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Short-latency disparity vergence eye movements: dependence on the preëxisting vergence angle

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Abstract

We recorded the vergence eye movements that are elicited at ultra-short latencies when binocular disparities are applied to large-field patterns (Busetini et al., 1996) and determined their dependence on the *preëxisting vergence angle* (*PVA*). The search coil technique was used to record the movements of both eyes in four healthy subjects (two with presbyopia). Using dichoptic viewing, the two eyes saw identical images each consisting of a fixation cross at the center of a random dot pattern in a circular aperture. The subject fixated the crosses and then the images (crosses, random dots, windows) moved horizontally ($1.5^\circ/\text{s}$) in opposite directions so as to bring the eyes to the desired horizontal vergence position without changing the accommodation demand. After a further 800–1200 ms to permit fusion at this new vergence angle (now, the *PVA*), a disparity step was applied and, 200ms later, the screen changed to uniform gray, marking the end of the trial. The disparity steps could have one of 6 magnitudes and four directions (crossed, uncrossed, right-hyper, left-hyper) while the *PVA* was varied systematically. The horizontal and vertical DVRs of one of the presbyopes consistently showed robust linear dependence on the *PVA* ($r^2 > 0.96$). The horizontal DVRs of the other three subjects showed no sensitivity to the *PVA* and their vertical DVRs showed only very weak dependence. The experiment was repeated on one of the non-presbyopes after cycloplegia, but the outcome was the same, indicating that the negative findings were not due to the influence of the vergence-accommodation response. Our data indicate that the DVRs can be scaled by the *PVA*, but most subjects do not show this effect, perhaps because they relied on other distance cues that are uninformative in our experimental situation.

Keywords

Disparity Vergence Eye Movements

Introduction

When the images seen by the two eyes are slightly misaligned (binocular disparity) vergence eye movements are elicited at ultra-short latencies in humans and monkeys (Busetini et al., 2001; Busetini et al., 1996; Masson et al., 1997; Sheliga et al., 2006; 2007; Takemura et al., 2001). The direction of these disparity vergence responses (DVRs) is as expected of a negative feedback control system that uses binocular parallax to eliminate vergence errors: convergent with crossed disparities, divergent with uncrossed disparities, left sursumvergent with left-hyper disparities, and right sursumvergent with right-hyper disparities (Busetini et al., 2001). The DVR is one of three oculomotor reflexes that share much in common: for review, see Miles (1998). One of these other reflexes, the Radial Flow Vergence Response (RFVR),

has a gain that is a linear function of the preexisting vergence angle (*PVA*) in humans (Yang *et al.*, 1999). The other reflex, the Ocular Following Response (OFR), has a gain that is inversely related to viewing distance in monkey (Busettini *et al.*, 1991) but modulation with viewing distance was very variable in humans unless subjects were placed on a sled to encourage the expectation of ego-motion (Busettini *et al.*, 1994). In the case of the OFR it was felt that the modulation with viewing distance was linked to *perceived distance* with possible contributions from efference copies of the vergence angle and the accommodative state, but other depth cues (e.g., texture size) and context also seem to play an important rôle in humans (Busettini *et al.*, 1991; Busettini *et al.*, 1994). In the present study we recorded the initial open-loop DVRs that were elicited when binocular disparities were applied to random dot patterns and examined their dependence on the *PVA*. The data indicate that only one of four subjects used the *PVA* to scale the DVR.

Methods

We recorded the initial DVRs elicited by disparities applied to large textured patterns. Some of the techniques were very similar to those used previously (Sheliga *et al.*, 2006; 2007; Yang *et al.*, 2003) and will be described only in brief here. Four subjects participated in this study: One was an author (FAM), two were experienced in eye-movement recordings but uninformed about the purpose of the experiments (BMS, DSZ), and the fourth was both inexperienced and uninformed (ST). All subjects had normal or corrected-to-normal vision. Experimental protocols were approved by the NEI Institutional Review Board concerned with the use of human subjects. Two of the subjects were presbyopic (FAM and DSZ) and two were emmetropic (BMS and ST). Otherwise, the eye examination in all subjects was normal.

The horizontal and vertical positions of both eyes were recorded with the electromagnetic induction technique (CNC Engineering, Seattle, USA) using scleral search coils embedded in silastin rings (Skalar, Delft, The Netherlands), and each eye was sampled at 1KHz (Collewyn *et al.*, 1975; Robinson, 1963). At the beginning of each recording session a calibration procedure was performed for each of the two eyes independently with defined fixations targets as previously described (Sheliga *et al.*, 2006; 2007).

Dichoptic stimuli were presented using a Wheatstone mirror stereoscope (Sheliga *et al.*, 2006; 2007). The visual stimuli consisted of random-dot patterns (RDs) with centered gray fixation crosses (width 5°, height 5°, thickness 0.1°) that were identical at the two eyes. The RDs were presented inside a circular aperture (diameter, 30°) with a black surround. The individual dots were circular (diameter, 0.5°), covering 25% of the pixels, and were either black or white (contrast 70%) on a grey background (18.7 cd/m²). At the start of each trial a randomly chosen pair of identical RDs (from a lookup table) was presented, creating a single binocular image at the monitor distance (53 cm; approximate vergence angle, 6.5°). Both half images moved at 1.5°/s horizontally in opposite directions until the appropriate *PVA* was reached (range, 0°-18°). After a further 800-1200 ms to permit fusion of the two half images, a disparity step was applied and then, after 200ms, the screen changed to uniform grey (18.74 cd/m²) marking the end of the trial. After an inter-trial interval of 500ms the next pair of binocular images appeared signaling the start of another trial. The subjects were asked to fixate the center of the crosses whenever present and to refrain from blinking or making saccades after a beep tone was presented indicating the end of the ramp movement and the beginning of the fixation period before the disparity step was applied. If no saccades were detected during the requisite period the data were stored on a hard disk; otherwise, the trial was aborted and repeated later. Each block of trials consisted of 10 to 50 randomly interleaved stimulus presentations, and each block was repeated at least 50 times. There were 10 different patterns of dots in the RDs and one was randomly selected each trial. The RDs, including the circular aperture, were corrected for the tangent error so that the retinal images did not vary with the *PVA*.

The horizontal and vertical eye-position measures obtained during the calibration procedure were each fitted with second-order polynomials whose parameters were then used to linearize the corresponding eye-position data recorded during the experiment proper. The linearized eye-position measures were smoothed with a 6-pole Butterworth filter (3 dB at 45 Hz) and mean temporal profiles were computed for each stimulus condition. Trials with saccadic intrusions (that had failed to reach the eye-velocity threshold of $18^\circ/\text{s}$ during the experiment) were deleted. The horizontal (vertical) vergence angle was computed by subtracting the horizontal (vertical) position of the right eye from the horizontal (vertical) position of the left eye. In our convention, rightward and upward eye movements were positive so that the DVRs were positive when convergent or left sursumvergent and negative when divergent or right sursumvergent. The initial horizontal and vertical DVRs (HDVRs, VDVRs) in each stimulus condition were quantified by measuring the changes in the horizontal and vertical vergence position measures over the 70-ms time periods commencing 90 ms after the onset of the disparity stimuli. The minimum latency of the DVRs was ~ 80 ms from the first appearance of the disparity stimuli so that these vergence-response measures were restricted to the initial open-loop period (i.e., twice the reaction time).

Results

Figure 1A shows sample HDVR temporal profiles obtained from one subject (FAM) when crossed and uncrossed disparities of 0.4° were applied to RDs at different PVAs as indicated by the numbers superimposed on the traces. Crossed disparities (X) elicited convergent (CONV) and uncrossed disparities (UX) elicited divergent (DIV) eye movements that increased in amplitude with increases in the PVA. With high PVAs (fixations at near) the vergence velocity traces showed oscillations that were especially prominent with crossed disparities: see Fig. 1A. The associated response measures, based on the change in vergence angle over the interval 70-160 ms from stimulus onset, are plotted in Fig. 1B and show clear linear dependence on the PVA, with regression coefficients for the HDVRs to crossed disparities of 0.090 (intercept:) and $0.006^\circ\text{--}1$ (slope) with an r^2 value of 0.999; similarly, the coefficients for the HDVRs to uncrossed disparities were -0.045 (intercept), $-0.009^\circ\text{--}1$ (slope) with an r^2 value of 0.998.

The VDVRs showed a very similar dependence on the PVA. Figure 1D shows sample VDVR temporal profiles obtained from the same subject when left-hyper and right-hyper disparities of 0.2° were applied to RDs at different PVAs. Left-hyper disparities (LH) elicited left sursumvergent (LSSV) and right-hyper disparities (RH) elicited right sursumvergent (RSSV) eye movements that increased in amplitude with increases in the PVA. The associated response measures plotted in Fig. 1E show clear linear dependence on the PVA, with linear regression coefficients for the VDVRs to left-hyper disparities of 0.047 (intercept:) and $0.0026^\circ\text{--}1$ (slope) with an r^2 value of 0.999; similarly, the coefficients for the VDVRs to right-hyper disparities were -0.035 (intercept), $-0.037^\circ\text{--}1$ (slope) with an r^2 value of 0.998.

To determine if the dependence of the DVRs on the PVA was evident with all disparity stimuli we obtained disparity tuning curves at two different PVAs (3° and 15°). The two tuning curves for the HDVRs are shown in Fig. 1C and for the VDVRs are shown in Fig. 1F (subject FAM). All curves were well fitted by Gabor functions (Busetini *et al.*, 2001), which explained over 96% of the variance (Table 1). The scale factors of the best-fit Gabor functions, G , were significantly greater when the PVA was 18° than when it was 3° : 13.1 vs 7.2 (HDVR) and 5.5 vs 3.8 (VDVR). Other parameters of the best-fit Gabor functions—offset (A), width (σ) and phase shift (θ)—were not significantly different for the two PVAs.

We also explored the effect of horizontal disparity offsets (0 - 2.5° , crossed and uncrossed disparities) on the VDVR elicited by given vertical disparity steps (0.2° right-hyper, 0.2° left-

hyper) at two PVAs (3° , 15°) for subject FAM. The orthogonal (horizontal) disparity offsets were applied at the same time as the vertical disparity steps, i.e., the disparity vector was oblique. Figure 2 shows the dependence of the mean VDVRs ($\pm$ SE) on the horizontal disparity offset for the two PVAs (filled symbols, 3° ; open symbols, 15°). The dependence on the horizontal offset was always well described by a Gaussian function (r^2 : 0.989 ± 0.010) as previously reported by Yang *et al* (2003). The parameters of the best-fit Gaussian functions for the DVRs to left-hyper (right-hyper) disparities with the two PVAs differed significantly only in the scale factor, g : see Table 2.

The HDVRs of the other three subjects showed no significant dependence on the PVA and the VDVRs showed only a very minor increase with increases in the PVA. In fact, this effect was rather subtle and only visible in the velocity traces. Linear regression of the DVRs to the PVA had r^2 values >0.99 (mean $\pm$ SD, slope of HDVRs to X: -0.0041 ± 0.0044 , UX: -0.0038 ± 0.0051 ; VDVRs to RH: 0.0013 ± 0.0204 , LH: -0.013 ± 0.0287).

In our setup, the changes in the PVA were not accompanied by changes in the accommodation demand and the non-presbyopes occasionally reported problems maintaining focused images, presumably due to the influence of vergence-accommodation (Fincham and Walton, 1957). The experiments were repeated on one of the non-presbyopes (BMS) after cycloplegia (Cyclopentolate, 1% solution, Cyclogyl[®]), but there were no significant changes in this subject's data, suggesting that vergence-accommodation was not responsible for the lack of dependence of this subject's DVRs on the PVA (slope: HDVRs to X: 0.0003, UX: -0.0004; VDVRs to RH: 0.0000, LH: -0.0004).

Discussion

The data in Figs. 1 and 2 from one subject clearly indicate that horizontal and vertical DVRs can be scaled (linearly) by the PVA. This is in line with the unpublished observations of C. Busetini, G.S. Masson and F.A. Miles [cited by Miles (1998)] who did essentially the same experiments as in the present study but used a somewhat different setup from the present one. In fact, these workers used the same setup that Yang *et al* (1999) subsequently used to demonstrate that the initial RFVR was a linear function of the PVA. The only difference between those two studies was that one used radial-flow steps and the other used disparity steps. The random-dot patterns in those studies were somewhat larger in extent than in the present one ($90^\circ \times 90^\circ$) and no correction was made for the slight changes in the retinal images of the patterns as the PVA changed (due to the tangent error). The scaling of the DVRs by the PVA in Fig. 1 is very similar to that previously reported for the RFVR by Yang *et al* (1999), who postulated that radial-flow vergence operates synergistically with the translational vestibulo-ocular reflex (TVOR) during fore-aft motion of the observer to maintain binocular alignment on objects in the scene ahead and that the two reflexes share a pathway whose gain modulates with vergence angle. The data in Fig. 1 suggest that the DVR might also share this same pathway and operate in synergy with the RFVR and TVOR mechanisms. Interestingly, Busetini *et al* (1991) had earlier invoked a similar synergy between the OFR and TVOR to compensate for lateral and vertical accelerations of the head and showed that, in monkeys, both reflexes have gains that modulate linearly with vergence angle, an effect that they also attributed to shared pathways and neural gain elements. These explanations imply that the modulation arises rather late in the neural pathways, i.e., on the motor side, and our finding that the PVA merely scales the disparity tuning curves (Fig. 1C, F) and the curves describing the dependence on orthogonal disparity offsets (Fig. 2) is consistent with this.

Unlike the RFVR, the DVR showed clear dependence on the PVA in only one of our four subjects, casting doubt on the notion that the modulation arises from a gain element shared by the two reflexes. The subject showing the dependence was one of two presbyopes, but since

the other did not show this dependence, presbyopia does not seem to be the determining factor. One problem in trying to rationalize these differences between subjects is that it isn't clear what purpose is served by modulating the DVR gain with the *PVA*. In particular, what advantage is gained from increasing the sensitivity of the DVR for near fixations? High gains can cause instability and this might be the reason for the oscillations that we observed with near viewing (Fig. 1A). [Note that the period of these oscillations was less than half the response latency of the DVR and hence must involve internal feedback loops rather than the external visual feedback loop.] Busetini et al (1991) pointed out that the OFR shows progressive saturation with image speed, the peak eye velocity being inversely related to the viewing distance, indicating that the speed saturation occurs upstream of the dependence on viewing distance. These workers postulated that, under normal viewing conditions, this speed saturation would tend to offset the dependence on viewing distance because the retinal slip speeds experienced by the moving observer tend to vary inversely with viewing distance, resulting in a greater tendency for the OFR to saturate with near viewing. It is known that the DVR saturates with retinal image speed at a point in the visual pathways before the inputs from the two eyes are combined (Masson et al., 2002), opening up the possibility that under normal viewing conditions this saturation will tend to offset the DVR's dependence on the *PVA*.

Why would the DVR of most subjects in our study not show this dependence on the *PVA*? One factor might be cue redundancy. There are many potential cues to viewing distance in addition to the vergence angle—accommodation, size, perspective, overlay, motion parallax (Howard and Rogers, 2002)—and different subjects might assign different weights to these cues at different times depending on the context. In our experiment, the depth indicated by these other cues is generally fixed and in conflict with the vergence angle so that any subject who used them would not show dependence on the vergence angle. Similar arguments were advanced to explain inter-subject variability in a study on the dependence of the human OFR on viewing distance (Busettini et al., 1994). This last study also found contextual effects, whereby dependence of the OFR on viewing distance became much clearer when the subject was placed on a sled, raising the possibility that the visual motion stimulus could result from ego-motion. This all implies that there might be much more flexibility in the deployment of these reflexes than generally supposed and, in our present study, this might be responsible for the failure to see a dependence on the *PVA* in three of our four subjects.

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Figure 1.

Dependence of the DVRs on the PVA (subject FAM). **A:** Mean horizontal vergence velocity profiles; *numbers* on traces indicate the PVA. **B:** Mean changes in horizontal vergence angle as a function of the PVA; straight lines are linear regressions. **C:** Horizontal disparity tuning data when the PVA was 3° (filled symbols) and 15° (open symbols); curves are best-fit Gabor functions (parameters in Table 1). **D:** Mean vertical vergence velocity profiles; *numbers* on traces indicate the PVA. **E:** Mean changes in vertical vergence angle as a function of the PVA; straight lines are linear regressions. **F:** Vertical disparity tuning data when the PVA was 3° (filled symbols) and 15° (open symbols); curves are best-fit Gabor functions (parameters in Table 1). Means based on data from 49-55 trials. Abbreviations: X, crossed disparities; UX,

uncrossed disparities; RH, right-hyper disparities; LH, left-hyper disparities; CONV, convergence; DIV, divergence; LSSV, left-sursumvergence; RSSV, right-sursumvergence.

Figure 2.

The effect of horizontal disparity offsets on the mean VDVRs to right-hyper and left-hyper disparities of 0.2° with two different PVAs: 3° (filled symbols) and 15° (open symbols). Curves are best-fit Gaussian functions (parameters in Table 2). Subject, FAM. Abbreviations as for Fig. 1.

Table 1
Parameters of the best-fit Gabor functions in Fig. 1C and 1F (subject FAM).

PVA	B	G	d^F	σ	f	ϕ	r^2
3°	0.042	7.16	0.026	0.40	0.010	-90	0.966
15°	0.025	13.06	0.019	0.45	0.010	-90	0.970
3°	0.012	3.76	-0.025	0.26	0.014	-90	0.976
15°	0.009	5.53	-0.029	0.26	0.017	-90	0.971

The Gabor function had the form, $A + G * e^{\left[-\frac{(D - d^F)^2}{2\sigma^2} \right]} * \cos \left[2\pi f (D - d^F) + \phi \right]$, where A is y-offset, G is gain, d^F is x-offset, D is applied disparity, σ is standard deviation, ϕ is phase in degrees, and f is spatial frequency in cycles/deg.

Table 2
Parameters of the best-fit Gaussian functions in Fig. 2 (subject FAM).

<i>PVA</i>	<i>A</i>	<i>g</i>	μ	σ	r^2	
3°	0.012	0.04	-0.01	0.31	0.994	LSSV
15°	0.011	0.07	-0.04	0.27	0.989	
3°	0.010	-0.05	0.01	0.44	0.974	RSSV
15°	0.012	-0.10	0.00	0.39	0.993	

The Gaussian had the form, $A + g * e^{\left[-\frac{(d-\mu)^2}{2\sigma^2}\right]}$, where *A* is y-offset, *g* is a scale factor, σ is the width, μ is the x-offset of the peak, and *d* is the applied disparity. All units are in degrees.