Exp Brain Res (1997) 116:153–159

RESEARCH ARTICLE

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The dynamics of vertical vergence

Received: 11 September 1996 / Accepted: 28 January 1997

Abstract We measured the gain and phase of vertical vergence in response to disjunctive vertical oscillations of dichoptic textured displays. The texture elements were m-scaled to equate visibility over the area of the display and were aperiodic and varied in shape so as to avoid spurious binocular matches. The display subtended 65° and oscillated through peak-to-peak amplitudes from 18 arc min to 4° at frequencies from 0.05 to 2 Hz – larger ranges than used in previous investigations. The gain of vergence was near 1 when the stimulus oscillated at 18 arc min at a frequency of 0.1 Hz or less. As the amplitude of stimulus oscillation increased from 18 arc min to 4°, vergence gain decreased at all frequencies, which is evidence of a nonlinearity. Gain declined with increasing stimulus frequency but was still about 0.5 at 2 Hz for an amplitude of 18 arc min. Phase lag increased from less than 10° at a stimulus frequency of 0.05 Hz to between 100° and 145° at 2 Hz. Overall, the dynamics of vertical vergence resemble the dynamics of horizontal vergence and cyclovergence.

Key words Vertical vergence · Eye movements · Vertical disparity

Introduction

When the eyes converge on a point in the midline, the locus of zero vertical disparity is the median plane and the horizontal plane containing the point of fixation. Thus, when a person moves the gaze from a straight-ahead position to an oblique position, vertical vergence is required to bring the images of the newly fixated object into vertical correspondence. For instance, a vertical vergence of 3 prism dioptres is required to fixate a point 24° up and 24° to one side on a frontal plane, at a distance of 33 cm (Ogle and Prangen 1953). The required vergence for a given direction of gaze varies with the distance of the surface. Thus, we are constantly changing our vertical vergence as we shift our direction or distance of gaze, although the range of required vertical vergence is smaller than that of horizontal vergence. Many people have a vertical phoria which manifests itself as an elevation of one eye relative to the other when there is no fusional stimulus in view. Under normal viewing conditions the vertical misalignment of the images which a phoria would introduce triggers a corrective vertical vergence. Any uncorrected vertical misalignment is defined as a vertical fixation disparity.

Houtman et al. (1981) used scleral search coils to measure open-loop vertical vergence. In open-loop vergence a negative-feedback signal from the eye-movement monitor is fed back to the stimulus so that, as the eyes move, the images on the two retinas remain in the same locations. As far as we can tell from the incomplete description, they used a display of letters subtending 11°. An open-loop, 35 arc min vertical displacement of one image produced a saturation level of vergence of about 40 arc min at a velocity of about 15 arc min/s. Vergence velocity appeared to be independent of stimulus magnitude. For closed-loop sinusoidal image displacements of 33 arc min, response gain fell from near 1 at 0.03 Hz to about 0.3 at 1 Hz. Gains were lower for an amplitude of 65 arc min (Houtman and van der Pol 1982).

Kertesz (1981) also used scleral search coils to measure vertical vergence in one subject. The maximum amplitude of vertical vergence in one direction was 1.9° for a stimulus subtending 5°, and 5.2° for a stimulus subtending 57.6°. Perlmutter and Kertesz (1982) used a Purkinje Eyetracker and the same stimulus which subtended 8.5°. An open-loop step of vertical disparity of 14.8 arc min produced a vertical vergence with a latency of 180 ms and a velocity of 39.6°/s to reach a final value of 54 arc min which was maintained for 250 ms. The velocity of open-loop vertical vergence was proportional to the magnitude of disparity, as Rashbass and Westheimer (1961) had found for open-loop horizontal disparity, although Houtman et al. (1981) did not find this propor-

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tionality. For sinusoidal modulations of vertical disparity the open-loop gain was about 9 dB at frequencies up to 0.4 Hz and fell to 0 dB at about 0.7 Hz. For closed-loop modulations of disparity of 9.3 arc min the gain was about 3.2 dB up to a frequency of 0.4 Hz and fell to 0 dB at 0.9 Hz. Gain decreased as the amplitude of disparity modulation increased from 3.3 to 28 arc min, showing that the mechanism is nonlinear. The phase lag increased from about 30° to 90° as frequency increased from 0.1 to 0.9 Hz and was the same for a sinusoidal (predictable) modulation of disparity as for an unpredictable modulation of disparity, demonstrating that the mechanism does not involve a predictor. Perlmutter and Kertesz (1982) used a stimulus consisting of 50 notched horizontal lines 10 arc min apart. With such a stimulus, the horizontal lines come into coincidence at every multiple of 10 arc min of vertical offset and provide a stimulus for vertical fusion. This stimulus is therefore unsatisfactory for studying the range of vertical vergence.

Boman and Kertesz (1983) claimed that vertical vergence amplitudes decrease and vertical vergence reaction time increases in the presence of a horizontal disparity but that horizontal vergence is not affected by the presence of a vertical disparity. But their stimulus had a strong horizontal/vertical anisotropy – it contained several prominent vertical lines which would provide a horizontal fusional stimulus at several horizontal disparities, but no such horizontal lines.

The following experiment was designed to measure the dynamics of vertical vergence using a larger stimulus than used in previous experiments and for a wide range of frequencies and amplitudes of stimulus displacements.

Materials and methods

Eye movement monitoring

Scleral search coils (Robinson 1963) were used to record the movements of both eyes. Coils were inserted into each eye after administering a topical ocular anesthetic (Collewijn et al. 1975). The subject was seated with the head supported on a custom-fitted bite board at the center of the magnetic field coils wound on a 1-m cubic frame. Horizontal and vertical field coils provided independent measurements of vertical and horizontal eye position. Eye movements were less than 3°, a range within which the voltage induced in each search coil is a linear function of horizontal and vertical eye rotation.

The instrument was calibrated by recording the demodulated coil voltage as the subject looked at fixation points between ± 5° along horizontal and vertical axes. Positive angles refer to downward and rightward positions of an eye relative to the primary position. Vergence responses were obtained from the difference between the responses of the left and right eyes. The relationship between eye position and coil voltage was defined by the best fitting line using a least squares criterion. This formula was then used to convert raw coil voltages into angular eye position. There was no noticeable deviation from linearity of each coil and no noticeable crosstalk between horizontal and vertical channels. We measured the amplitude of vergence modulation in response to disjunctive vertical motion of the dichoptic displays. This measure is insensitive to slow drifts in eye position. The absence of any significant drift in mean eye position indicated that the search coils effectively adhered to the eyes.

Display

The displays used in earlier reports either suffered from correspondence ambiguity, were not described adequately, or did not provide a strong stimulus for vertical fusional movements. We investigated the frequency response of vertical vergence for several amplitudes of disjunctive stimulus motion using a well-defined textured stimulus which filled the binocular field of view.

Translucent rear projection screens were attached to the field coils to the right and left of the subject. Stimuli on photographic slides were projected onto the screens and viewed through mirrors in a Wheatstone stereoscope configuration (Howard and Zacher 1991). When viewed dichoptically the two images formed a single binocular image subtending 65° in the frontal plane at a distance of 57 cm directly ahead of the subject. Care was taken to ensure that the screens were not visible directly. The pattern consisted of randomly positioned geometrical figures as shown in Fig. 1. To prevent any suppression of vergence movements by surrounding features with zero disparity, the figures were light elements on a dark background and all surrounding objects were matte black so that only the dichoptic textured pattern was visible. The stimulus elements in each monocular display had a mean luminance of 13 cd/m^2 on a background of mean luminance of less than 1 cd/m^2. Luminance was reduced by approximately 50% after reflection off the semi-silvered mirrors.

The stimulus had a wide range of spatial frequencies and a mixture of horizontal and vertical features to drive vertical vergence and control cyclovergence and horizontal vergence. A central vertical fixation line was also provided as a horizontal fusion lock. A regular pattern of line elements was avoided since the eyes have a tendency to misconverge on such a stimulus, as in the well-known wallpaper illusion (Howard and Rogers 1995). The size of the display elements increased outwards from the center to compensate for decreased acuity in the visual periphery (Anstis 1974). We used a simple proportional scaling, although there are no data on the scaling factor used by the vergence system.

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 up and down by a rocker arm. The two rocker arms were driven by the same servo-motor so that the two images oscillated in counterphase at a frequency determined by the speed of the motor. A microswitch on the motor shaft indicated the start of each cycle and allowed calibration of the oscillation frequency. A micrometer on the rocker arm allowed the amplitude of oscillation of each image 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

Four subjects, two male and two female, between the ages of 22 and 32 years performed the experiment. The experiment was approved by York University ethics committee in accordance with the standards in the 1964 Helsinki Declaration. All had normal stereoscopic vision and gave their informed consent. Three of the subjects were myopes who normally wore spectacles or contact lenses. One subject wore her spectacles during the experiment. The other subjects did not wear their spectacles but reported that they could see the display clearly. The subjects were seated in the coil frame and asked to maintain fixation on the center of the display. The two images were oscillated in counterphase at frequencies of 0.05, 0.1, 0.5, 1.0 and 2.0 Hz with 18′, 33′, 1.0°, 2.0° and 4.0° of arc peak-to-peak disjunctive vertical displacement. The frequencies were presented in a random order for each amplitude and amplitudes were presented in a different order for each subject. Vergence eye movements were recorded for at least five complete cycles of vertical oscillation. Eye movement records and the

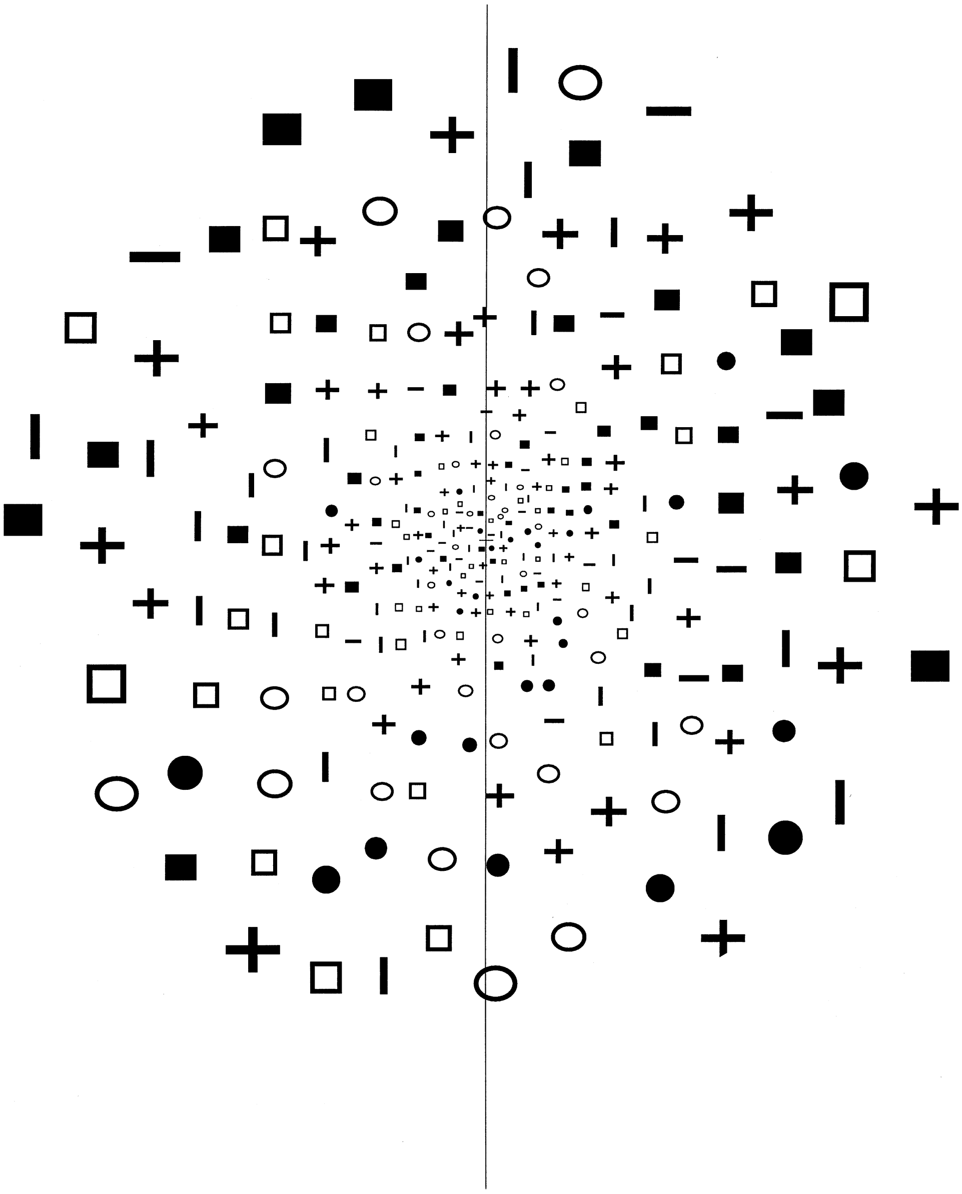


Fig. 1 Display used to induce vertical vergence. The display consisted of well-spaced texture elements of various shapes so as to avoid false binocular matches. Texture element size was m-scaled in the periphery to compensate for decreasing visual acuity

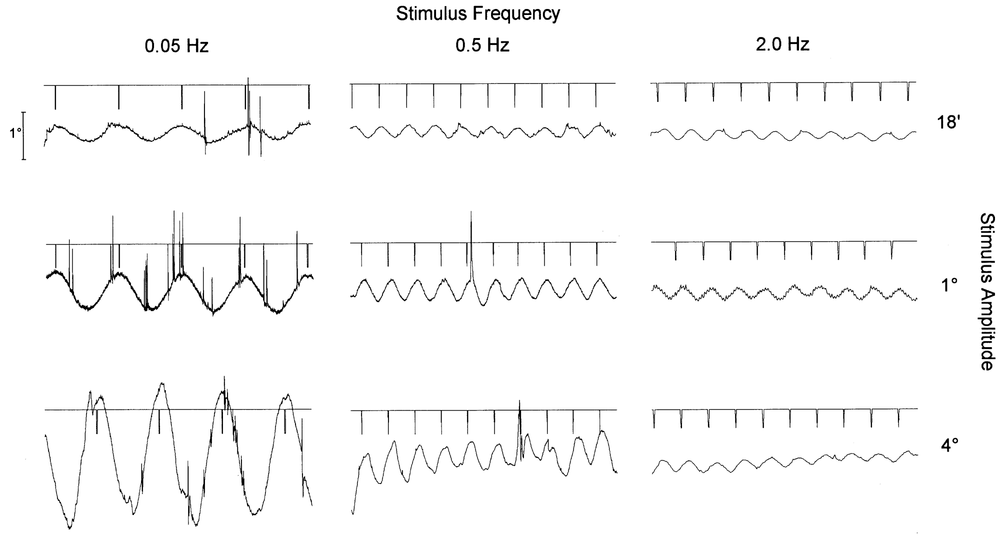
marker indicating the start of a cycle were transferred onto digital tape. The data were digitized at 100 Hz with 12-bit resolution. For a sinusoidal variation in stimulus disparity, vergence gain is defined as peak amplitude of vergence divided by peak amplitude of stimulus displacement. Gain and phase for each condition were estimated by averaging the response calculated from vergence amplitude and delay over all recorded cycles.

Results

A sample of vergence records of one subject is shown in Fig. 2. Figure 3 shows the magnitude of vertical vergence as a function of the frequency of stimulus oscillation for each of four subjects. Multivariate analysis of variance indicated a significant effect of stimulus amplitude [$F(4,12) = 159.242$, $P < 0.01$] and frequency [$F(4,12) = 103.088$, $P < 0.01$] on the gain of vertical vergence. Analysis of variance also indicated a significant effect of stimulus frequency [$F(4,12) = 489.617$, $P < 0.01$] and a small but significant effect of amplitude [$F(4,12) = 5.118$, $P < 0.05$] on the phase lag of vertical vergence. The gain and phase appeared to change in a similar manner with increasing stimulus frequency for all stimulus amplitudes. However, a small but significant interaction between amplitude and frequency existed for both response gain [$F(16,48) = 3.458$, $P < 0.01$] and phase [$F(16,48) = 2.186$, $P < 0.05$] but these interaction terms accounted for less than 3% of the variance in the model.

Figure 4a shows the mean gain of vergence for the four subjects as a function of stimulus frequency for each of five stimulus amplitudes. At a stimulus frequency of 0.1 Hz or less and amplitude of 18 arc min the gain of vergence was almost one and there was no appreciable phase lag (Fig. 4b). This probably represents the normal operating range of the response. Although the amplitude

Fig. 2 Records of vertical vergence for one subject for a set of frequency and amplitude combinations. The pulse trains on each record indicate the peak of each disparity oscillation and provide an indication of time scale



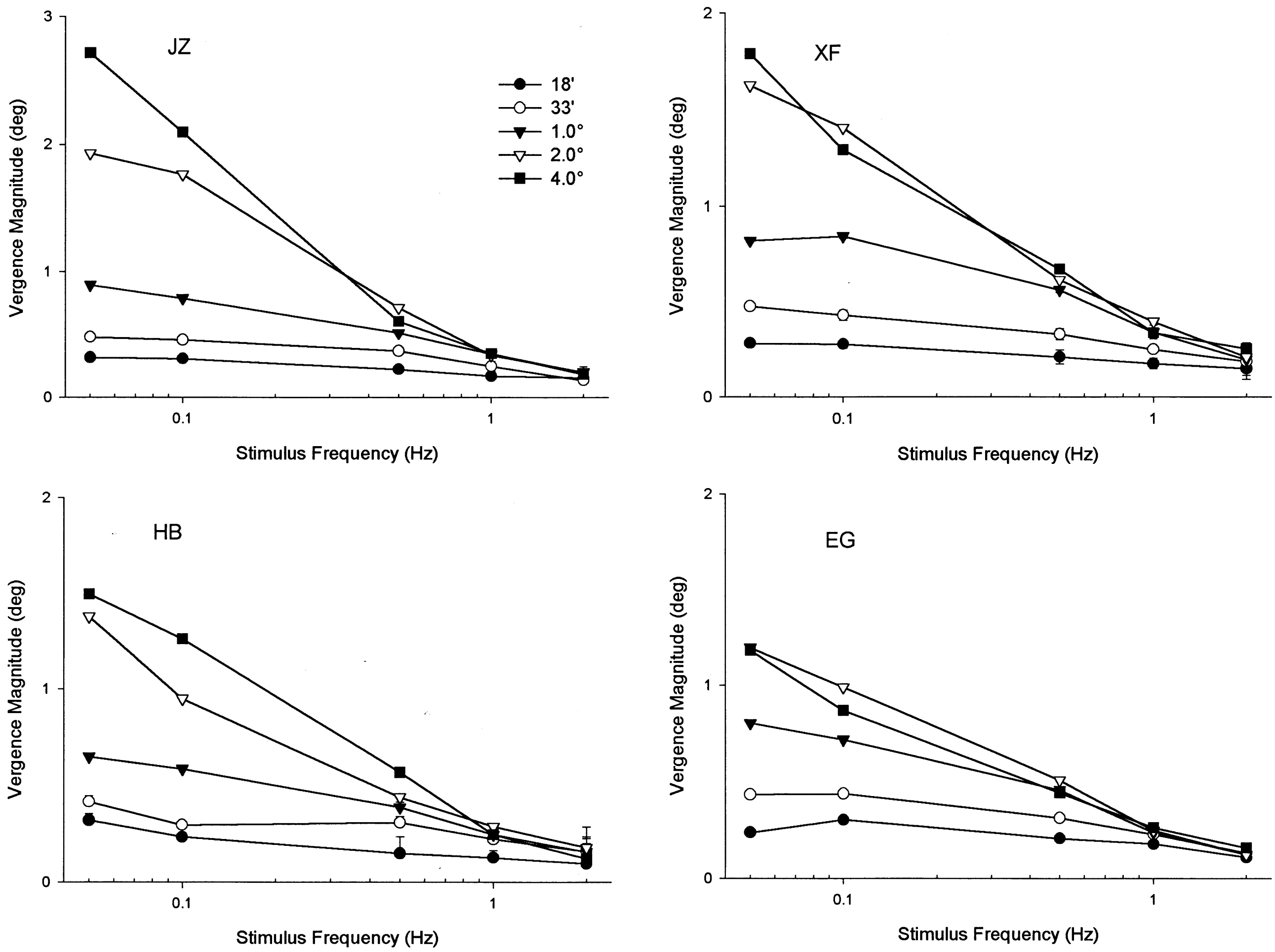


Fig. 3 Magnitude of peak-to-peak vertical vergence of the four subjects (JZ, XF, HB, EG) as a function of the frequency of stimulus oscillation for each of five amplitudes of stimulus oscillation

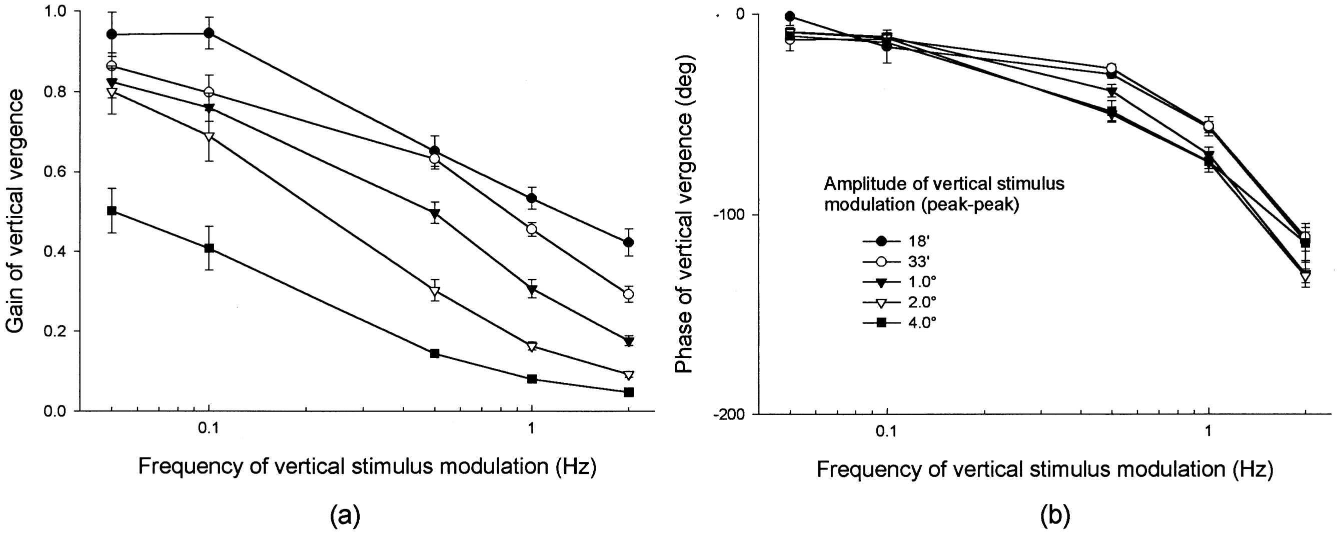


Fig. 4 **a** Gain of vertical vergence averaged across the four subjects as a function of frequency of stimulus oscillation. **b** Phase lag of vergence averaged across the four subjects as a function of the frequency of stimulus oscillation for each of five amplitudes of stimulus oscillation

of vergence increased with increasing stimulus amplitude, response gain (peak response amplitude over peak stimulus amplitude) declined. Thus the increase in vergence amplitude did not match the increase in stimulus amplitude and hence vergence gain dropped with disparity amplitude. Both response amplitude and response gain declined with increasing stimulus frequency for all stimulus amplitudes.

At the highest frequencies, however, vergence amplitude showed less dependence on stimulus amplitude and the response curves in Fig. 3 converged. At 2 Hz the response tended to saturate at a peak-to-peak vergence amplitude of approximately 0.2°. This response differed from the saturation noted for low-frequency, large-amplitude conditions in that the response remained sinusoidal in appearance and did not appear to be clipped. As a result, although vertical vergence amplitude fell more significantly with frequency for larger stimulus amplitudes, vergence gain did not show the same strong frequency-amplitude interaction.

With a stimulus amplitude of 4° the response of some subjects was decidedly nonsinusoidal and significant clipping occurred (Fig. 5). One subject responded with conjugate eye movements, presumably because he suppressed one of the disparate images and followed the remaining image with both eyes.

Figure 4b shows the mean phase lag of the four subjects as a function of stimulus frequency for each of five stimulus amplitudes. There was a small but significant increase in phase lag as stimulus amplitude increased but the increase was not always systematically related to stimulus amplitude. At the lowest stimulus frequency and amplitude, vergence gain was near 1 and phase lag was typically less than 10°. Above a frequency of 0.1 Hz, phase lag increased linearly with increasing

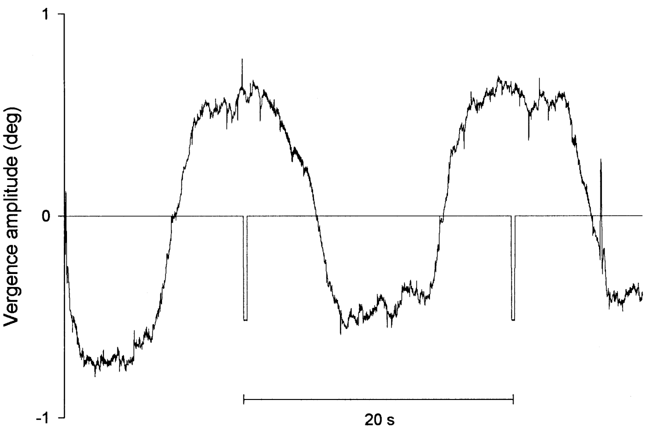


Fig. 5 Record of vertical vergence to an amplitude of stimulus modulation of 4° at a frequency of 0.05 Hz in subject EG. In this condition, this subject showed the lowest gain and most pronounced nonlinearity for large-amplitude, low-frequency oscillation. The pulse train on the record indicates the peak of each disparity oscillation and provides an indication of time scale

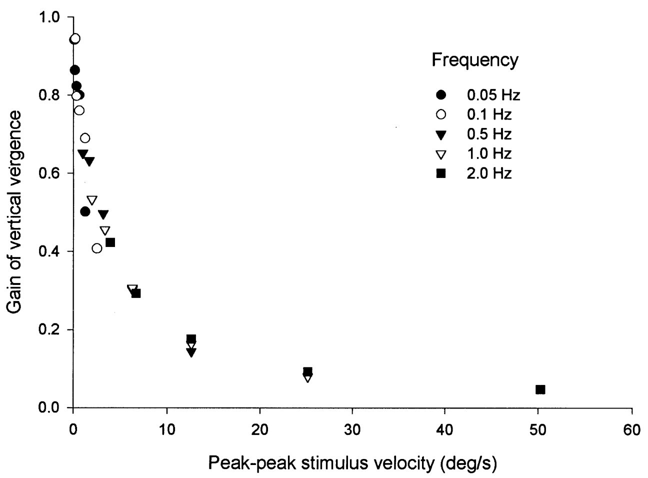


Fig. 6 Gain of vertical vergence as a function of peak-to-peak stimulus velocity

stimulus frequency for all stimulus amplitudes. At 2 Hz, phase lag reached a value of 123° averaged across the five amplitudes and four subjects.

Figure 6 shows that the gain of vertical vergence decreases exponentially with increasing peak stimulus velocity in a similar fashion for all stimulus amplitudes. Thus vergence gain is more closely related to stimulus velocity than to stimulus frequency or amplitude.

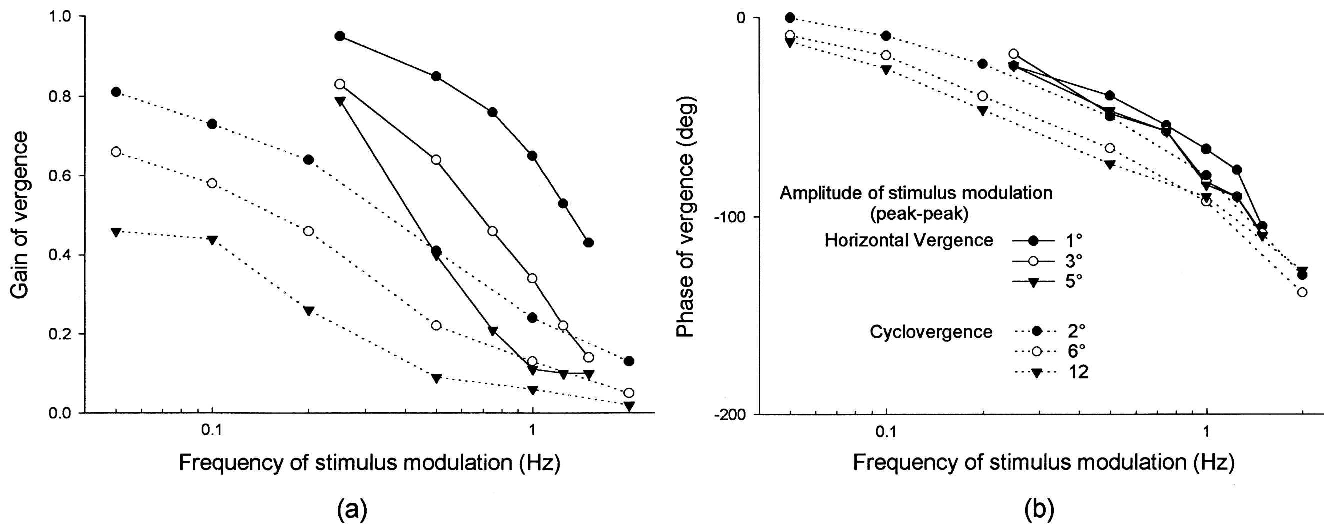
Discussion

There are two previous studies of vertical vergence with which our study can be compared. Houtman et al. (1981) used 33 and 65 arc min amplitudes of stimulus disparity comparable to our 33 arc min and 1.0° amplitudes and frequencies up to 1 Hz. For comparable conditions our two studies report similar reductions in vergence gain with increasing stimulus amplitude and frequency. For 33 arc min amplitude they report a somewhat higher gain at 0.05 Hz (near 1.0 vs 0.86) with a faster gain rolloff by 1.0 Hz (0.3 compared with 0.46). Their 65 arc min amplitude and our 1.0° amplitude resulted in a similar falloff in response gain. Phase showed a similar weak decrement with stimulus amplitude in both studies. The display used by Houtman et al. (1981) was considerably smaller than that used in our study. Their display was described as “complex” which presumably meant that it contained a variety of distinct features and was difficult to misconverge. Unfortunately the display was not fully described and thus it is not possible to compare the stimulus features which may be responsible for small quantitative differences in the results.

Fig. 7 **a** Gain and **b** phase of horizontal vergence and cyclovergence. Horizontal vergence was evoked by sinusoidal modulation of horizontal disparity of a 30° × 30° textured pattern as a function of frequency of modulation for three stimulus amplitudes. Adapted from Erkelens and Collewijn (1985). Cyclovergence was evoked by sinusoidal modulation of cyclodisparity of a 75° × 75° textured pattern as a function of frequency of modulation for three stimulus amplitudes. From Howard and Zacher (1991)

In marked contrast to our study and that of Houtman et al. (1981), Perlmutter and Kertesz (1982) reported closed-loop gains much larger than 1 for all stimulus amplitudes between 3.3 and 27.9 arc min. Although gain declined with increasing frequency, it remained above 1 even at a frequency of 1 Hz. This high gain would result in overcompensation for vertical stimulus misalignment. In contrast, we found no large overshoots of vergence under any condition, including conditions with similar stimulus amplitudes, frequencies and viewing distance as those used by Perlmutter and Kertesz. The phase lags reported by Perlmutter and Kertesz were similar to those reported here. Unlike the results and conclusions reached by Perlmutter and Kertesz, our study indicates that vertical vergence is designed to compensate for vertical disparity at moderate amplitudes and frequencies of stimulus misalignment. We argued in the Introduction that the display used by Perlmutter and Kertesz was subject to an artifact resulting from correspondence ambiguity between the mainly horizontal features of their stimulus. In an earlier study with line stimuli which did not suffer from this ambiguity, Perlmutter and Kertesz (1978) found no systematic overcompensation of vertical vergence.

We can compare the gain and phase lag of vertical vergence with the gain and phase lag of horizontal vergence. Krishnan et al. (1973) measured the gain and phase lag of horizontal vergence of one subject in response to a sinusoidally changing disparity of a pair of dichoptic vertical lines through an amplitude of 3.5°. Gain was close to 1 for frequencies up to about 1 Hz and fell off rapidly above 1.5 Hz. Erkelens and Collewijn (1985) measured the gain and phase lag of horizontal vergence evoked by sinusoidal oscillation of a 30° × 30° display of random dots. The results are shown in Fig. 7. It can be seen that for stimulus amplitudes between 1° and 5° the gain was between 0.8 and 1 at a frequency of 0.25 Hz. As with vertical vergence, the gain of horizontal vergence fell with increasing stimulus amplitude at a greater rate for larger amplitudes and was more closely related to peak velocity of stimulus oscillation than to



frequency or amplitude. Also the phase lag of horizontal vergence was about 20° at a frequency of 0.25 Hz and increased to about 100° at a frequency of 1.5 Hz in much the same way for all amplitudes. Thus the phase lag of horizontal vergence in response to a 30°-diameter display of random dots resulted from a constant delay of about 210 ms. The comparable value of delay from our 60° display is 158 ms.

We can also compare vertical vergence with cyclovergence. The gain and phase lag of cyclovergence for three amplitudes of disconjugate cyclorotation of a circular textured display subtending 75° are shown in Fig. 7. Like the gain of vertical vergence, the gain of cyclovergence declined from a similar high value at a frequency of 0.05 Hz to a similar low value at 2 Hz. Also, the gain of both responses declined with increasing stimulus amplitude. However, the two responses cannot be compared quantitatively because the stimulus amplitudes are in different dimensions. Like the phase lag of vertical vergence, the phase lag of cyclovergence is weakly dependent on stimulus amplitude and increases to well over 100° at a frequency of 2 Hz. Overall, the dynamic characteristics of horizontal vergence, vertical vergence and cyclovergence are remarkably similar. Whether this arises from the fact that they all involve overlapping sets of oculomotor muscles or because of similarities in neural control is not known. In experiments we are still conducting we are finding that the three types of vergence differ in the extent to which they depend on the area of the stimulus and on stimulation of the central retina (Howard and Sun 1994).

Acknowledgements This work was supported by a grant from the National Science and Engineering Council of Canada. We thank Xueping Fang and Holly Bridge for help in running the experiment.

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