

Increased vergence response with increasing stimulus size would indicate spatial integration. For vertical and cyclovergence, vergence response increases with stimulus size over a fairly large range (Howard and Zacher 1991; Howard et al. 1994, 2000). However, for horizontal vergence, Howard et al. (2000) showed that even an isolated 0.75°-diameter central stimulus could evoke vergence tracking with a gain of 1. An extrafoveal stimulus initiated vergence with a gain that depended on its area and eccentricity (see also Francis and Owens 1983; Hampton and Kertesz 1983; Hung et al. 1991). While vergence is not saturated, an increase in vergence gain with stimulus area is an indication of spatial integration. However, since vergence is a closed-loop response, once gain approaches unity we expect no increase in gain with a 'stronger' stimulus. With isolated horizontal vergence stimuli this occurs for small stimuli, leaving no room for an effect of stimulus size to show itself.

Another indication of spatial integration is the influence of surrounding stimuli on the vergence response to a target. Several investigators have enquired whether vergence in response to a central target is affected by superimposed or neighbouring stimuli. For example, Winkelman (1951, 1953) found that disparate images presented suddenly in the parafoveal region induced temporary diplopia in a small centrally fixated object.

Stevenson et al. (1997) studied the ability of subjects to maintain binocular fixation on a stationary, central spot superimposed on a textured background undergoing continuous changes in vertical and horizontal disparity. Horizontal vergence induced by the background was small when subjects tried to fixate the stationary spot but it had a gain of about 0.85 when they attended to the background. In a later study, Stevenson et al. (1999) measured the stability of vergence on a stationary central point as a function of the eccentricity and size of a random-dot patch with changing disparity. The smallest patch that had any effect increased with eccentricity, in much the same way that the mean size of receptive fields of cortical cells increases with eccentricity (the cortical magnification factor). A large patch induced weak vergence even when there was a 7° gap between spot and patch. These studies demonstrate that vergence is driven by disparities pooled over a certain area with a pronounced effect of attention and a bias for central stimuli. However, stimuli beyond a certain eccentricity are not combined with central stimuli to form a stimulus for vergence.

Popple et al. (1998) used a flashed nonius procedure to measure the initial vergence response to a 12.5-arcmin step change in disparity of the central region of a random-dot stereogram. The magnitude of the response increased with increasing size of the disparate region and reached a maximum with a diameter of about 6°. The diminished response with smaller disparate regions was presumably due to averaging of the target disparity with the unchanging disparity in the surround. By this criterion, disparities in the central retina are pooled over an area subtending 6°.

We thus have two criteria for specifying the area over which disparities are pooled for driving horizontal vergence. By the criterion of the smallest isolated stimulus required to produce a gain near unity, the area subtends less than 1°. By the criterion of the area over which competing disparity signals are pooled, the area subtends about 6°.

In all previous experiments, the target stimulus and the competing stimuli fluctuated about the same mean disparity. There is evidence that the stimulus for vergence is derived from the mean disparity in a given region. Mallot et al. (1996) presented planes of dots 18 arcmin in front of and beyond a prefixation target for 230 ms. The vergence response, measured by a flashed nonius method, was determined by a weighted mean of the disparities in the two planes, with greater weight given to the plane containing more dots or higher contrast dots. However, the authors did not study the range of disparities over which this averaging occurs. Jones and Stephens (1989) found that peripheral stimuli increased the horizontal fusional range for a central target, but only when the disparity between target and peripheral lines was less than about 0.5°. In this paper we, also, find that the interference effect of a competing stimulus falls off rapidly with relative disparity between it and the target.

Vertical disparity in a textured background prevents people from vertically fusing the images of a central horizontal line (Burian 1939). Allison et al. (2000) showed that a textured background ceased to have any effect on the ability of subjects to vertically fuse a central stimulus when the horizontal disparity of the background was increased to 6°. The effectiveness of a stimulus with a given vertical disparity to evoke vergence depends on its horizontal disparity. Yang et al. (2003) found that the initial 150-ms open-loop component of vertical vergence to a 2° step of vertical disparity in a random-dot display fell to zero when the horizontal disparity of the dots was increased to about 4°. We can thus say that vertical disparity signals are averaged over an area and over a certain range of horizontal disparity.

In the present study, we ask whether the ability of subjects to remain converged on a central target depends on the mean horizontal disparity of the target relative to that of the background. We measured the effects of three variables: (1) whether the horizontal disparity of the surround was modulated while that of the central target remained constant, or the disparity of the target was modulated while that of the surround remained constant; (2) whether the target and the background stimulus were superimposed, adjacent, or separated by a blank area; (3) whether the target and background had a mean disparity of zero or the background had a pedestal disparity of plus or minus 1° and 2°. The aim of this pedestal disparity manipulation was to discover whether disparity signals for driving vergence are integrated over a volume rather than just over an area.

Materials and methods

Subjects

Three subjects, ranging in age from 27 to 35 years, participated in this study. One subject was naïve to the purposes of the studies and one subject was one of the authors. All subjects had normal stereoscopic vision. One subject was myopic and wore his glasses during the experiments. 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 prior to inclusion in the study.

Eye movement monitoring

Eye movements were measured by the scleral search-coil technique (Robinson 1963) using equipment made by CNC Engineering (Seattle, WA, USA). A search coil (Skalar Medical, Delft, The Netherlands) was placed on each eye after application of a drop of anaesthetic. Each subject sat with the head supported on a bite at the centre of the magnetic field coils contained in a cubic frame one meter along each side. The root-mean-square noise in the eye-monitoring system was of the order of 0.01°.

Visual display

Each dichoptic display consisted of a central target stimulus that the subject attempted to fuse, combined with a larger display with competing disparity. Examples of the target and competing stimuli are shown in Fig. 1.

The target and competing stimuli consisted of randomly distributed white texture elements (squares, plus signs, lines, and circles) displayed on a black background. The diameter of the stimulus elements increased linearly from 0.4° at the centre to 3° at an eccentricity of 32.5°. Their density decreased proportionately. This scaling compensated for the decrease in visual acuity with increasing eccentricity (Anstis 1974). A horizontal line was projected across the centre of the whole 65° display area. It provided no horizontal disparity and helped subjects maintain zero vertical vergence and cyclovergence.

The target consisted of a single texture element subtending 0.75° or a textured disc subtending 5, 10, 20, 45 or 65° (the full-field condition). Each target had a 0.75°-diameter central texture element that bisected the horizontal line. When the target was stationary, this intersection provided a fixation target. When the target changed disparity, the intersection provided a vergence-tracking target. This comprised the stimulus for the 0.75°-diameter target; additional texture elements were added for the larger targets.

The competing display was a 65° full-field disc or an annulus with an outer diameter of 65° and a black centre with diameter 5°, 10°, 20° or 45°. The target and competing stimuli were combined in the following ways: (1) the target was superimposed upon the full competing textured disk, (2) the target just filled the centre of a competing annulus, and (3) the 0.75°-diameter target was placed at the centre of the blank area of a competing annulus. In all cases, care was taken to ensure that the elements of the target stimulus and the background did not overlap over the range of disparities tested. The texture elements of the target differed in shape from the texture

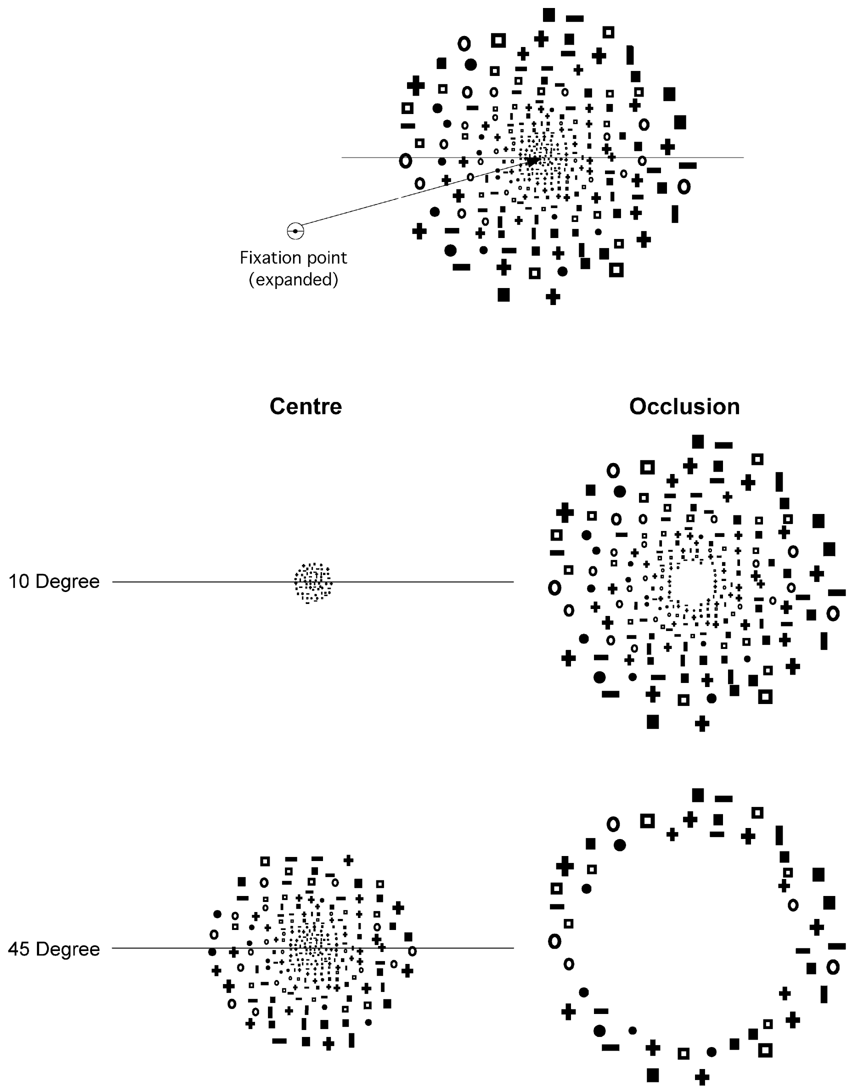

Fig. 1 Subset of stimulus patterns used in these experiments. Pairs of these dichoptic images were presented on each trial: one a target fixation/tracking stimulus the other as a competing interference stimulus. The *top* pattern illustrates the full-field background stimulus. The *bottom* four patterns show central disc targets (*left side*) and annular surrounds (*right side*) for 10°- and 45°-diameter discs or annuli

elements of the competing background to prevent their images being mismatched.

The stimuli were computer-generated and prepared as slides. One pair of projectors held the left- and right-eye slides for the target, and a second pair of projectors held the slides for the competing stimulus. For each eye, the images for the two stimuli were combined by a beam splitter and rear-projected onto a screen. The two screens were mounted on opposite sides of the frame containing the field coils. Fiducial marks in the projected images were accurately superimposed on reference marks on the screens, outside the area visible to the subject. The subject viewed the images through mirrors set at ±45° to the frontal plane so that the fused image appeared in the frontal plane 57 cm directly ahead of the subject. The average luminance of the stimulus after reflection off the mirror was about 0.5 cd/m^2. The area surrounding the stimulus was matt-black so that only the fused textured stimulus was visible.

We used an optically produced display since it has higher resolution than a computer-generated display. Also, mechanical movement of the slides provided a smoother and more rapid movement than could be achieved in a computer-generated display. Identical left and right images were made into 35-mm slides. Each one was mounted in a custom slide-holder, which could be oscillated sinusoidally left and right by an eccentric movement. The two slides were driven by the same servomotor so that the two images oscillated in counterphase at a frequency determined by the speed of the motor with accurate control of phase. A microswitch on the motor shaft indicated the start of each cycle and allowed calibration of the oscillation frequency. The amplitude of oscillation was controlled by a micrometer that allowed the image movement to be set with a resolution of 1 min arc. Since the two images oscillated symmetrically in counterphase, the peak disparity was twice the individual peak image displacement.

Procedure

Subjects were seated with their heads supported on a bitebar at the centre of the magnetic field coils. In some conditions, the slides for the target were stationary while those for the competing stimulus oscillated in antiphase from side to side. In other conditions the slides for the competing stimuli were stationary while those for the target oscillated.

The images of the stationary competing stimulus were set at zero screen disparity or with a fixed pedestal disparity of ±1° or ±2°. When the disparity of the competing stimulus was modulated, the images were set at an initial disparity of zero or a pedestal disparity of ±1° or ±2°. During the trial, a servomotor oscillated the slides in antiphase around the pedestal disparity through a peak-to-peak amplitude of 0.5° at 0.1 Hz.

The eye-movement system was calibrated using data obtained while subjects fixated targets at defined eccentricities. During each trial, subjects fixated on the central element of the target stimulus. The display was presented for 60 s. Each condition was repeated twice for each subject in a counter-balanced manner.

Data analysis

The eye-position signals and a reference signal that indicated the peak of each stimulus oscillation were recorded on a digital tape and later sampled by a 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. A computer program was used to fit the vergence record to a sinusoid by the method of least squares. The 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. The peak amplitude of response for each sinusoidal oscillation of the stimulus was measured and the peak vergence values within each condition were 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.

Results

Experiment 1: vergence tracking as a function of the diameter of a central target superimposed on a stationary 65° background

This experiment was designed to investigate whether a stationary competing background affects the horizontal vergence response to a central target oscillating in depth through a peak-to-peak amplitude of 0.5° at 0.1 Hz. The target was 0.75°, 5°, 10°, 20°, or 45° in diameter and was superimposed on a stationary 65°-diameter background. Subjects were instructed to track the changing disparity of the target while eye movements were recorded. The percept was of two transparent planes, one moving in depth through the other. An example of the eye-movement records is shown in Fig. 2.

Figure 3 shows the mean gains of horizontal vergence for three subjects as a function of the diameter of the disparity-modulated central target. A 0.75°-diameter target failed to evoke full-gain vergence in the presence of the stationary background. Gain increased as the diameter of the target increased from 0.75° to 5°. Gain was just below unity and remained constant as the diameter of the central target increased from 5° to 45° for two subjects (JZ and XF). For one subject (EK), the gain for a 10°-target was lower than the gains for a target with diameter of 5°, 20° or 45°.

It seems that vergence tracking of a small stimulus is degraded by the presence of a unchanging background stimulus. Repeated measures analysis of variance indicated a significant effect of the diameter of the target on

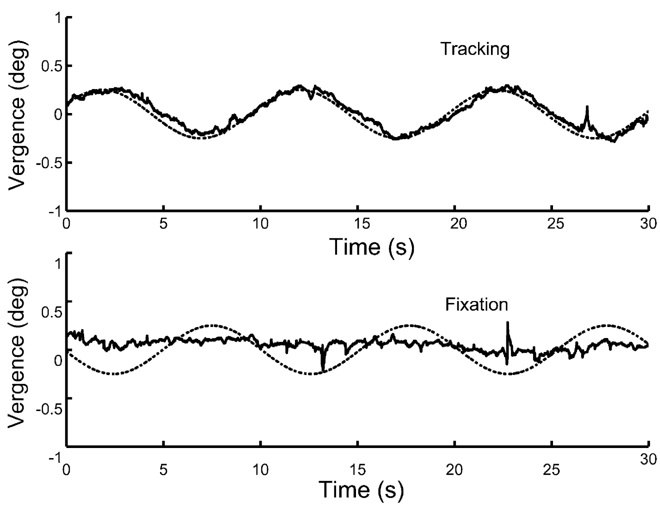

Fig. 2 Example typical vergence data during tracking of a central target superimposed upon a static background (*top*) and fixation of a stationary target while the background changed disparity (*bottom*). In both cases, the background was a 65° textured disc and the target subtended 0.75°. *Solid lines* show the recorded vergence data and *dotted lines* show the changing disparity signal

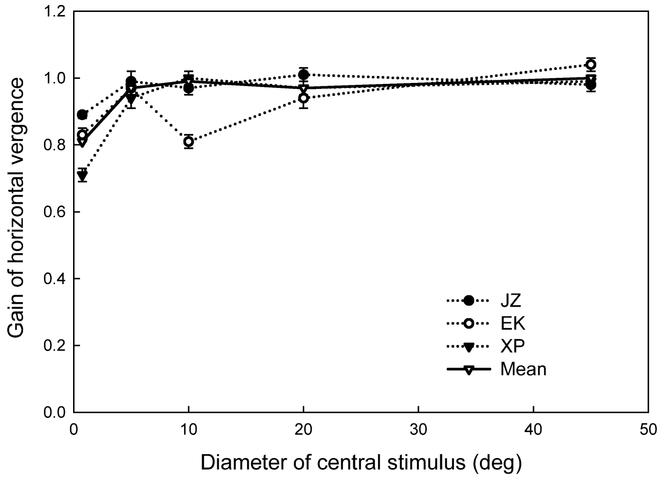

Fig. 3 Results of experiment 1. The gain of vergence as a function of the diameter of a disparity-modulated central stimulus superimposed upon a 65° static background. An outlying point has been excluded from the mean at 10° eccentricity. Data shown are for each subject together with the mean across subjects; *error bars* for each subject indicate ±SEM

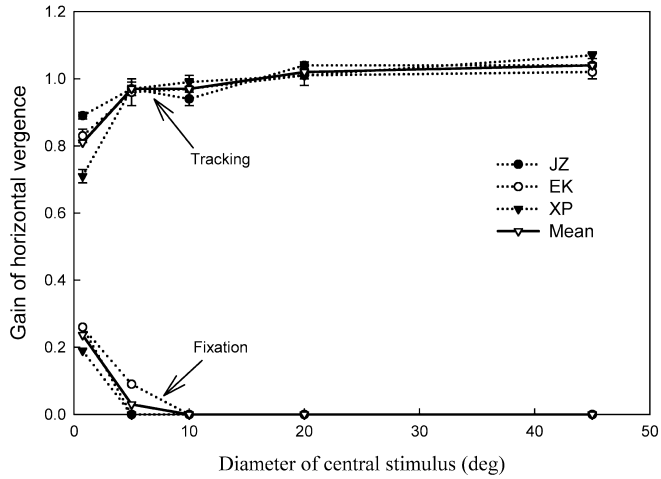

Fig. 4 Results of experiments 2 and 3. *Upper curves* show the gain of vergence as a function of the diameter of a disparity-modulated central stimulus set in a static 65° annulus. *Lower curves* show the gain of induced vergence during fixation of a static central stimulus set in a disparity-modulated 65° annulus. In both cases, the inner diameter of the annulus was matched to the outer diameter of the central stimulus. Data shown are for each subject together with the mean across subjects; *error bars* for each subject indicate ±SEM

the gain of vergence ($F_{(4,8)}$=3.97, p<0.05). Tukey's HSD test revealed a significant difference in gain between target diameters of 0.75° and 5° (p<0.01), 0.75° and 10° (p<0.05), 0.75° and 20° (p<0.01), and 0.75° and 45° (p<0.01), but no significant difference in gain between stimuli diameters of 5°, 10°, 20°, or 45°. Thus, disparity signals from the changing central target and from the unchanging background are integrated over an area of around 5° to 10°. Popple et al. (1998) obtained a similar estimate of integration area defined by this criterion.

Experiment 2: vergence tracking as a function of the diameter of a central target filling a stationary annulus

In this experiment, we measured the gain of horizontal vergence evoked by the changing disparity of a target that filled the centre of a stationary competing annulus with an outer diameter of 65°. The diameter of the target was 0.75°, 5°, 10°, 20° or 45°. Subjects were instructed to track the motion in depth of the central element in the target while eye movements were recorded.

Figure 4 shows the mean results for the three subjects. A 0.75°-diameter target failed to evoke full-gain vergence in the presence of a stationary background. Gain increased as the diameter of the target increased from 0.75° to 5°. Gain remained about 1 as the diameter of the target increased from 5° to 45°. Repeated measures analysis of variance indicated a significant effect of the diameter of the target on the gain of horizontal vergence ($F_{(4,8)}$=15.88, p<0.01). Tukey's HSD test revealed a significant difference in gain between target stimuli with diameters of 0.75° and 5° (p<0.01), 0.75° and 10° (p<0.01), 0.75° and 20° (p<0.01), 0.75° and 45° (p<0.01), and 5° and 45° (p<0.05), but no significant difference in gain between stimuli with diameters of 10°, 20° or 45°.

Experiment 3: vergence induced by changing disparity in an annulus while subjects attempted to fixate a stationary target, as a function of the diameter of the target

In this experiment, we measured the gain of vergence induced by the changing disparity of an annulus with an outer diameter of 65°, while subjects attempted to fixate a stationary central target that filled the centre of the annulus. The diameter of the stationary target was 0.75°, 5°, 10°, 20° or 45°. Subjects were instructed to fixate the centre of the stationary target and ignore the motion in depth of the annular background while eye movements were recorded.

For all subjects, the changing disparity of the annular background induced vergence when the subjects attempted to fixate the static 0.75-diameter stationary target. The mean gain of induced vergence was 0.24. For one subject, the annulus induced vergence with the 5°-diameter target. However, there was no induced vergence for any subject when the diameter of the target was between 10° and 45°. Vergence induced by the oscillating annulus while subjects attempted to fixate the central target was much smaller than that produced when subjects tracked the changing disparity of the target in experiment 2.

Experiment 4: vergence tracking of a 0.75°-diameter target set in a stationary annulus, as a function of the inner diameter of the annulus

The object of this experiment was to measure how far a competing stimulus had to be from a small central target before it ceased to affect vergence tracking of the target. A central 0.75°-diameter target with changing disparity was

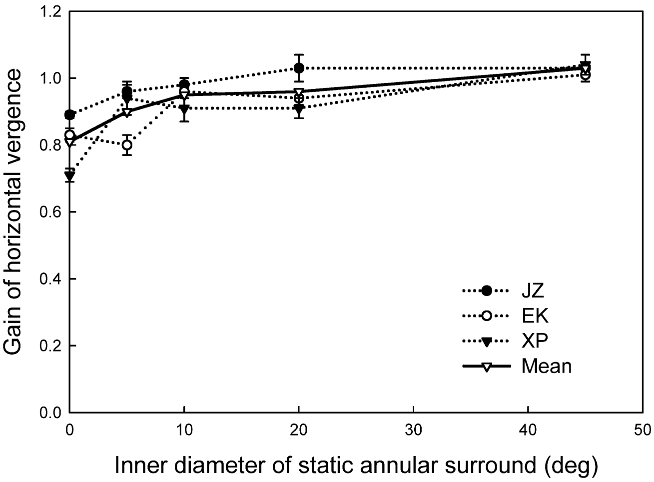

Fig. 5 Results of experiment 4. The vergence stimulus was a disparity-modulated central, 0.75°-target superimposed upon a static annulus of 65°outer diameter. The plot shows the gain of vergence as a function of the inner diameter of the annulus. Data shown are for each subject together with the mean across subjects; *error bars* for each subject indicate ±SEM

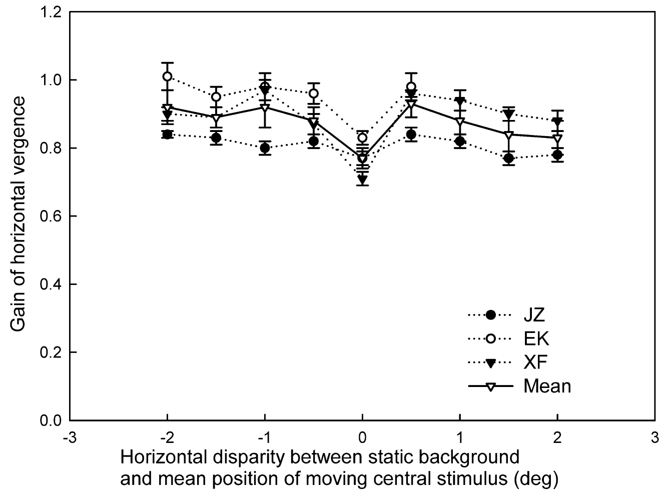

Fig. 6 Results of experiment 5. The gain of vergence as a function of the relative disparity between a disparity-modulated central stimulus and the 65° static background, upon which it was superimposed. Data are missing for subject EK at disparities greater than +1.0° because the subject could not fuse the stimuli. Data shown are for each subject together with the mean across subjects; *error bars* for each subject indicate ±SEM

set at the centre of a stationary annular background. The background had an outer diameter of 65° and an inner diameter of 0°, 5°, 10°, 20°, or 45°. Subjects were instructed to track the motion in depth of the target while their eye movements were recorded.

Figure 5 shows the mean gain of vergence for three subjects. When the stationary stimulus was a full background, the 0.75°-diameter target failed to evoke full-gain vergence, which means that the background interfered with the changing disparity of the target. When the inner diameter of the annulus was 5°, the interference effect was diminished for two subjects (JZ and XF), but remained strong for one subject (EK). When the inner diameter of the annulus was 10° or larger, the gain evoked by the 0.75°-diameter target was near unity for all subjects, which means that the annular background had no effect on vergence tracking. Repeated measures analysis of variance indicated a significant effect of increasing the inner diameter of the annular background on the gain of horizontal vergence ($F_{(4,8)}$=6.98, p<0.05). Tukey's HSD test revealed a significant difference in gain between the full-background and the 10°-annulus (p<0.05), the full background and the 20°-annulus (p<0.01), the full background and the 45° annulus (p<0.01), but no significant difference in gain between the full background and the 5° annulus.

Experiment 5: vergence tracking of a 0.75°-diameter target superimposed on a stationary 65°-diameter background, as a function of the pedestal disparity of the background

In this experiment, we measured vergence in response to changing disparity of a 0.75°-diameter central vertical line superimposed on a stationary 65°-diameter textured background with various horizontal pedestal disparities. This experiment was designed to measure the depth range of horizontal disparities that are integrated to drive horizontal vergence. The background had a pedestal disparity of 0°, ±0.5°, ±1.0°, ±1.5° or ±2.0°. Subjects were instructed to track the motion in depth of the central target while their eye movements were recorded.

Figure 6 shows the mean gains of vergence for the three subjects. The extent to which the stationary background reduced the gain of vergence tracking of the 0.75°-diameter target depended on the depth plane of the background. The interference effect of the background was less when the background was either nearer than, or beyond, the target. One exception was for subject JZ when the target was beyond the background with large relative horizontal disparities. We believe this is due to the difficulty fusing the small target when it lay beyond the textured background. For example, one subject (EK) could not fuse the target at all when the background was nearer than the target with a relative disparity of 1° or more.

Repeated measures analysis of variance indicated a significant effect of the relative horizontal disparity pedestal on the gain of horizontal vergence ($F_{(5,10)}$=6.14, p<0.01). Tukey's HSD test revealed a significant difference in gain between the coplanar background and the background with −2° horizontal disparity (p<0.05), the coplanar background and the background with −1° horizontal disparity (p<0.05), and the coplanar background and the background with +0.5° horizontal disparity (p<0.05).

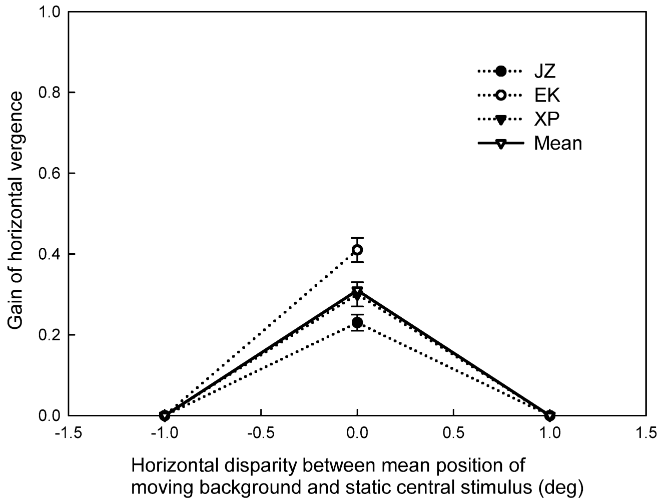

Fig. 7 Results of experiment 6. The mean gain of vergence induced by disparity modulation of a 65° background as a function of the relative disparity between the background and a static, central fixation stimulus. Data are missing for subject EK at +1.0° disparity because the subject could not fuse the stimulus. Data shown are for each subject together with the mean across subjects; *error bars* for each subject indicate ±SEM

Experiment 6: vergence induced by changing disparity in a full background while subjects attempted to fixate a stationary target, as a function of the pedestal disparity of the background

In this experiment, we measured the gain of vergence induced by the changing disparity of a 65°-diameter background while subjects attempted to fixate a 0.75°-diameter stationary target superimposed on the background. The disparity of the background was modulated sinusoidally at 0.1 Hz through a peak-to-peak amplitude of 0.5° about a pedestal disparity of 0°, +1°, or −1° relative to the fixation stimulus. The background contained a central fixation cross that coincided with the target when the stimuli were coplanar. Subjects were instructed to fixate the stationary target and ignore any motion in depth of the background while their eye movements were recorded.

Figure 7 shows the mean gain of vergence induced by disparity modulation of the background as a function of the pedestal disparity of the background. The moving background induced vergence only when it had zero pedestal disparity, that is, when it appeared to pass through the depth plane of the fixation target. Stevenson et al. (1997) obtained induced vergence under these conditions. There was no measurable induced vergence when the pedestal disparity placed the background either in front of or beyond the fixation target. However, subject (EK) could not fuse the fixation target when the pedestal disparity placed the background nearer than the target.

Discussion

Integration areas versus response saturation

The magnitude of horizontal disparity increases with the depth of the object from the horopter. Thus, horizontal disparity indicates relative depth between objects but not distance from the observer. When the eyes are converged on an object, the volume of space around that object may contain objects with a wide variety of horizontal disparities. For the most precise detection of relative disparities in the region of interest, one needs to be able to converge on one object and ignore vergence signals arising from neighbouring objects. This means that horizontal vergence must be controlled by disparities in a selected local region.

Popple et al. (1998) measured the initial change in vergence induced by a step change in disparity of the central area of a random-dot stereogram, while the remainder of the stereogram had a competing constant disparity. They concluded from their results that disparities driving the initial open-loop component of vergence are integrated over texture elements in a central 6°-diameter region of the retina. We used a similar stimulus arrangement in experiment 2. The subject attempted to remain converged on a central disc with modulating disparity, while the disparity of the surround remained constant. The surround reduced the gain of vergence tracking for discs up to a diameter of 5°. Beyond a diameter of 5°, we observed no significant effect of the surround. These results are in substantial agreement with those of Popple and colleagues. We conclude that the differences between Popple et al. (1998) and Howard et al. (2000) were due to the presence of the stationary surround in the former experiments and response saturation in the latter.

Although a small stimulus can evoke vergence with a gain of 1, vergence gain is reduced when there are objects with different disparities within the 6°-diameter integration area. This local pooling of disparities for driving vergence is probably an advantage because it brings the point of binocular fixation to a position of mean disparity. This optimises the working range of the stereoscopic system. We are more sensitive to a relative disparity between two objects when the absolute disparities are minimal (Badcock and Schor 1985).

In contrast, at a given vergence, pooling disparities over a diameter of 6° for use in stereoscopic processing would be a disadvantage. Thus, we would expect more restricted spatial integration for stereopsis than for vergence. The finding that a depth interval between two vertical lines can be detected most easily when the lines are only about 2 arcmin apart confirms this expectation (Westheimer and McKee 1980; Kumar and Glaser 1995). The minimum separation for stereopsis is similar to the limit of resolution.

In experiment 2, the central vergence stimulus increased in area while the annular surround decreased in area. The change in vergence could therefore have been due to either an increase in the area of the central stimulus or to a decrease in the area of the surrounding stimulus. In experiment 4, the size of the central target was constant. The increase in vergence gain as the distance between the central target and the annulus increased to 5° can therefore be attributed to the increasing distance between the central stimulus and the surround. The decrease in the area of the surround could not have been the crucial factor because Howard et al. (2000) showed that a 65°-diameter display evokes vergence with a gain of near unity when the central 10° is occluded. Clearly, stimuli beyond an eccentricity of 5° can drive vergence in their own right but they are not combined with central stimuli. Experiment 1 was the complementary case. The stationary background was a constant 65°-diameter display while the central disparity-modulated target varied in size. Here, vergence gain saturated when the diameter of the target reached 5°. Thus, these three different measures, combined with the results of Popple et al. (1998), suggest that vergence signals are averaged over an area 5° in diameter. There were hints of small differences between the conditions but a detailed investigation of these differences would require the use of occlusions of between 0 and 10°.

Initial versus transient vergence

Disparity-induced vergence serves a number of purposes including holding binocular fixation on a target; tracking a target moving in depth, changing fixation between targets at different disparities, and providing feedback for adaptation of phoria, disjunctive saccades and accommodative–vergence interactions. Given the varied roles of vergence, it is not surprising that it is context-dependent. For example, there is considerable evidence for separate sustained and transient vergence systems. The transient mechanism initiates vergence whereas the sustained mechanism acts as a ‘fusion lock’ to hold binocular fixation on the target. Robust transient vergence is elicited by dichoptic stimuli that differ widely in orientation, contrast, spatial frequency and luminance polarity (Edwards et al. 1998; Pope et al. 1999; Sato et al. 2001). Vergence is sustained only by stimuli that have relatively similar features. Edwards et al. (1998) proposed a model of the transient vergence system based upon a single spatial-frequency channel with relatively low-frequency peak sensitivity (between 0 and 1 cycles per degree). This suggests that stimuli evoking transient vergence are coarser than those used by the fusion-lock mechanism. We studied steady-state vergence to modest amplitude oscillations of disparity between similar images, which presumably activated mainly the fusion-lock mechanism. Nevertheless, our estimates of retinal integration area match well with the 6° estimate made by Popple et al. (1998) for transient initial vergence.

Tracking versus suppression

In experiment 3, we found that the gain of vergence induced by disparity-oscillation of the background was small compared with that found when subjects tracked the central stimulus in the presence of a stationary surround (experiment 2). The extent to which a modulated background induced vergence with a 0.75°-diameter stationary target was approximately equal to the extent to which a stationary background reduced the gain of vergence pursuit of a disparity modulated target. We found little evidence for a difference in the spatial integration area between the fixation and tracking conditions. Stevenson et al. (1997), also, found that subjects could not hold vergence on a fixation target in the presence of a disparity-modulated surround. Our results and those of Stevenson and colleagues demonstrate that horizontal vergence is driven by a weighted mean of competing signals from a certain area.

Depth selectivity

We have shown that a competing peripheral stimulus interferes with the ability to maintain vergence on a fixed central target or to track the changing vergence of a central target. In experiment 5, we found that the interference was maximal when the target and the competing surface were coplanar and diminished with increasing relative horizontal disparity between the two stimuli. The tuning is relatively sharp with the disparity integration range being roughly ±1.0°. In experiment 6 we showed that disparity modulation of a surrounding stimulus had no effect on the ability to remain fixated on a stationary target when the stimuli had a relative disparity of ±1.0. Thus, disparity signals evoking horizontal vergence are integrated over both a retinal area and a relative disparity range. It is thus more useful to think of an integration volume for vergence rather than a two-dimensional retinal integration area. This conclusion is similar to that drawn by Allison et al. (2000) for vertical vergence.

The disparity integration range and the operational range of disparity-evoked vergence may both reflect the range of the underlying disparity detectors. Images with a horizontal disparity of more than about 0.5° do not fuse. However, with isolated objects, disparities of 7° or more can support stereoscopic depth perception (Westheimer and Tanzman 1956). With random-dot displays, exposed for 150 ms, relative disparities of more than about 1° failed to produce depth (Glennerster 1998). Random-dot displays become subject to spurious binocular matches as disparity exceeds half the mean dot spacing. For this reason, it becomes difficult to detect the interocular correlation of random-dot displays at about 1° of relative disparity (Stevenson et al. 1992). Busettini et al. (2001) showed that the amplitude and velocity of the initial 100-ms vergence response to disparity steps in a large random-dot display were proportional to step size up to about ±1° and reached a peak with a step of about ±2°. Responses to larger disparity steps tended to consist of idiosyncratic 'default responses' unrelated to the sign of the disparity. We minimized the matching problem by using a mixture of well spaced texture elements. In monkey, the cortical disparity sensitive cells in V1, generally believed to form part of the neural pathways for disparity vergence, are sensitive to absolute retinal disparity (Cumming and Parker 1999), as would be expected for cells mediating vergence. In cat striate cortex, von der Heydt et al. (1978) reported that disparity selective cells have a range of preferred disparity with a mean preferred disparity of zero and a standard deviation of about 0.5°. This range roughly agrees with the disparity tuning range of ±1.0° for vergence integration found here if we assume a detection range of ±2 or 3 standard deviations. Similarly, Prince et al. (2002) found that few cells in macaque V1 had preferred disparity greater than ±1.0°. Although the typical receptive fields of these cells are too small to explain the retinal integration area they presumably form the inputs to later pooling.

In summary, the results of this study confirm that horizontal vergence of maximum gain can be elicited by a central stimulus under 1° in diameter. By this criterion, the stimulus integration area for horizontal vergence is under 1°. However, the ability to maintain vergence on a central target is affected by neighbouring stimuli closer than about 5°. Stimuli beyond this eccentricity are not combined with central stimuli to form a combined disparity signal. This agrees with previous findings of a 6°-diameter integration area for the initiation of vergence to step change in disparity (Popple et al. 1998). However, stimuli beyond this central integration area can drive vergence in their own right. We also found that a competing stimulus had less effect on vergence responses when separated from the target by a disparity pedestal. As a result, we propose that it may be more useful to think in terms of an integration volume of disparity signals for vergence rather than a two-dimensional retinal integration area.

Acknowledgements The support of NSERC Canada to I.P. Howard and R.S. Allison is gratefully acknowledged. The authors would like to thank Jim Zacher for his technical expertise and his assistance in running the experiments.

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