Short-Latency Disparity Vergence in Humans

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Busettini, C., E. J. FitzGibbon, and F. A. Miles. Short-latency disparity vergence in humans. J Neurophysiol 85: 1129–1152, 2001. Eye movement recordings from humans indicated that brief exposures (200 ms) to horizontal disparity steps applied to large random-dot patterns elicit horizontal vergence at short latencies (80.9 ± 3.9 ms, mean ± SD; n = 7). Disparity tuning curves, describing the dependence of the initial vergence responses (measured over the period 90–157 ms after the step) on the magnitude of the steps, resembled the derivative of a Gaussian, with nonzero asymptotes and a roughly linear servo region that extended only a degree or two on either side of zero disparity. Responses showed transient post-saccadic enhancement: disparity steps applied in the immediate wake of saccadic eye movements yielded higher vergence accelerations than did the same steps applied some time later (mean time constant of the decay, 200 ms). This enhancement seemed to be dependent, at least in part, on the visual reafference associated with the prior saccade because similar enhancement was observed when the disparity steps were applied in the wake of saccadephase-like shifts of the textured pattern. Vertical vergence responses to vertical disparity steps were qualitatively similar: latencies were longer (on average, by 3 ms), disparity tuning curves had the same general form but were narrower (by ~20%), and their peak-to-peak amplitudes were smaller (by ~70%). Initial vergence responses usually had directional errors (orthogonal components) with a very systematic dependence on step size that often approximated an exponential decay to a nonzero asymptote (mean space constant ± SD, 1.18 ± 0.66°). Based on the asymptotes of these orthogonal responses, horizontal errors (with vertical steps) were on average more than three times greater than vertical errors (with horizontal steps). Disparity steps ~7° generated “default” responses that were independent of the direction of the step, idiosyncratic, and generally had both horizontal and vertical components. We suggest that the responses depend on detectors that sense local disparity matches, and that orthogonal and “default” responses result from globally “false” matches. Recordings from three monkeys, using identical disparity stimuli, confirmed that monkeys also show short-latency disparity vergence responses (latency ~25 ms shorter than that of humans), and further indicated that these responses show all of the major features seen in humans, the differences between the two species being solely quantitative. Based on these data and those of others implying that foveal images normally take precedence, we suggest that the mechanisms under study here ordinarily serve to correct small vergence errors, automatically, especially after saccades.

INTRODUCTION

Vergence eye movements are critical for good binocular vision, serving to align both eyes on the same object: the nearer the object of regard, the greater the required convergence. The visual control of vergence depends heavily on the slight difference in the positions of the images on the two retinas, which is referred to as binocular disparity and effectively defines the vergence error. Although there are a number of complex visual cues to viewing distance that can influence vergence, here we shall be concerned solely with disparity, which is the most potent (for recent review, see Collewijn and Erkelens 1990). The ability of pure disparity errors to drive vergence was first demonstrated by Rashbass and Westheimer (1961), who used a Wheatstone stereoscope to present identical targets independently to the two eyes. Targets with crossed disparity errors (equivalent to objects nearer than the plane of fixation) elicited increased convergence, and targets with uncrossed disparity errors (equivalent to objects farther than the plane of fixation) elicited decreased convergence, exactly as expected of a negative feedback system working to achieve and maintain appropriate binocular alignment. Most studies have been concerned with horizontal vergence, perhaps in large measure because it is the means by which binocular alignment is shifted between objects in different depth planes. However, good binocular vision requires that the two lines of sight be aligned vertically as well as horizontally, and vertical disparities have been shown to elicit appropriate vertical vergence, although the effective range of disparities is much smaller, the responses have much more sluggish dynamics, show more extensive spatial integration, and are less sensitive to instruction, than the horizontal vergence responses associated with horizontal disparities (Howard et al. 1997, 2000; Kertesz 1983; Stevenson et al. 1997).

In the present study on humans, we have been concerned solely with the initiation of vergence by disparity steps applied to large random-dot stereograms. Previous studies on humans have generally, although not always, used small targets and reported latencies ranging from 150 to 200 ms (Erkelens and Collewijn 1991; Houtman et al. 1977, 1981; Jones 1980; Mitchell 1970; Rashbass and Westheimer 1961; Westheimer and Mitchell 1956). Using monkeys, we have recently reported that, when large textured patterns are used, horizontal disparity steps of suitable magnitude consistently elicit horizontal vergence eye movements with latencies of ~55 ms (Busettini et al. 1994a, 1996b). These short-latency vergence responses were in the appropriate direction only when steps were small (~2–3°), and large steps (up to 12.8°) yielded responses with both isogonic and orthogonal components that were largely independent of whether the steps were crossed or uncrossed, horizontal or vertical (so-called, “default” responses). We ar-

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argued that the responses to small disparity steps reflected the operation of a servomechanism that normally functions to correct residual vergence errors, and the (default) responses to large steps were due to residual local correlations. We also reported that small disparity steps applied in the immediate wake of a saccadic eye movement yielded appropriately directed vergence eye movements with much higher initial accelerations than did the same steps applied some time later. Further, this transient post-saccadic enhancement seemed to be dependent, at least in part, on the visual stimulation associated with the prior saccade because similar, although sometimes weaker, enhancement was observed when the disparity steps were applied in the wake of saccadlike shifts of the textured pattern (so-called, "simulated saccades"). In the present paper on humans, we report similar findings: latencies are short (although 25 ms or so longer than in monkeys), there are default responses with large steps, and there is transient enhancement in the wake of real and simulated saccades. The only significant methodological difference between the present study and our previous one on monkeys was the visual stimulus: the collage of arbitrary geometrical shapes used previously was replaced by a random-dot pattern, permitting a more formal description of the stimulus. We also report here that initial vergence responses have orthogonal components that reach an asymptote with steps of a few degrees and persist (as default responses) with large steps. Further, we show that the initial vergence responses to small disparity steps (2–3°) are relatively insensitive to eightfold changes in the size of the texture elements (random dots), although responses to steps of intermediate size (3–6°) are larger with larger elements. In addition, we report that the vertical vergence responses to vertical disparity steps have only slightly longer latencies but are appreciably smaller in magnitude than the horizontal responses to horizontal steps, although the general form of the disparity tuning curves is very similar. Finally, we use the same new random-dot stimuli to extend our earlier report on monkeys and show that the initial vergence responses of monkeys share most of the features of the human, the differences between the two species being quantitative rather than qualitative. Some of these findings on humans have been published in abstract form (Busetttini et al. 1994b).

METHODS

The eye movements evoked by brief exposure to disparity steps applied to large projected random-dot patterns were recorded from seven adult human subjects. All procedures were approved by the Institutional Review Committee concerned with the use of human subjects, and all subjects provided informed consent. Three of the subjects (FM, RK, and GM) each participated in numerous recording sessions, and four more (MB, KP, HA, and JG) each participated in only a few sessions on selected abbreviated paradigms. All of these subjects had stereacuities better than 40 s of arc (Titmus test) and no known oculomotor or visual problems other than refractive errors that were corrected with spectacles when necessary. Only two subjects (FM and RK) had prior experience (as subjects) in eye-movement studies. We also recorded the vergence responses of three rhesus monkeys using the exact same stimuli as for the human recordings to permit a quantitative comparison between the two species. Except for the details of the stimuli (described in Recording and stimulation procedures), the methodology used on monkeys was exactly the same as in our earlier study and will not be described here (Busetttini et al. 1996b).

Recording and stimulation procedures

The presentation of stimuli and the acquisition, display, and storage of data were controlled by a PC (Hewlett Packard Vectra, 486) using a Real-time EXperimentation software package (REX) developed by Hays et al. (1982). The horizontal and vertical positions of both eyes were recorded with an electromagnetic induction technique (Robinson 1963) using scleral search coils embedded in silastin rings (Collewijn et al. 1975). Coils were placed in each eye following application of 1–2 drops of anesthetic (proparacaine HCl), and wearing time ranged up to 73 min for the three main subjects and 30 min for all others. The AC voltages induced in the scleral search coils were led off to a phase-locked amplifier that provided separate DC voltage outputs proportional to the horizontal and vertical positions of the two eyes with corner frequencies (3 dB) at 1 kHz (CNC Engineering). The outputs from the coils were calibrated at the beginning of each recording session by having the subject fixate small target lights located at known eccentricities along the horizontal and vertical meridia. Peak-to-peak voltage noise levels were equivalent to an eye movement of 1–2 min of arc. Interocular distance was measured to the nearest millimeter.

The subject was seated in a fiberglass chair with his/her head stabilized by means of a chin support and forehead rest combined with a head strap and faced a translucent tangent screen (distance, 33.3 cm; subtense, 85 × 85°) onto which two identical, overlapping patterns were back-projected. Orthogonal polarizing filters in the two projection paths and matching filters in front of each eye ensured that each pattern was visible to only one eye: dichoptic stimulation. The screen was constructed of material specially designed to retain the polarization (Yamaboshi, Tokyo, Japan). The patterns consisted of black circular dots with randomly distributed centers on a white background; overlaps were freely allowed, resulting in irregular clustering, and the screen image had equal amounts of black and white (50% coverage). Dot diameters were 2° except for one special study in which this parameter was varied systematically (when all dots had one of the following diameters in a given experiment: 0.5, 1.1, 2.2, or 4.4°). The luminance of the images on the screen was measured with a photometer (Spectra Pritchard), sampling the screen through the polarizing filters so as to mimic the subjects’ view. With this arrangement, the luminance measured through the polarization filtering was 0.13 cd/m² in the light areas of the patterns and 0.0026 cd/m² in the dark areas. The equivalent measures through the nonmatching (orthogonal) polarizing filters were 0.0011 cd/m² in the light areas and 0.00060 cd/m² in the dark areas. Subjects were unaware of the “ghost” images seen through the orthogonal filters. Pairs of mirror galvanometers (General Scanning, M3-S with vector tuning) positioned in each of the two light paths in an X/Y configuration were used to control the horizontal and vertical positions (and thereby the horizontal and vertical disparities) of the two images. These galvanometers were driven by the DAC outputs of the PC at a rate of 1 kHz with a resolution of 12 bits (optical range, ±50°). Voltage signals separately encoding the horizontal and vertical positions of both eyes together with the positions of the four mirror galvanometers were low-pass filtered (Bessel, 6-pole, 180 Hz) and digitized to a resolution of 16 bits, sampling at 1 kHz. All data were stored on a hard disk and, after completion of each recording session, were transferred to a workstation (Silicon Graphics) for subsequent analysis. The rise time of the mirror galvanometers was <2 ms, and to determine their true dynamics and exact timing they were monitored with a Tektronix digital storage oscilloscope linked to a PC (386).

Paradigms

In a given experiment, the stimulus parameter(s) under study were varied from trial to trial in a pseudorandom sequence, in part to discourage prediction/anticipation, and in part to distribute any effects due to short-term changes in nonvisual factors such as arousal, atten-
STANDARD PARADIGM. At the beginning of each trial, the two responsive range with stimuli of marginal efficacy. Through averaging) even when we were exploring the limit of the sessions until each condition had been repeated a sufficient number of

tion, fatigue, and so forth. It was usual to collect data over several sessions until each condition had been repeated a sufficient number of times to permit good resolution of the responses to be achieved (through averaging) even when we were exploring the limit of the responsive range with stimuli of marginal efficacy.

Preliminary experiments (Bussetti et al. 1994b) had revealed that, like ocular following (Gellman et al. 1990), disparity vergence was subject to transient postsaccadic enhancement, and we now conducted a series of experiments in which the postsaccadic delay was varied systematically to characterize the time course of the enhancement. Stimuli were 1.6° crossed- and uncrossed-disparity steps, and the postsaccadic delay intervals were 50, 100, 200, 400, and 800 ms (randomly interleaved). The possibility that the enhancement in the wake of a saccade was due to the visual reafference produced by the saccade sweeping the image of the pattern across the retina was investigated by applying the disparity steps in the wake of a saccadeline shift of the pattern on the screen. The saccadeline shift (or simulated saccade) was applied 800 ms after the initial centering saccade, pilot studies having indicated that the postsaccadic enhancement of disparity vergence had decayed to negligible levels within that period. These shifts were generated from a look-up table that reproduced the profile of a representative centering saccade previously recorded from the subject under study. Because all of the centering saccades were leftward, the simulated saccades had to be rightward to replicate the retinal events correctly. Preliminary experiments, however, indicated that subjects often made anticipatory tracking responses to these simulated saccades, despite attempts to avoid doing so. For this reason we used both rightward and leftward simulated saccades, randomly interleaved, which largely eliminated the problem. The disparity steps (crossed and uncrossed, 1.6°) were then applied in the wake of these simulated saccades with delay intervals of 50, 100, 200, 400, and 800 ms (randomly interleaved). Only the data obtained with the rightward saccadeline shifts were used for the comparison with the data obtained with real (leftward) saccades.

OCULAR FOLLOWING: DEPENDENCE ON A PRIOR SACCADE OR SIMULATED SACCADE. To allow a direct comparison of the effects of a prior saccade or simulated saccade on disparity vergence with those on ocular following (Gellman et al. 1990), additional experiments were undertaken that were identical to those just described except that the disparity steps were replaced with conjugate steps in which the patterns seen by both eyes stepped together 0.8° (leftward or rightward): ocular following stimulus. Note that the previous study of the dependence of human ocular following on a prior saccade used velocity step stimuli (Gellman et al. 1990).

Data collection and analysis

The horizontal and vertical eye position data obtained during the calibration procedure were each fitted with a third-order polynomial that was then used to linearize the horizontal and vertical eye position data recorded during the experiment proper. The latter were then smoothed with a cubic spline of weight 0.33, selected by means of a cross-validation procedure (Eubank 1988), and all subsequent analyses utilized these splined data. To be consistent with our conventions for defining the polarity of the disparity stimuli, rightward and upward eye movements were defined as positive, and vergence position was computed by subtracting the horizontal (or vertical) position of the right eye from the horizontal (or vertical) position of the left eye. This meant that horizontal vergence was positive (denoting increased convergence) when the left eye moved rightward with respect to the right eye, or the right eye moved leftward with respect to the left eye. Likewise, vertical vergence was positive when the left eye moved upward with respect to the right eye, or the right eye moved downward with respect to the left eye (so-called, left sursumvergence or
right deorsumvergence). Horizontal (or vertical) version position, equivalent to cyclopean gaze position, was computed by averaging the horizontal (or vertical) positions of the two eyes. Vergence (or version) velocity was obtained by two-point backward differentiation of the vergence (or version) position data.

The vergence position and vergence velocity temporal profiles recorded in all of the trials using a given stimulus condition were displayed together (synchronized to the disparity step) with an interactive graphics program that allowed the deletion of the occasional trials with saccades or blinks.

To best illustrate the temporal structure of the responses, mean vergence velocity profiles were computed for each stimulus condition. To eliminate any effects due to post-saccadic vergence drift, the mean vergence velocity profile recorded during the control saccade-only trials was subtracted from the mean vergence velocity profiles obtained for each stimulus condition. All of the vergence velocity traces in the figures have been so adjusted, and upward deflections of these traces represent convergent or left sursumvergence velocities.

LATENCY MEASURES. An objective algorithm was used to estimate the latency of onset of vergence using data obtained with disparity steps that gave close-to-maximal responses. Visual inspection of the mean vergence velocity profiles had indicated that the average latencies were generally 75–85 ms. Accordingly, the individual vergence velocity profiles over the time window, 52–118 ms (measured with respect to the onset of the disparity step), were fitted with a function that assumed that, up to a time, $T$, the response profiles were flat (preresponse period), and then incremented linearly (response period). The fitting was done using the nonlinear regression method implemented in BMDP 3R (Dixon et al. 1990), based on a modified Gauss-Newton algorithm (Jennrich and Sampson 1968). For times $t < T$, the function had a constant value ($P_1$), and for times $t \geq T$, the function had a value, at time $t$, of $P_1 + [P_2 (t - T)]$. The value of the baseline ($P_1$), the starting point of the linear segment ($T$, which was our estimate of the response latency), and the slope of the linear segment ($P_2$), were all free parameters. Starting values were 75 ms ($T$), 0°/s ($P_1$), and 0°/s$^2$ ($P_2$).

AMPLITUDE MEASURES. Estimates of the amplitude of the initial disparity vergence response were obtained by measuring the change in vergence position over a 67-ms time interval starting 90 ms after the onset of the disparity step. It will be seen that the mean latency of onset is about 80 ms so that this amplitude measure is restricted to the period prior to the closure of the feedback loop, when eye movements begin to influence the disparity: initial open-loop response. The measures from all trials were then used to calculate the mean change in vergence, together with the SD, for each stimulus condition. Of course, sampling the response at a fixed time with respect to the onset of the stimulus meant that the sample would be sensitive to changes in the latency of onset of the response. The latency of vergence showed little dependence on any of the stimulus parameters examined in the present study, although the initial vergence responses could become vanishingly small as the limits of the response range were explored. (At such times, response-locked measures would default to later components of the response.) To eliminate any effects due to post-saccadic vergence drift, the mean change in vergence during the saccade-only (control) trials was subtracted from the mean change in vergence for each stimulus condition, and these adjusted measures are the ones given in the text and plotted in the figures (where they are referred to as “change in vergence position”).

OCULAR FOLLOWING. The analysis of the ocular following data was very similar to that of the vergence data except that it was carried out on the splined position measures obtained from the right eye. Quantitative estimates of the amplitudes of the initial responses were obtained by measuring the change in eye position during the 67-ms time interval starting 90 ms after the onset of the conjugate position step, and two-point backward differentiation was used to obtain eye velocity profiles. The position measures and velocity temporal profiles obtained for all trials were then averaged for each stimulus condition, and any effects due to post-saccadic drift were eliminated by subtracting the data obtained from saccade-only (control) trials. These adjusted eye-position measures (referred to as “change in eye position”) and eye-velocity temporal profiles are used for all figures and textual references.

Phoria measurement

Dissimilar target images were presented to the two eyes dichoptically, and the subjects’ verbal reports of their relative positions were used to bring the targets into subjective alignment using a staircase procedure, thereby providing an estimate of each subject’s phoria. Subjects viewed the tangent screen in the usual way, and separate projectors with orthogonal polarizers were used to present an upright cross (+) continuously to one eye and an oblique cross (×) transiently to the other. Each cross was black on a white background and spanned 2.3° with arms 10 min of arc thick. The subject fixated the upright cross, and, following a warning tone, the oblique cross appeared for 50 ms. The subject was required to report the horizontal and vertical position of the oblique cross with respect to the upright cross, i.e., right/left/aligned, above/below/aligned. If the subject reported misalignment, then, on the next trial, the oblique cross was repositioned, by a discrete amount, so as to reduce its apparent horizontal and vertical separation from the upright cross. If the subject reported alignment along one or the other axis, no adjustment was made along that axis for the next trial. At the start of each block of trials, the oblique cross could have horizontal and vertical offsets (relative to the upright cross) of 0, ±5, or −5° (varied randomly). The repositioning steps were initially 2°, and then reduced with each successive report of alignment or reversal in the apparent misalignment, to 1°, then to 0.5°, and finally to 0.2°. When the horizontal and vertical steps had both decremented to 0.2°, the oblique cross had invariably reached an asymptotic position, and the block was continued for 20 more trials before starting a new block with a new misalignment. Each subject completed 9–20 blocks of trials, and his/her phoria was estimated from the average misalignment of the 2 crosses for the last 20 trials in each block.

RESULTS

Vergence responses to horizontal disparity steps

Horizontal disparity steps of suitable amplitude applied to large random-dot patterns elicited consistent horizontal vergence responses at short latencies. Figure 1 shows sample horizontal vergence velocity temporal profiles from 1 subject in response to 174 horizontal crossed-disparity steps of 2° applied 50 ms after 10° leftward centering saccades. Data are shown for all trials except the few (8) contaminated with saccades. Also shown in Fig. 1 is the mean horizontal vergence velocity profile (±SD), together with the mirror galvanometer feedback signals indicating the horizontal positions of the images seen by the left and right eyes. The estimated mean latency (objectively determined, see METHODS) for the data shown in Fig. 1 was 82.5 ms and is indicated by the arrows. For 2° crossed-disparity steps such as those used in Fig. 1, the mean latency for seven subjects was 80.9 ± 3.9 (SD) ms. Individual mean latencies (±SD), together with the number of measures contributing to the estimates (when the latency algorithm converged) and the total number of trials from which the data were drawn (after rejecting trials with saccades or blinks), were as follows: 82.5 ± 4.8 ms (subject RK, n = 174/174), 86.0 ± 8.7 ms (FM, 140/144), 84.6 ± 11.6 ms (GM, 147/177), 78.0 ± 6.2 ms (JG, 147/148), 77.7 ± 9.2 ms (KP, 165/168),...
Because our major concern was with the initial open-loop vergence responses, the temporal profiles in all figures are discontinued 180 ms after the onset of the disparity steps.

**BINOCULAR RESPONSE TO A BINOCULAR STIMULUS.** These short latencies are similar to those reported for the ocular following elicited by conjugate ramps applied to large textured patterns (Gellman et al. 1990). Because visual motion detectors can integrate position steps over time to generate an apparent motion signal (Mikami et al. 1986a,b; Newsome et al. 1986), it was possible that the short-latency vergence responses resulted from independent monocular tracking, in which each eye tracked the apparent motion that it saw, rather than from the binocular misalignment per se. To test this idea, we restricted the step to one eye only, leaving the other eye to view a stationary pattern. The movements of the eye that saw the stationary pattern were of particular interest; any effects on this eye due to the monocular apparent-motion cues should have been in the direction *opposite* to the apparent motion stimulus.

Figure 2 shows the data from one such experiment in which horizontal crossed-disparity steps of 2.4° were applied by 1) shifting the pattern seen by the left eye 1.2° rightward and the pattern seen by the right eye 1.2° leftward (—), 2) shifting the pattern seen by the left eye 2.4° rightward (···), or 3) shifting the pattern seen by the right eye 2.4° leftward (-----). There was good convergence regardless of whether the displacement step was seen by one or both eyes, although the initial vergence acceleration was slightly smaller when only one eye saw the step. Further, the eye that saw the stationary pattern always moved in a direction appropriate for a stereo-driven response, that is, in the direction *opposite* to the apparent motion stimulus: when only the right eye saw a step (leftward), the left eye moved to the right, and when only the left eye saw a step...

*FIG. 2.* The effect on the horizontal vergence and version velocity responses of restricting the horizontal disparity step to one eye. Crossed-disparity steps of 2.4° were applied by 1) shifting the images seen by the left and right eyes equally (—), 2) shifting the image seen by the right eye leftward while the other image remained stationary (-----), or 3) shifting the image seen by the left eye rightward while the other image remained stationary (···). All traces are means ($n = 183$). Zero on the abscissa indicates the time of onset of the disparity steps. *Subject RK.*
then the right eye moved to the left. It is of interest that the version responses were always extremely weak (see bottom traces in Fig. 2), despite the fact that in the asymmetric cases there were changes in the apparent cyclopean alignment of the stimuli. Essentially identical data were obtained from two other subjects (FM and GM).

**DEPENDENCE ON THE MAGNITUDE AND DIRECTION OF THE STEPS.** Vergence responses were often not exactly aligned with the direction of the disparity steps and could include appreciable orthogonal components (“directional errors”). That is, responses to horizontal steps included vertical vergence, and responses to vertical steps included horizontal vergence. Like the isogonal components, these orthogonal components showed a highly systematic dependency on the amplitude and direction of the disparity step, but the form of this dependency differed markedly for the two components and will be described separately.

**Isogonal components.** With small horizontal disparity steps (<3°), the very earliest isogonal (i.e., horizontal) components of the vergence responses were always in the compensatory direction, i.e., the direction that reduced the seen disparity, so that crossed steps resulted in increased convergence and uncrossed steps resulted in decreased convergence. This is evident from the horizontal vergence velocity profiles shown for each of three subjects in the middle rows of Fig. 3 (stimuli, crossed steps) and Fig. 4 (stimuli, uncrossed steps): see data labeled \( \dot{V}_h \). Over the range approximately ±1°, larger steps resulted in larger responses, as expected of a disparity-driven, depth-tracking servo system: see traces in continuous line. Responses began to saturate with larger stimuli, however, generally reaching a maximum with steps of only 1.6–2.4°. As steps exceeded these levels, response profiles declined in amplitude but then gradually assumed a form that persisted with even the largest steps (12.8°) and was idiosyncratic: see traces in dashed line. (It will become apparent later, when we discuss the quantitative details, that all responses of all subjects reached asymptotic levels as steps reached ~7°.) Thus some subjects (RK, FM, KP, and HA) responded to the largest steps with increased convergence and others (GM and MB) with decreased convergence, regardless of whether the steps were

![Graphs](http://jn.physiology.org/)

**FIG. 3.** The vergence-velocity responses elicited by crossed-disparity steps: dependence on the amplitude of the step (sample mean traces for 3 subjects). **Top row:** vertical vergence velocity (\( \dot{V}_v \)) over time (ordinate) is plotted against horizontal vergence velocity (\( \dot{V}_h \)) over time (abscissa); dots on traces at 100, 120, 140, and 160 ms measured from the onset of the step; tick marks on the axes are at 1°/s intervals. **Middle and bottom rows:** temporal profiles for horizontal vergence velocity (\( \dot{V}_h \)) and vertical vergence velocity (\( \dot{V}_v \)), respectively; numbers at ends of traces, disparity steps (in deg); continuous lines, responses (to small disparity steps) that increment as stimulus amplitude increases; dashed lines, responses (to larger steps, indicated by numbers in parentheses) that decrement as stimulus amplitude increases; calibration bars, 2°/s; abscissa, time from onset of the disparity steps; upward deflections represent convergent (\( \dot{V}_h \)) and left-sursumvergent (\( \dot{V}_v \)) velocities. **Column A,** subject RK; **column B,** subject FM; **column C,** subject GM.
crossed or uncrossed. In fact, for a given subject, the vergence responses to the largest steps were always roughly the same, regardless of whether the steps were positive or negative, horizontal or vertical. This is made clear in Fig. 5, which shows the vergence velocity temporal profiles that were elicited when the 12.8° steps were applied in each of the four directions: crossed, uncrossed, left hyper, and right hyper. It follows from this that the initial responses were anticompensatory with large steps in one or the other direction: uncrossed steps in some subjects (RK, FM, KP, and HA) and crossed steps in others (GM and MB).

It is also evident from Figs. 3 and 4 that the time course of the individual vergence response profiles could vary considerably, some showing a gradual climb toward a peak, others peaking rapidly (especially in GM), and yet others showing a reasonably steady climb except for a brief dip here and there. These declines and dips began at latencies considerably less than twice the reaction time and were unrelated to the closing of the visual feedback loop. The response profiles of subject GM clearly differed from those of RK and FM in their transiency (as well as in their polarity with large steps).

The dependence of the initial (open-loop) isogonal responses on the magnitude and direction of the horizontal disparity steps was examined quantitatively by measuring the change in horizontal vergence position over the 67-ms time interval starting 90 ms after the onset of the disparity step. Disparity tuning curves based on these measures had the general form of the derivative of a Gaussian and are shown in Fig. 6A (●, ■, and ♦) for each of the three subjects whose response profiles are shown in Figs. 3–5. In these plots, responses are compensatory when they fall in either the top right quadrant (in which crossed disparity steps produced increases in convergence) or the bottom left quadrant (in which uncrossed disparity steps produced decreases in convergence). For small steps (<1°), the curves all have roughly linear positive slopes passing through zero: this is the servo range over which small increases in the input elicited roughly proportional increases in the output in the appropriate (compensatory) direction. (We will return to this issue later.) All curves peak with steps of 1–2° and then decline toward an asymptote that, for a given subject, is very similar for crossed and uncrossed steps, so that responses to steps in one direction are compensatory (in the top right or bottom left quadrants), whereas the responses to steps in the other direction are anticompensatory (in the top left or bottom right quadrants). Figure 6A also includes the horizontal vergence measures for the responses to the largest vertical disparity steps (12.8°): see the open symbols plotted at the right and left extremes labeled “Vertical steps (left hyper),” and “Vertical steps (right hyper).” Student’s t-test failed to reveal any significant differences at the 0.05 level among the horizontal responses of a given subject to the four 12.8° stimuli (crossed, uncrossed, left hyper, and right hyper).
Orthogonal components. The vergence responses to horizontal disparity steps also included orthogonal (i.e., vertical) components that were smaller, slower to develop, and generally less transient than the isogonal responses: see Figs. 3 and 4 (\(\dot{V}_v\) traces). The vergence velocity profiles in Figs. 3 and 4 suggest that the latency of the orthogonal components was generally 20–30 ms longer than that of the isogonal components. Unfortunately, this could not be confirmed with our objective algorithm because of the small amplitude of the orthogonal components, and we used the same measurement interval as for the isogonal components (90–157 ms). The response measures plotted in Fig. 6 indicate that these orthogonal responses developed roughly exponentially with increases in step size, generally reaching an asymptote with steps of only a few degrees. These orthogonal components were not simply methodological artifacts due to misalignment of the visual stimuli with respect to the eye coil signals or \(x/y\) coil cross talk because 1) for a given stimulus, the orthogonal responses could be in opposite directions in different subjects (the sign was idiosyncratic); 2) for a given subject, the temporal response profiles and disparity tuning curves for the orthogonal component (\(V_v\) traces in Figs. 3 and 4, curves in Fig. 6B, respectively) were not simply scaled down versions of those for the isogonal component (\(V_h\) traces in Figs. 3 and 4, curves in Fig. 6A, respectively); 3) for a given subject, the orthogonal vergence responses for crossed and uncrossed steps had the same sign: compare the \(V_v\) traces in Figs. 3 and 4, and also compare the data for positive and negative disparity steps in Fig. 6B. Like the isogonal (horizontal) vergence responses, for a given subject, the orthogonal (vertical) vergence responses to the largest horizontal steps (12.8°) were the same regardless of whether the steps were crossed, uncrossed, left hyper, or right hyper: see the traces labeled, \(V_v\), in Fig. 5, and the data plotted at the right and left extremes of Fig. 6B. Student’s \(t\)-test failed to reveal any significant differences at the 0.05 level among the vertical vergence responses to the largest steps in the four directions tested.

It is now clear that the (default) responses to large horizontal (or vertical) steps were “oblique,” with both horizontal and vertical components that were idiosyncratic: three subjects showed increased convergence combined with left sursumvergence (RK, FM, and HA), two showed decreased convergence with right sursumvergence (GM and MB), and one showed increased convergence with right sursumvergence (KP).

Dynamic directional errors. Compared with the isogonal components, the orthogonal components were small and slow to develop, so that directional errors were generally modest for the very earliest vergence responses to horizontal disparity steps. The temporal development of the directional errors is best appreciated from \(x/y\) plots of the horizontal and vertical vergence velocity over time: top row of Figs. 3 and 4. For steps less than \(\approx 2^\circ\), the \(x/y\) vergence velocity traces start out near the origin and keep fairly close to the horizontal (isogonal) axis before gradually veering away. (Note that the dots on the \(x/y\)
vergence velocity traces occur 100, 120, 140, and 160 ms, after
the onset of the step.) As steps exceeded 2°, the amplitudes
of the isogonal components now shifted toward the asymp-
totes, allowing the orthogonal components, which were now
maximal, to introduce increasingly large directional errors.
Note that the similarity of the responses to large steps in each
of the four directions is evident not only from superimposing
the temporal profiles of $V_\dot{h}$ and of $V_\dot{v}$ but also from superim-
posing the $x/y$ plots in which these two parameters are plotted
against one another (see Fig. 5, top row).

Vergence responses to vertical disparity steps

Vertical disparity steps of suitable amplitude elicited con-
sistent vertical vergence responses at short latencies. Using the
vertical vergence velocity data obtained with 1.2° left-hyper
steps, mean latency (±SD) determined by our objective
method was 85.1 ± 3.4 ms for four subjects. Individual mean
latencies (±SD), together with the number of measures con-
tributing to the estimates and the total number of trials from
which the data were drawn, were 86.9 ± 12.4 ms (subject RK,
$n = 159/179$), 84.9 ± 12.3 ms (FM, 122/145), 88.2 ± 14.3 ms
(GM, 152/177), and 80.5 ± 11.5 ms (HA, 26/31). These laten-
ties are on average 3 ms longer than those listed earlier for the
isogonal vergence responses (of these same 4 subjects) to
horizontal disparity steps.

Binocular response to a binocular stimulus

Once again, we tested the possibility that these short-latency (isogonal)
vergence responses might have resulted from independent
monocular tracking, rather than from disparity per se, by re-
stricting the steps to one eye only, leaving the other eye to view
a stationary pattern. The results of one such experiment on
subject RK are shown in Fig. 7, in which vertical positive-
disparity steps (that is, left-hyper steps) of 1.2° were applied by
1) shifting the pattern seen by the left eye 0.6° upward and the
pattern seen by the right eye 0.6° downward (—), 2) shifting
the pattern seen by the left eye 1.2° upward (•••••••), or 3) shifting
the pattern seen by the right eye 1.2° downward (•••••••••). The
outcome was essentially the same as for horizontal vergence in
that monocular steps were almost as effective as binocular ones
in producing (isogonal) vergence, and the eye that saw the
stationary pattern always moved in a direction appropriate for
a stereo-driven response: when only the right eye saw a step
(downward), the left eye moved upward, and when only the left
eye saw a step (upward) then the right eye moved downward.
or less, and used a logarithmic scale. The most salient features of the data in Fig. 11 are as follows: 1) the highest features for the vertical-step data overlap the lowest curves for the horizontal-step data; 2) over the range of low disparities examined here, the shapes of the curves undergo a transition from convex upward (lowest curves) to concave upward (highest curves), one consequence being that, 3) the lower curves tend to peak earlier (i.e., at lower disparities) than the higher curves; 4) for stimuli in a given plane (horizontal or vertical), the curves tended to be steeper for the steps that evoked responses in the direction of the default: crossed and left hyper for RK and FM, uncrossed and right hyper for GM.

The orthogonal (horizontal) responses to vertical steps were much stronger than the orthogonal (vertical) responses to horizontal steps, with latencies this time that were comparable with those of the isogonal components. One consequence was that vergence directional errors could be much greater with vertical disparity steps. In fact, for vertical steps greater than \( \approx 1.5^\circ \), the orthogonal responses were actually greater than the isogonal responses. For vertical steps \( >5^\circ \), default responses predominated, and both the horizontal and the vertical vergence response measures were independent of whether the steps were positive or negative, horizontal or vertical (see also Fig. 5). The large directional errors with vertical disparity steps are most easily appreciated from the \( x/y \) plots of the horizontal and vertical vergence velocity over time (Figs. 8 and 9, top rows). These \( x/y \) vergence velocity traces all start out near the origin, but only the traces resulting from very small steps \( (0.4^\circ) \) consistently kept fairly close to the vertical (isogonal) axis; most responses to vertical steps \( >0.4^\circ \) veered off in a horizontal direction almost immediately, although occasional ones kept fairly close to the vertical axis at first. Of course, the \( x/y \) trajectories obtained with the largest vertical steps are essentially the same as those obtained with the largest horizontal steps (Fig. 5).

**Quantitative comparison of the disparity tuning curves for horizontal and vertical steps**

We fitted mathematical functions to the change-in-vergence measures for both the isogonal and orthogonal components of the vergence responses, and these functions are plotted as smooth curves in Figs. 6 and 10. The function parameters provide a succinct summary of the data and permit quantitative comparisons of the responses of the different subjects and, for a given subject, of the responses to horizontal versus vertical steps. Later, the function parameters will be used to compare the data for different stimulus patterns (large-dot patterns vs. small-dot patterns), as well as for human versus monkey.

The following exponential function (Eq. 1) was fitted to the mean orthogonal responses of each subject

\[
C + A_o \cdot \left(1 - e^{-\theta/\theta_o}\right)
\]

where \( d \) is the disparity error created by the step, \( A_o \) is the asymptotic level of the exponential, \( C \) is an offset, and \( \theta_o \) is the space constant. It is clear from the curves in Figs. 6B and 10B that Eq. 1 generally provided a good fit to the orthogonal data with the exception of the responses of FM to crossed steps, which were unusual in showing a slight overshoot before settling at the asymptotic level. The best-fit parameters for all three subjects are listed in Table 1, which also includes an
estimate of the goodness of fit, $r^2$, based on the percentage of the disparity-induced variation in vergence explained by the sum of squares due to regression, with compensation for the mean: mean corrected $r^2$ (Cumming and Parker 1999; Engelman 1999). Most of the fits were clearly very good, $r^2$ averaging more than 90%, despite the poor fit for the data of FM. Table 1 indicates that the space constant, $B_0$, showed considerable inter-subject variation (range: 0.39 –3.35°) and, for a given subject, could show substantial directional asymmetries for crossed versus uncrossed and right-hyper versus left-hyper stimuli. Excluding the crossed-step data for FM (because the fit was poor), $B_0$ was always larger for the vertical vergence responses than for the horizontal, on average, by 130% (1.93 vs. 0.84°). It is also evident from Table 1 that $A_o$ and $C$ were generally negatively correlated. For example, on average, $C$ is $-21\%$ of $A_o$ (correlation coefficient 0.96) for the horizontal responses to vertical steps and $-11\%$ of $A_o$ (0.74) for the vertical responses to horizontal steps. This means that the exponential fit generally showed a reversal in sign for the smallest disparities. Often, this reversal occurred below 0.2° (the smallest step that we used), and no reversal was evident in the recorded data. In such cases, it is possible that the $y$-offset in Eq. 1 (C) actually compensates for a small $x$-offset in the data, such as might occur, for example, if there were a small dead zone within which disparity is ineffective. This raises the possibility that an $x$-offset might be more appropriate in Eq. 1 than the $y$-offset that we have used. However, in other cases, the recorded responses to the smallest steps showed a clear reversal in sign: for examples, see the data of GM (uncrossed) and RK (crossed) in Fig. 6B. In such cases, where the fitted exponential function must show sign reversal, a separate $y$-offset term is critical.

The following function (Eq. 2) was fitted to the isogonal responses

$$A_o[1 - e^{-(d/D_o)}] + G \exp\left[-\frac{(d' - D)^2}{2\sigma^2}\right] \cos\left[2\pi(d' - D) + \phi\right]$$

The first term in Eq. 2 accounts for the nonzero asymptote, and, because this was independent of the direction of the step, we assumed that it shared the exponential development of the
response to the orthogonal stimulus. Accordingly, the first term is an exponential function with an asymptotic level, $A_i$, and a space constant, $B_i$. The latter was fixed at the value of the space constant that was obtained when Eq. 1 was fitted to the pooled orthogonal data: for the horizontal isogonal fits, we pooled the horizontal responses to right-hyper and left-hyper steps, and for the vertical isogonal fits, we pooled the vertical responses to crossed and uncrossed steps. The second term in Eq. 2 is a Gabor function, in which $s$ is the Gaussian width, $f$ and $f'$ are the spatial frequency and phase of the cosine term, and $G$ is a gain factor. Because the data were usually not symmetrical about zero, we incorporated a parameter, $D$, to allow the peak of the Gaussian to shift, and, because the rate at which responses incremented (with small disparities) was sometimes appreciably greater than the rate at which they decremented (with higher disparities), we scaled the disparity, $d$, by a compression factor, $F$, which could have values ranging downward from unity. A value for $F$ of unity indicates no asymmetry, and lower values indicate that the rising phase of the tuning curve was steeper than the falling phase (increased skew). It is clear from the curves in Figs. 6A and 10A that Eq. 2 provided a good fit to the isogonal data for all three subjects, and the best-fit parameters for these curves are listed in Table 2, together with an estimate of the goodness of fit (again, $r^2$), and $P$, the peak-to-peak amplitude of the best-fit functions. The mean $r^2$ indicates that, on average, the fit accounted for 99.4% of the disparity-induced variation in vergence. Table 2 indicates that the amplitude ($P$), Gaussian width ($\sigma$), and compression factor ($F$) were consistently greater for the responses to horizontal steps than for the responses to vertical steps: on average, $P$ by 241%, $s$ by 43%, and $F$ by 31%. The spatial frequency ($f$) and phase ($f'$) were quite variable (range for $f$, 0.028–0.164 cycles/deg; range for $f'$, 263.5–278.6°), but neither showed consistent differences between horizontal and vertical. The differences in $F$ indicate that the asymmetry in the rising and falling phases of the tuning curves was greater for the vertical data.

**Dependence on the size of the elements in the visual patterns**

All of the above vergence responses were obtained with random-dot patterns in which the individual dots each had a
diameter of 2°, and we now report the effects of changing the diameter of the dots up to eightfold while maintaining the same overall coverage (50%). These experiments were carried out on monkeys as well as humans to allow a comparison of the two species. We know from the study of Busettini et al. (1996b) that the disparity tuning curves for the isogonal horizontal responses of the monkey have the same general form as the curves of humans, resembling the derivative of a Gaussian with a nonzero asymptote. However, that earlier study did not document the orthogonal responses or the responses to vertical disparity steps and employed visual stimuli (irregular patterns) that cannot be formally described, so that direct quantitative comparisons with the present human data were not possible. We therefore undertook a comparison study on three monkeys and three humans using the same stimulus patterns.

The vergence responses of humans and monkeys showed a similar dependence on the size of the individual dots in the disparity stimuli, and Fig. 12 shows some representative data from one human subject. The most obvious effect on the isogonal disparity tuning curves was on the falling phase: for both horizontal and vertical steps, the transition from the peak to the asymptote tended to be more gradual as the dot size increased. The peak responses tended to occur at slightly higher disparities with the larger dots, but effects on the initial rapid rise to the peak were generally small and effects on the asymptote were somewhat variable. The latter was also evident in the orthogonal disparity tuning curves, and, in Fig. 12, B and D, this effect partially obscures a tendency for the space constant to increase with dot size.

Such quantitative effects were assessed by fitting Eq. 1 to the orthogonal data and Eq. 2 to the isogonal data, and the best-fit parameters are summarized in Tables 3 and 4, respectively, which show average data for the three humans and the three monkeys. The fits for the isogonal data were all extremely good for the human data (\(r^2, 99.4 \pm 0.2\% \text{ mean} \pm \text{SD}\)) and only slightly less so for the monkey data (\(r^2, 97.9 \pm 1.5\% \text{ mean} \pm \text{SD}\)). The fits for some of the orthogonal data were poor, especially for the monkey vertical responses (to horizontal steps), mostly because the latter were vanishingly small and sometimes showed a very slight transient overshoot similar to that of subject FM seen in Figs. 6B and 10B. (Note that this was of little consequence for the fits of Eq. 2 to the monkey’s vertical isogonal responses because the latter had correspond-

\[\text{FIG. 10. The dependence of vergence responses on the amplitude of the vertical disparity steps: tuning curves (3 subjects). Mean change-in-vergence measures (ordinate) are plotted (in filled symbols) against the amplitude of the disparity step (abscissa). A: vertical (isogonal) vergence responses; curves indicate the least-squares best fits obtained using Eq. 2, for which } r^2 \text{ averaged } 99.4\%. \text{ B: horizontal (orthogonal) vergence responses; curves indicate the least-squares best fits obtained using Eq. 1, for which } r^2 \text{ averaged } >90\% \text{ despite the poor fit for the left-hyper data of subject FM (} r^2 = 70.9\%). \text{ Open symbols are the mean change-in-vergence measures obtained with } 12.8° \text{ horizontal disparity steps (data for uncrossed steps shown at left, data for crossed steps shown at right). Key identifies the data from each of the 3 subjects. Error bars, 1 SD.}\]
FIG. 11. Isogonal vergence responses to horizontal and vertical disparity steps. Ordinate, absolute mean change-in-vergence measures; abscissa, amplitude of disparity step (logarithmic scale). Filled symbols and continuous lines, horizontal responses (thick: crossed steps; thin, uncrossed steps); open symbols and dashed or dotted lines, vertical responses (dotted: left-hyper steps; dashed, right-hyper steps). Circles, subject RK; squares, subject FM; diamonds, subject GM. Error bars, 1 SD.

...ing dot size. For example, for the fits for which \( r^2 \) values (\( A_i \) in Table 4) were smaller than two in monkeys and more than three in humans. Further, the Gaussian width, \( \sigma \), was larger for horizontal steps than for vertical, the values with horizontal steps exceeding those with vertical on average by more than 40% in both humans and monkeys. Also of interest was the compression factor, \( F \), which showed very little variation between subjects (on average, SDs were 11% of the mean for humans, and 13% for monkeys) but, for humans, was always a little larger for horizontal than for vertical (on average, by nearly 17%), consistent with there being greater asymmetry between the rising and falling phases of the tuning curves for the vertical data. However, Table 4 also indicates that this factor showed no consistent differences between horizontal and vertical in the monkey data. Regarding the orthogonal responses, the asymptotic values (\( A_o + C \)), for the horizontal responses (to vertical steps) were always appreciably larger than for the vertical responses (to horizontal steps), on average by a factor of 25 in monkeys and more than 3 in humans.

HUMANS VERSUS MONKEYS. The spatial tuning was broader in the humans than in the monkeys. This was apparent from the space constant, \( B_o \), and the Gaussian width, \( \sigma \), which decreased with increasing dot size for the horizontal responses (to vertical steps) on average by 47% in humans (horizontal, 41%; vertical, 53%) and 152% in monkeys (133%, 172%). The compression factor, \( F \), and the spatial frequency, \( f \), sometimes showed a slight tendency to decrease with increasing dot size, and this, together with the changes in \( \sigma \), largely accounted for the more gradual transition from the peak to the asymptote as the dot size increased. The only orthogonal parameter consistently showing a systematic dependence on dot size was the space constant, \( B_o \), which increased with increasing dot size. For example, for the fits for which \( r^2 > 0.8 \), the value of \( B_o \) with the largest dots exceeded that with the smaller ones (on average) by 68% in humans (for both horizontal and vertical vergence responses) and by 159% in monkeys (horizontal responses).

HORIZONTAL VERSUS VERTICAL RESPONSES. In general, responses were larger and the spatial tuning was slightly broader for the horizontal responses than for the vertical. Thus the peak-to-peak measure, \( P \), was always much greater for horizontal steps than for vertical, on average by a factor of more than two in monkeys and more than three in humans. Further, the Gaussian width, \( \sigma \), was larger for horizontal steps than for vertical, the values with horizontal steps exceeding those with vertical on average by more than 40% in both humans and monkeys. Also of interest was the compression factor, \( F \), which showed very little variation between subjects (on average, SDs were 11% of the mean for humans, and 13% for monkeys) but, for humans, was always a little larger for horizontal than for vertical (on average, by nearly 17%), consistent with there being greater asymmetry between the rising and falling phases of the tuning curves for the vertical data. However, Table 4 also indicates that this factor showed no consistent differences between horizontal and vertical in the monkey data. Regarding the orthogonal responses, the asymptotic values (\( A_o + C \)), for the horizontal responses (to vertical steps) were always appreciably larger than for the vertical responses (to horizontal steps), on average by a factor of 25 in monkeys and more than 3 in humans.

Could the default responses with large disparity steps be due to the emergence of a phoria?

Because the responses to large steps were independent of the direction of the step, it was possible that they were not actively generated by the binocular visual stimuli but rather represented the emergence of a phoria. This explanation assumes that the largest steps exceeded the system’s ability to sense disparity and that the two eyes then passively assumed a (mis)alignment characteristic for each subject (Leigh and Zee 1999). We measured the subjects’ steady-state phorias in our near-viewing situation by assessing the binocular alignment of the eyes during monocular viewing (see METHODS), and the findings are listed in Table 5. (Note that the phoria values listed in Table 5 are given with respect to the plane of the screen, 0 indicating that the 2 lines of sight intersected exactly at the screen, positive values that the eyes converged in front of the screen, and negative values that the eyes converged beyond the screen.) Vertical phorias were generally very small and showed little variability, the absolute values averaging only 0.30° and the SDs averaging only 0.11°. The corresponding values for the horizontal phorias were appreciably larger: 3.71 and 0.55°. Table 5 also lists (under the heading “Default”) the average change-in-vergence measures for the largest (12.8°) disparity steps for each of the subjects, and it is clear that these measures often have the opposite sign to the subjects’ phorias. In particular, all (6) subjects had negative horizontal phorias, indicating that, with monocular viewing, their eyes were converged...
TABLE 1.  Best-fit parameters when Eq. 1 was fitted to the mean orthogonal responses obtained with horizontal and vertical disparity steps

<table>
<thead>
<tr>
<th>Stimulus</th>
<th>Subject</th>
<th>$A_i$</th>
<th>$B_i$</th>
<th>$C$</th>
<th>$r^2$, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Horizontal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Right-Hyper</td>
<td>RK</td>
<td>0.201</td>
<td>0.81</td>
<td>−0.036</td>
<td>97.8</td>
</tr>
<tr>
<td></td>
<td>FM</td>
<td>0.091</td>
<td>1.11</td>
<td>−0.027</td>
<td>88.3</td>
</tr>
<tr>
<td></td>
<td>GM</td>
<td>−0.118</td>
<td>0.71</td>
<td>0.026</td>
<td>95.2</td>
</tr>
<tr>
<td>Left-Hyper</td>
<td>RK</td>
<td>0.217</td>
<td>1.22</td>
<td>−0.045</td>
<td>97.1</td>
</tr>
<tr>
<td></td>
<td>FM</td>
<td>0.084</td>
<td>0.47</td>
<td>−0.039</td>
<td>70.9</td>
</tr>
<tr>
<td></td>
<td>GM</td>
<td>−0.134</td>
<td>0.70</td>
<td>0.027</td>
<td>93.1</td>
</tr>
<tr>
<td>Vertical</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crossed</td>
<td>RK</td>
<td>0.029</td>
<td>3.35</td>
<td>−0.003</td>
<td>97.9</td>
</tr>
<tr>
<td></td>
<td>FM</td>
<td>0.024</td>
<td>0.39</td>
<td>−0.005</td>
<td>59.8</td>
</tr>
<tr>
<td></td>
<td>GM</td>
<td>−0.034</td>
<td>1.53</td>
<td>0.000</td>
<td>95.4</td>
</tr>
<tr>
<td>Uncrossed</td>
<td>RK</td>
<td>0.025</td>
<td>1.53</td>
<td>−0.002</td>
<td>97.8</td>
</tr>
<tr>
<td></td>
<td>FM</td>
<td>0.023</td>
<td>1.55</td>
<td>0.000</td>
<td>97.9</td>
</tr>
<tr>
<td></td>
<td>GM</td>
<td>−0.032</td>
<td>1.67</td>
<td>0.008</td>
<td>91.4</td>
</tr>
</tbody>
</table>

An iterative procedure with a least-squares criterion was used to obtain the best fits with each of the parameters resolved to the number of decimal places shown. $r^2$ is an estimate of the goodness-of-fit based on the percentage of the disparity-induced variation in vergence explained by the sum of squares due to regression, with compensation for the mean: mean corrected $r^2$ (SYSTAT). Parameters $A_i$, $B_i$, and $C$ are in degrees. Disparity tuning curves based on these best-fit parameters are shown in Figs. 6B and 10B.

well beyond the screen, yet the horizontal default responses of four subjects (RK, FM, HA, and KP) were positive and involved increased convergence.

Dependence on a prior saccadic eye movement

All of the above vergence responses were obtained with disparity steps applied 50 ms after the centering saccade. Busetti et al. (1996b) showed that, in monkey, disparity steps applied at such times generated much more vigorous responses than when applied some time later: disparity vergence showed transient postsaccadic enhancement. That the same is true of human disparity-vergence responses is readily apparent from the sample data in Fig. 13A (left side), which shows the mean horizontal vergence velocity responses elicited in subject FM, by 1.6° crossed-disparity steps applied at selected times after the centering saccades. Effects on response latency were generally minor, and our usual change-in-vergence measures were used to quantify the dependence on postsaccadic delay by expressing them as a percentage of the measures obtained with the shortest delay interval (50 ms). The (isogonal) data obtained from two subjects using crossed and uncrossed horizontal disparity steps are plotted in filled symbols and continuous lines in Fig. 14A. The magnitude and time course of the postsaccadic decay in response amplitude clearly varied considerably between the two subjects and the two kinds of disparity step. For example, the response with the longest postsaccadic interval ranged from 15 to 67% (mean ± SD 43 ± 23%) of that with the shortest interval. The decay over time was roughly exponential, and the following function (Eq. 3) was fitted to the isogonal responses:

$$[100 - A] \cdot e^{(-t/\tau)} + A$$

where $psd$ is the postsaccadic delay (in ms), $A$ is the asymptotic level (%), and $\tau$ is the time constant (in ms). The best-fit values for $\tau$ were 157 ms (FM) and 120 ms (GM) for crossed steps, 343 ms (FM) and 181 ms (GM) for uncrossed steps (mean ± SD 200 ± 98 ms). It was apparent that the orthogonal vergence responses to horizontal steps also showed postsaccadic enhancement, but responses were always very small and quantitative measures were not attempted.

COMPARISON WITH OCULAR FOLLOWING. These effects of a prior saccade on the vergence responses to disparity steps were reminiscent of the transient postsaccadic enhancement of ocular following described by Gellman et al. (1990), and we made a direct comparison of the two phenomena. For this, the disconjugate steps used to elicit disparity vergence were replaced with conjugate steps to elicit ocular following (see METHODS). Some sample ocular following data obtained from subject FM are assembled in Fig. 13B (left side), which shows the mean (right) eye velocity profiles elicited by 0.8° rightward conjugate steps applied at selected times after the centering saccades. Effects on latency were again clearly negligible, and mean change-in-eye-position measures were used to quantify the dependence on postsaccadic delay by expressing them as a percentage of the measures obtained with the shortest delay interval (see METHODS). These data are plotted as open symbols and discontinuous lines in Fig. 14A, and it is immediately apparent that the ocular following data strongly resemble the disparity vergence data. Once more the magnitude of the enhancement varied considerably between the two subjects and the two kinds of conjugate steps. For example, the response at the longest interval ranged from 15 to 56% (mean ± SD 32 ± 18%) of that at the shortest interval, the average decrement being 19% greater than that seen (at the same interval) with disparity vergence. As previously reported by Gellman et al., the decay over time was roughly exponential, and the time

An iterative procedure with a least-squares criterion was used to obtain the best fits with each of the parameters resolved to the number of decimal places shown. $P$ is the peak-to-peak amplitude of Eq. 2, $r^2$ is an estimate of the goodness-of-fit, as in Table 1. $A_i$, $B_i$, $D$, $G$, $\sigma$, $\phi$, and $P$ are in degrees, $f$ is in cycles/deg, and $F$ is dimensionless. Disparity tuning curves based on these best-fit parameters are shown in Figs. 6A and 10A.

TABLE 2.  Best-fit parameters when Eq. 2 was fitted to the mean isogonal responses obtained with horizontal and vertical disparity steps

<table>
<thead>
<tr>
<th>Stimulus</th>
<th>Subject</th>
<th>$A_i$</th>
<th>$B_i$</th>
<th>$G$</th>
<th>$\sigma$</th>
<th>$D$</th>
<th>$f$</th>
<th>$\phi$</th>
<th>$F$</th>
<th>$r^2$, %</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Horizontal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Right-Hyper</td>
<td>RK</td>
<td>0.169</td>
<td>1.00</td>
<td>1.05</td>
<td>1.83</td>
<td>0.58</td>
<td>0.046</td>
<td>278.6</td>
<td>0.96</td>
<td>99.6</td>
<td>0.678</td>
</tr>
<tr>
<td></td>
<td>FM</td>
<td>0.047</td>
<td>0.76</td>
<td>1.50</td>
<td>1.60</td>
<td>0.36</td>
<td>0.028</td>
<td>273.4</td>
<td>0.91</td>
<td>99.3</td>
<td>0.514</td>
</tr>
<tr>
<td></td>
<td>GM</td>
<td>−0.092</td>
<td>0.57</td>
<td>0.57</td>
<td>1.85</td>
<td>−0.32</td>
<td>0.064</td>
<td>263.5</td>
<td>0.92</td>
<td>98.9</td>
<td>0.478</td>
</tr>
<tr>
<td>Vertical</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crossed</td>
<td>RK</td>
<td>0.025</td>
<td>2.12</td>
<td>0.50</td>
<td>1.03</td>
<td>0.20</td>
<td>0.029</td>
<td>271.8</td>
<td>0.70</td>
<td>99.5</td>
<td>0.117</td>
</tr>
<tr>
<td></td>
<td>FM</td>
<td>0.020</td>
<td>0.66</td>
<td>0.11</td>
<td>1.38</td>
<td>0.03</td>
<td>0.164</td>
<td>268.3</td>
<td>0.70</td>
<td>99.2</td>
<td>0.147</td>
</tr>
<tr>
<td></td>
<td>GM</td>
<td>−0.028</td>
<td>1.63</td>
<td>0.23</td>
<td>1.28</td>
<td>−0.01</td>
<td>0.113</td>
<td>269.5</td>
<td>0.73</td>
<td>99.6</td>
<td>0.225</td>
</tr>
</tbody>
</table>
constants estimated from best-fitting exponentials (Eq. 3) were 151 ms (subject FM) and 230 ms (GM) for rightward steps, 124 ms (subject FM) and 149 ms (GM) for leftward steps (mean ± SD 164 ± 46 ms). These values are on average 18% smaller than those for the disparity-vergence data, but the differences for a given individual again clearly varied widely. Thus on average, the postsaccadic enhancement of ocular following was slightly greater and more transient than that of disparity vergence.

Are the effects of a prior saccade due to the associated visual reafference?

We investigated the possibility that the effects of a prior saccade resulted from the visual reafference associated with the saccade sweeping the image of the pattern across the retina. For this, we applied the disparity steps in the wake of saccade-like (conjugate) shifts of the visual patterns (“simulated saccades”: see METHODS). Note that the trials yielding the data in this section were interleaved with others in which the disparity steps were delivered after real saccades (data in the previous section).

The simulated saccades resulted in transient enhancements of the initial isogonal vergence responses to horizontal disparity steps that roughly resembled those seen in the wake of real saccades: Figs. 13A (right side) and 14B (filled symbols, continuous lines). When expressed in terms of the responses at the shortest interval after the saccade shift, the responses at the longest interval ranged from 11 to 59% (mean ± SD 39 ± 20%), which values are comparable with those seen at the same interval after a real saccade, although there was considerable individual variation. The decay over time was only roughly exponential, and the time constants estimated from best-fitting exponentials (Eq. 3), were 221 ms (subject FM) and 33 ms (GM) for crossed steps, and 228 ms (subject FM) and 119 ms (GM) for uncrossed steps (mean ± SD 150 ± 93 ms). These values are on average 25% smaller than those for the disparity-vergence data in the wake of a real saccade, although again the differences for a given individual varied widely. Thus on average, the enhancement of disparity vergence after a simulated saccade was comparable in amplitude to, but somewhat more transient than, that after a real saccade.
TABLE 4.  Best-fit parameters when Eq. 2 was fitted to the mean isogonal responses obtained with horizontal and vertical disparity steps using patterns with dots of various sizes

<table>
<thead>
<tr>
<th>Subject</th>
<th>Size, deg</th>
<th>$A_i$</th>
<th>$G$</th>
<th>$\sigma$</th>
<th>$D$</th>
<th>$f$</th>
<th>$\phi$</th>
<th>$F$</th>
<th>$P$</th>
<th>$r^2$, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Human</td>
<td>0.5</td>
<td>0.021 ± 0.007</td>
<td>0.75 ± 0.58</td>
<td>0.007 ± 0.001</td>
<td>77 ± 25</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.1</td>
<td>0.021 ± 0.006</td>
<td>1.01 ± 0.69</td>
<td>0.004 ± 0.003</td>
<td>90 ± 10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2.2</td>
<td>0.027 ± 0.012</td>
<td>1.36 ± 0.77</td>
<td>0.006 ± 0.004</td>
<td>96 ± 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>4.4</td>
<td>0.019 ± 0.012</td>
<td>1.69 ± 0.53</td>
<td>0.003 ± 0.000</td>
<td>92 ± 6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Monkey</td>
<td>0.5</td>
<td>0.006 ± 0.005</td>
<td>1.73 ± 1.41</td>
<td>0.004 ± 0.003</td>
<td>40 ± 36</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.1</td>
<td>0.006 ± 0.005</td>
<td>1.76 ± 1.82</td>
<td>0.003 ± 0.004</td>
<td>42 ± 33</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2.2</td>
<td>0.006 ± 0.006</td>
<td>0.33 ± 0.08</td>
<td>0.003 ± 0.004</td>
<td>26 ± 20</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>4.4</td>
<td>0.005 ± 0.005</td>
<td>2.19 ± 2.66</td>
<td>0.003 ± 0.003</td>
<td>39 ± 29</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Values are means ± SD for 3 humans and 3 monkeys. Responses to crossed/uncrossed and to left-hyper/right-hyper steps were each first pooled for each subject. Parameters were then fitted to the data for each subject and subsequently averaged. An iterative procedure with a least-squares criterion was used to obtain the best fits with each of the parameters resolved to the number of decimal places shown. $r^2$ is an estimate of the goodness-of-fit, as in Table 1.

COMPARISON WITH OCULAR FOLLOWING. Simulated saccades were also used to examine the extent to which the postspaccadic enhancement of ocular following might also involve visual reafference. For this, the disconjugate steps used to elicit disparity vergence were again replaced with conjugate steps to elicit ocular following (see METHODS). A prior saccadelike shift of the pattern resulted in a transient enhancement of the initial ocular following responses to conjugate steps (Fig. 13B, right side; Fig. 14B, open symbols and discontinuous lines), although the response waveforms were rather different from those in the wake of a real saccade. When expressed in terms of the responses at the shortest interval after the saccadelike

TABLE 5.  Best-fit parameters when Eq. 3 was fitted to the mean responses obtained with horizontal and vertical disparity steps using patterns with dots of various sizes

<table>
<thead>
<tr>
<th>Subject</th>
<th>Size, deg</th>
<th>$A_i$</th>
<th>$G$</th>
<th>$\sigma$</th>
<th>$D$</th>
<th>$f$</th>
<th>$\phi$</th>
<th>$F$</th>
<th>$P$</th>
<th>$r^2$, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Human</td>
<td>0.5</td>
<td>0.050 ± 0.028</td>
<td>1.18 ± 0.30</td>
<td>1.26 ± 0.19</td>
<td>0.22 ± 0.15</td>
<td>0.043 ± 0.018</td>
<td>274 ± 4</td>
<td>0.90 ± 0.06</td>
<td>0.45 ± 0.08</td>
<td>99.5 ± 0.4</td>
</tr>
<tr>
<td></td>
<td>1.1</td>
<td>0.060 ± 0.029</td>
<td>0.87 ± 0.24</td>
<td>1.36 ± 0.19</td>
<td>0.22 ± 0.14</td>
<td>0.061 ± 0.008</td>
<td>274 ± 5</td>
<td>0.91 ± 0.05</td>
<td>0.52 ± 0.04</td>
<td>99.4 ± 0.1</td>
</tr>
<tr>
<td></td>
<td>2.2</td>
<td>0.057 ± 0.041</td>
<td>0.82 ± 0.35</td>
<td>1.74 ± 0.38</td>
<td>0.33 ± 0.13</td>
<td>0.058 ± 0.018</td>
<td>273 ± 7</td>
<td>0.89 ± 0.05</td>
<td>0.53 ± 0.08</td>
<td>99.4 ± 0.1</td>
</tr>
<tr>
<td></td>
<td>4.4</td>
<td>0.069 ± 0.037</td>
<td>1.21 ± 0.18</td>
<td>1.75 ± 0.12</td>
<td>0.36 ± 0.18</td>
<td>0.032 ± 0.012</td>
<td>273 ± 4</td>
<td>0.75 ± 0.04</td>
<td>0.50 ± 0.08</td>
<td>99.4 ± 0.3</td>
</tr>
<tr>
<td>Monkey</td>
<td>0.5</td>
<td>0.044 ± 0.031</td>
<td>0.24 ± 0.12</td>
<td>0.91 ± 0.06</td>
<td>0.24 ± 0.13</td>
<td>0.142 ± 0.060</td>
<td>276 ± 1</td>
<td>0.76 ± 0.07</td>
<td>0.19 ± 0.05</td>
<td>98.4 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>1.1</td>
<td>0.064 ± 0.033</td>
<td>0.29 ± 0.24</td>
<td>1.12 ± 0.11</td>
<td>0.27 ± 0.18</td>
<td>0.145 ± 0.085</td>
<td>274 ± 7</td>
<td>0.82 ± 0.14</td>
<td>0.22 ± 0.06</td>
<td>97.9 ± 0.3</td>
</tr>
<tr>
<td></td>
<td>2.2</td>
<td>0.068 ± 0.046</td>
<td>0.18 ± 0.07</td>
<td>1.68 ± 0.52</td>
<td>0.24 ± 0.09</td>
<td>0.163 ± 0.047</td>
<td>274 ± 4</td>
<td>0.74 ± 0.08</td>
<td>0.25 ± 0.11</td>
<td>96.5 ± 3.0</td>
</tr>
<tr>
<td></td>
<td>4.4</td>
<td>0.068 ± 0.044</td>
<td>0.17 ± 0.15</td>
<td>2.10 ± 0.32</td>
<td>0.39 ± 0.24</td>
<td>0.152 ± 0.076</td>
<td>276 ± 7</td>
<td>0.77 ± 0.19</td>
<td>0.20 ± 0.09</td>
<td>95.8 ± 0.6</td>
</tr>
</tbody>
</table>

Values are means ± SD for 3 humans and 3 monkeys. An iterative procedure with a least-squares criterion was used to obtain the best fits with each of the parameters resolved to the number of decimal places shown. Parameters were then fitted to the data for each subject and then averaged. Values for parameter, $B_i$, were not free but set at the values obtained from fitting Eq. 1 to the orthogonal data and their mean values are given in Table 3 under $B_i$ (see text). $P$ is the peak-to-peak amplitude of Eq. 2. $r^2$ is an estimate of the goodness-of-fit, as in Table 1. $A_i$, $D$, $G$, $\sigma$, $\phi$, and $P$ are in degrees, $f$ is in cycles/deg, and $F$ is dimensionless.
TABLE 5. Comparison of default vergence responses and phoria measures

<table>
<thead>
<tr>
<th>Subject</th>
<th>Horizontal</th>
<th>Vertical</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Phoria</td>
<td>Default</td>
</tr>
<tr>
<td>RK</td>
<td>-1.55 ± 0.47</td>
<td>0.17 ± 0.07</td>
</tr>
<tr>
<td>FM</td>
<td>-5.40 ± 0.37</td>
<td>0.05 ± 0.08</td>
</tr>
<tr>
<td>GM</td>
<td>-4.72 ± 1.24</td>
<td>-0.09 ± 0.09</td>
</tr>
<tr>
<td>HA</td>
<td>5.26 ± 0.44</td>
<td>0.01 ± 0.04</td>
</tr>
<tr>
<td>KP</td>
<td>5.90 ± 0.52</td>
<td>0.12 ± 0.09</td>
</tr>
<tr>
<td>MB</td>
<td>-2.06 ± 0.26</td>
<td>-0.01 ± 0.03</td>
</tr>
</tbody>
</table>

Values are means ± SD in degrees; numbers in parentheses are number of measures. Default responses are the mean vergence measures obtained with the largest steps, pooling responses for all 4 directions (12° crossed, uncrossed, left hyper, and right hyper). Positive values indicate eyes converged in front of the screen.

shift, the responses at the longest interval ranged from 11 to 47% (29 ± 15%), which averages 91% of that seen at the same interval after a real saccade. The decay over time was roughly exponential, and the time constants estimated from best-fitting exponentials (Eq. 3) were 159 ms (subject FM) and 139 ms (GM) for rightward steps, and 28 ms (subject FM) and 288 ms (GM) for leftward steps (mean ± SD 153 ± 106 ms). These values are on average only slightly smaller (7%) than those for the real-saccade data, but the differences for a given individual varied widely. Thus on average, the enhancement of ocular following after a simulated saccade was roughly comparable with that of disparity vergence in that it was slightly weaker and more transient than that after a real saccade.

**DISCUSSION**

**Short latencies and machinelike consistency**

The vergence responses induced by small disparity steps applied to large textured patterns had ultra-short latencies and almost machinelike consistency despite the fact that subjects were never given explicit instructions to respond to the steps. For example, the mean latencies of the horizontal vergence responses to 2° horizontal crossed-disparity steps ranged from 75.6 to 86.0 ms for the seven subjects examined, with individual SDs ranging from 4.8 to 11.6 ms. The data for vertical vergence responses to vertical disparity steps were very similar except that response amplitudes were much smaller and latencies were on average 3 ms longer. These latency measures were obtained using steps that were close to optimal, but it is evident from the vergence velocity temporal profiles in Figs. 3, 4, 8, 9, and 13 that latency was largely independent of the specific parameters of the steps and of the exact times at which the steps occurred with respect to a prior saccade. The small variance of the (objectively determined) latency estimates coupled with the total absence of any negative latencies indicates that these ultra-rapid responses were stimulus-driven and not the result of anticipation such as described by Kowler and Steinman (1979a,b). In a comparable study on monkeys, we previously reported mean latencies ranging from 52.2 to 53.4 ms with SDs ranging from 3.8 to 5.2 ms (Busettini et al. 1996b).

As pointed out in the Introduction, published estimates of the latency of disparity vergence in humans are generally in the range of 150–200 ms, and although most of these studies used small targets, some also used larger ones like our random-dot patterns (e.g., Erkelens and Collewijn 1991). Our use of a prior saccade (to boost response amplitudes), together with vergence velocity profiles rather than the more usual position profiles (to improve temporal resolution), might have increased the probability that the earliest responses would be detected sooner in our study. However, we think it unlikely that such methodological considerations can account for a difference that often exceeds 100 ms.

**Response to the binocular misalignment**

The experiments in which the step of disparity was applied to one eye only while the other eye viewed a stationary pattern (Figs. 2 and 7) indicate that the short-latency vergence responses were not the result of monocular visual tracking in which each eye independently tracked the apparent motion that it saw; the eye that saw the stationary scene always moved in a direction that was opposite to the motion seen by the other eye, exactly as expected of a stereoscopic mechanism that responds to the binocular misalignment.

It is also of interest that, even though the binocular stereoscopic cues here were asymmetric, they resulted in vergence eye movements that affected the two eyes almost equally. From Figs. 2 and 7 it is very evident that the version responses were appreciably weaker than the vergence responses. It seems unlikely that the low amplitude of the version was due merely to the fact that the version stimulus had only one-half the magnitude of the vergence stimulus (1.2 vs. 2.4°), especially given the vigorous version responses (ocular following) in Fig. 13B (left side) to 0.8° conjugate steps. A possible factor is that...
the earliest version responses to frontoparallel motion are best for binocular images moving in the plane of fixation and attenuate considerably if those images have disparity (Busettini et al. 1996a). Thus the version component of the response to the asymmetric steps may have been compromised by the fact that the 2.4° monocular steps shifted the binocular image out of the plane of fixation.

Dependence on a prior saccade

The initial horizontal vergence elicited by horizontal crossed-disparity steps showed clear transient enhancement in the immediate wake of a saccade (Figs. 13A, left side, and 14A). This enhancement was greatest with the shortest post-saccadic delay intervals, decreasing roughly exponentially as the delay interval increased, and was probably in part visual in origin because similar (although sometimes more transient) enhancement was seen after simulated saccades (Figs. 13A, right side, and 14B). Some of the differences in the enhancement due to real and simulated saccades might have resulted from the fact that the associated visual events did not exactly match (see Busettini et al. 1996b for discussion of the optical factors). Because of this, it is difficult to know how much weight to attach to the (sometimes minor) quantitative discrepancies between the effects of real and simulated saccades in our experiments. In sum, it is possible that the post-saccadic enhancement of disparity vergence is due in large part to the visual reafference resulting from the saccade sweeping the image of the pattern across the retina, but a contribution from nonvisual mechanism(s) cannot be excluded. Others have described nonvisual "priming effects" whereby stimulus-evoked eye movements can be influenced by another, prior eye movement (Cullen et al. 1991; Das et al. 1999; Lisberger 1998).

The post-saccadic enhancement of disparity vergence is strongly reminiscent of the post-saccadic enhancement of ocular following described by Gellman et al. (1990). In the present study we sought to compare the two directly using conjugate position steps to induce ocular following (in place of the conjugate position ramps in the study of Gellman et al.). On average, the peak enhancement after real and simulated saccades was slightly less for vergence than for ocular following (Fig. 14, A and B), although the enhancement of ocular following was sometimes slightly more transient. These data clearly suggest that the effects of a prior saccade on vergence and ocular following have a similar, if not exactly identical, etiology (for a discussion of the possible neural mechanisms...
that might mediate postsaccadic enhancement see Kawano and Miles 1986).

Busettini et al. (1996b) pointed out that most saccades involve a transfer of fixation between locations at different viewing distances and suggested that the postsaccadic enhancement of disparity vergence might help to speed the alignment of the two eyes on the newly acquired location. Kawano and Miles (1986) argued that by raising the gain only transiently (when needed most), the system avoids the potentially destabilizing effects of a permanently high gain. One possible problem with this scheme is that it assumes that the vergence control system can distinguish the object of regard from the background, yet our responses were obtained with very large stimuli. The recent findings of Howard et al. (2000) might offer a solution. These workers measured vergence responses while modulating disparity sinusoidally and found that the gain of the (isogonal) vergence responses for images centered on the fovea increased with stimulus size. Surprisingly, horizontal responses (to horizontal disparities) saturated when the stimulus subtended only 0.75°, whereas the vertical responses (to vertical disparities) did not saturate until the stimulus subtended 20°. This accords with the optical challenges faced by the two systems: the horizontal system must be able to respond to local differences in horizontal disparity to produce a convergent angle appropriate for the viewing distance of the object in the fovea, whereas a large integration area is preferred for the maintenance of the vertical alignment of the two eyes (see Howard et al. 2000 for detailed discussion of this point). One of the several differences between our study and that of Howard et al. was that the latter examined the closed-loop performance of the disparity vergence mechanism, whereas our analysis dealt solely with the initial open-loop response. Popple et al. (1998) used nonius lines to monitor the initial vergence responses elicited by brief disparity steps applied to the center part of a random-dot stereogram (while the surround remained at a fixed depth) and found that the initial vergence response increased with the area of the central region but, idiosyncratically, saturated when this region subtended 2–16° (average, 6°). The recent study of Stevenson et al. (1999) also indicates that foveal inputs carry much more weight than peripheral inputs, as though scaled in accordance with the cortical magnification factor. These studies raise the possibility that vergence responses similar to those we have studied might be obtainable with images much smaller than the ones we have used.

Responses of monkeys are similar to those of humans

The earlier studies of Busettini et al. (1996b) on the ultra-short-latency vergence responses of monkeys were largely restricted to horizontal isogonal responses. The present report extends this earlier study by including the disparity tuning of orthogonal as well as isogonal responses (vertical as well as horizontal) and is the first to provide such data for humans. As a result, it is now clear that the short-latency disparity-vergence responses of monkeys and humans have much in common: their disparity tuning curves, based on isogonal (or orthogonal) responses to horizontal (or vertical) disparity steps, have qualitatively similar forms and show a similar pattern of dependence on a prior saccade as well as on stimulus factors such as dot size. Of course, there are clear quantitative differences between the responses of the two species. For example, the monkey’s responses have a shorter latency (on average, by about 25 ms) and narrower disparity tuning curves (on average, the spatial frequency of the isogonal components, \( f \), is more than 2 times higher and the space constant of the orthogonal components, \( B_{\alpha} \), is about \( \frac{1}{2} \)). The responses of both species also show transient enhancement after saccades, real or simulated, although again, there are quantitative differences. For example, the time constants of the best fitting exponentials for the decay in postsaccadic enhancement averaged 52 ms in monkeys (Busettini et al. 1996b) and 200 ms in the two subjects in the present study. (Unfortunately, the 2 studies employed different visual stimuli: irregular geometrical patterns vs. random dots.) In our view, most of the differences between the two species involve scaling factors, and we conclude that the monkey is an excellent model for studying the neural basis of human short-latency disparity vergence.

Negative feedback depth-tracking system using disparity selective neurons?

It has often been pointed out that disparity-selective neurons provide a direct measure of vergence error and so have the potential to provide the primary drive for vergence eye movements like those described in the present paper. Such neurons have been recorded in a number of areas in monkey cortex, including striate and extrastriate visual areas (Burkhalter and Van Essen 1986; Cumming and Parker 1999, 2000; Felleman and Van Essen 1987; Hubel and Livingstone 1987; Hubel and Wiesel 1970; Poggio and Fischer 1977; Poggio and Talbot 1981; Poggio et al. 1988; Prince et al. 2000; Smith et al. 1997; Trotter et al. 1996), as well as the middle temporal (MT) area (Bradley and Andersen 1998; Bradley et al. 1995; DeAngelis and Newsome 1999; DeAngelis et al. 1998; Maunsell and Van Essen 1983), the medial superior temporal (MST) area (Eifuku and Wurtz 1999; Roy et al. 1992; Takemura et al. 1999), the posterior parietal area (Sakata et al. 1983), the lateral bank of the intraparietal sulcus (LIP) (Gnadt and Mays 1995), and the frontal eye field (FEF) (Ferraina et al. 2000; Gamlin and Yoon 2000; Gamlin et al. 1996). The recent preliminary findings of Takemura et al. (1999) in MST are of particular interest because they were obtained using stimuli and behavioral paradigms identical to those in the present study. Takemura et al. reported that the earliest vergence eye movements were attenuated after chemical lesions in MST and that, although the individual MST cells encoded only some aspect(s) of the disparity stimulus, the disparity tuning curve for the summed activity of the population of disparity-selective cells in MST resembled the derivative of a Gaussian and closely matched the entire tuning curve for the associated (isogonal) vergence responses.

The large random-dot patterns that we (and Takemura et al.) have used, confront the disparity-sensing mechanisms with a matching problem because a given dot at one eye can be matched to many dots at the other eye, even though only one match is globally “correct.” In fact, disparity-selective neurons in V1 have been shown to respond solely to local matches regardless of whether globally “correct” or “false” (Cumming and Parker 2000). One consequence of this is that most of these neurons respond to the disparity of patterns that have opposite contrast in the two eyes: so-called, anticorrelated patterns.
(Cumming and Parker 1997). It is further known that disparities applied to anticorrelated patterns generate (isogonal) vergence eye movements at short latency that are very similar to those in the present study except that they are in the opposite (i.e., “wrong”) direction (Masson et al. 1997). This is consistent with the idea that the vergence eye movements in the present study rely on disparity-selective neurons that respond to purely local matches between the two visual images. Interestingly, such anticorrelated stimuli are seen as rivalrous and do not give rise to percepts of depth (Cogan et al. 1993; Cumming and Parker 1997; Cumming et al. 1998; Masson et al. 1997), leading to the suggestion that the associated vergence eye movements are reflexlike and generated independently of perception (Miles 1998). Takemura et al. (1999) also reported that individual MST cells responded to (horizontal) disparity steps applied to anticorrelated patterns and that the summed activity of the population once more closely matched the associated (“wrong”) vergence responses. The clear suggestion is that, in the monkey, horizontal vergence eye movements like those described in the present study are mediated at least in part by the aggregate activity of disparity-selective neurons in MST. The neuronal mediation of the vertical vergence responses remains open. Neurons sensitive to vertical disparity have been described in cat visual cortex (Bishop et al. 1971; Ferster 1981; Nikara et al. 1968; von der Heydt et al. 1978) as well as monkey MT (Maunsell and Van Essen 1983), but there have been no formal studies concerning the neural mediation of vertical vergence. It is commonly assumed that vertical vergence is entirely involuntary, and there is strong evidence that human subjects are unable to ignore small vertical vergences in the foveal region (see Stevenson et al. 1997 for recent review).

Functional neuroimaging studies have identified a human homologue of area MT-MST (Greenlee 2000; Tootell et al. 1995; Watson et al. 1993; Zeki et al. 1991), although there is some debate as to whether MST lies adjacent to MT in the human (de Jong et al. 1994). These human studies have all identified MT-MST on the basis of its motion sensitivity, and none have looked for sensitivity to disparity stimuli or vergence eye movements. Studies in monkeys have identified direct, subcortical pathways by which MST might produce horizontal vergence eye movements, including the dorsolateral pontine nuclei (Boussaoud et al. 1992; Glickstein et al. 1980, 1985), which contain cells that discharge in relation to horizontal vergence (Zhang and Gamlin 1997) and project in turn to regions of the cerebellum known to be concerned with eye movements (for review, see Leigh and Zee 1999). There have been some preliminary reports that MST projects to the superior colliculus (Colby and Olson 1985; Lock et al. 1990), a structure also recently implicated in the production of vergence (see Chaturvedi and Van Gisbergen 2000 for recent review). Other studies in monkeys indicate that MST projects to two cortical areas that are interconnected and contain neurons that discharge in relation to horizontal disparity stimuli and/or horizontal vergence eye movements: LIP (Gnadt and Mays 1995) and FEF (Ferraina et al. 2000; Gamlin and Yoon 2000; Gamlin et al. 1996). Neurons in LIP that carry depth-related information project directly to the superior colliculus (Gnadt and Beyer 1998), and FEF neurons project directly to the medial part of the nucleus reticularis tegmenti pontis (Huerta et al. 1986; Leichnetz et al. 1984; Stanton et al. 1988), which shows vergence-related activity (Gamlin and Clarke 1995) and projects in turn to the premotor neurons for vergence (in the supraoculomotor and adjacent reticular formation) via the posterior interposed and fastigial nuclei of the cerebellum (see Gamlin et al. 1996 and Gamlin 1999 for review).

Default responses and directional errors (orthogonal components)

The isogonal vergence responses in the present study peaked with disparity steps of only 1°–3°, so that the servo operating range, over which increases in disparity gave rise to roughly proportional increases in vergence, was often restricted to disparities of less than 1° (Figs. 6A and 10A). We infer from this that the disparity-selective mechanism mediating our responses has a relatively small range and is able to make globally “correct” matches only for disparities up to a degree or two. The power spectrum of our random-dot patterns indicated that most of the power in our stimuli is at low spatial frequencies, the overall screen size (85° in our case) setting the lower limit, and the dot size determining the high-frequency roll-off. Thus increasing the dot size reduced the high-frequency content: −3 dB points were ∼0.15 cycles/deg with the 4.4° dots and ∼0.75 cycles/deg with the 1.1° dots. This indicates that the limited servo-range is not due to a lack of low spatial frequencies in our stimuli. Large disparity steps (12.8°), which far exceeded what we are defining as “the servo range,” generated vergence responses that were independent of the direction of the step (crossed, uncrossed, right hyper, left hyper). Because these so-called “default” responses often had the opposite sign to the subjects’ phorias (Table 5), we conclude that they were not simply a passive response to a loss of binocular fusion but were actively generated by a disparity-driven mechanism. Busettini et al. (1996b) were the first to report nonselective vergence responses to large disparity steps (in monkeys) and suggested that such large stimuli are seen as uncorrelated by the disparity detectors, hence the vergence system’s indifference to their direction. Interestingly, it is known that at least some of the disparity-selective neurons in visual cortex respond when the patterns at the two eyes change from correlated to anticorrelated (Gonzalez et al. 1993; Poggio 1989, 1990; Poggio et al. 1988). Our default vergence responses to large disparity steps were presumably generated by globally “false” matches and had both isogonal and orthogonal components that varied in amplitude from one subject to another (although, for a given subject, were always greatest in the horizontal direction; see Figs. 6 and 10). Being independent of stimulus direction, the isogonal components of the default responses were often anticomplementary.

We have failed to find any mention of orthogonal components (i.e., directional errors) in the literature on the disparity-

2 Although Busettini et al. (1996b) emphasized the relative insensitivity to direction, their data showed small, idiosyncratic anisotropies in the default responses for the different directions. We noticed similar response differences in our initial pilot studies on humans and attributed them to slight differences in the net (local) matches between the disparity detectors (that are assumed to mediate the vergence responses) and the dots in our stimulus pattern. For all of the experiments described here, we decided to randomize the initial starting position of the random dot stereo pairs on each trial (see METHODS), hypothesizing that this would reduce the likelihood of consistent local correlations and thereby homogenize the responses to large steps. With randomization, the mean vergence responses of a given subject to the largest steps generally showed only very weak dependence on the direction of the step (Fig. 5).
induced vergence eye movements of normal humans. Further, we found only one report of anticipatory responses unrelated to any phoria; Jones (1977) used small, briefly presented, visual stimuli and described anomalous vergence responses that were clearly very different from those in the present study in that they were found in <20% of subjects and invariably consisted of small decreases in convergence with crossed disparity steps.

The disparity tuning curves for the orthogonal component of the vergence responses were often well fitted by an exponential with a space constant that averaged 1.18 ± 0.66° (SD); see Figs. 6B and 10B and Table 3. (Some curves, especially those of the monkeys, showed slight overshoot, and this, combined with the fact that some orthogonal responses were very weak, rendered some of the exponential fits less satisfactory; see Table 3.) One might expect that the shape of the orthogonal tuning curves would in part reflect the orthogonal structure of the binocular receptive fields of the disparity detectors: clearly, whatever the disparity detection mechanism, it must be two-dimensional and show dependence on orthogonal as well as isogonal disparities. The only data available on the two-dimensional field structure of disparity-selective neurons are in the study of Maunsell and Van Essen (1983), who plotted the responses of monkey MT neurons to horizontal and vertical disparities. These plots, which were of low resolution, did not always show clear orientation (elongation), and no attempt was made to define isogonal and orthogonal axes. However, whereas the optimal horizontal disparity varied from cell to cell, “the optimal vertical disparity was never significantly different from zero,” which we take to indicate that the primary disparity-encoding (isogonal) axis was probably horizontal in most of the (19) units so studied. Not surprisingly, these plots were too sparse to define the exact mathematical form of the dependency on disparity. An attempt has been made to construct very detailed three-dimensional surface plots of the binocular receptive fields of V1 cells from the two monocular receptive fields, which are commonly represented by Gabor functions along the primary disparity-encoding (isogonal) axis and by Gaussian functions along the orthogonal axis (Cumming and DeAngelis 2001). In these models, the responses to orthogonal disparities have a roughly Gaussian envelope, which is slightly different from the exponential form that we chose to fit to our orthogonal data. In fact, we found that Gaussian functions fitted the orthogonal data in Figs. 6 and 10 as well as the exponentials did, insofar as both functions accounted, on average, for 90% of the disparity-induced variation in vergence. Given the steepness of the initial rise in the orthogonal components, however, it is perhaps not surprising that the Gaussian functions were sometimes less successful than the exponentials in fitting the responses to the very smallest disparity steps. On the basis of this, we feel that the exponential is a slightly more appropriate function for describing our data.

We have suggested that the short-latency vergence responses are mediated by disparity detectors that respond solely to local disparity matches, and further that the so-called default responses to large disparity steps are a product entirely of globally “false” matches. In fact, it seems likely that, in our experiments, the recorded isogonal vergence responses were never solely the product of globally “correct” matches and were always “contaminated” by responses to globally “false” matches. One possibility is that the contributions from these two sources are effectively given by the two terms of Eq. 2 that we have used to describe the isogonal tuning curves. In our attempts to provide a mathematical description of the isogonal responses (Eq. 2), we at first sought to use simple Gabor functions, which have been much used to describe and compare the disparity tuning curves of neurons in various regions of the cortex (see Cumming and DeAngelis 2001 for recent review). However, an additional term was required to provide the nonzero asymptote (default), and, because this was independent of the direction of the step, we assumed that it shared the exponential development of the response to the orthogonal stimulus. This might indicate that the two terms in Eq. 2 approximate the contributions of globally false matches (the exponential function) and globally correct matches (the Gabor function).

Automatic correction of small vergence errors

The (isogonal) disparity tuning curves in our study resemble the derivative of a Gaussian, with a roughly linear servo region that extends only a degree or two on either side of zero disparity, indicating that the vergence mechanism that we have studied can deal only with small disparities. Erkelens (1987) used line targets and random-dot patterns to study horizontal vergence responses to crossed disparity steps that were stabilized on the retina (using eye-movement feedback) and reported that responses were sustained only for steps up to 2°; responses to larger steps were transient, as though beyond the position-servo range. We envisage a rapid automatic (reflex?) mechanism that functions solely to correct small (i.e., residual) vergence errors independently of perception. This means that another, voluntary, mechanism would be needed to deal with the larger disparities involved when shifting binocular alignment to other surfaces in other depth planes, a process requiring some kind of target selection and a depth-sensing mechanism that can deal with disparities well beyond the range of the system that we have studied. Schor et al. (1992) already proposed such a dual vergence control mechanism, using inputs derived from perceived distance and disparity in a “coarse to fine sequence” in which “perceptual spatiotopic errors” are used to initiate the voluntary transfer of gaze to a target in a new depth plane and the disparity-driven subsystem then completes the binocular realignment by eliminating any residual vergence error.

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