Central and Peripheral Visual Interactions in Disparity-Induced Vergence Eye Movements: I. Spatial Interaction

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Purpose. To evaluate the interaction between central and peripheral disparities in the initiation of vergence eye movements.

Methods. Eye movements were recorded in eight normal subjects using an infrared limbus tracker. Three-dimensional visual stimuli were back projected onto a tangent screen by using two liquid crystal display (LCD) projectors through crossed polarizers. The central target was a vertical bar, which always jumped from 2 to 1 m. The peripheral target was a random-dot pattern that jumped from 2 to 0.75, 1, or 1.5 m (near planes), 2 m (no change), or 3 m (far plane) simultaneously with the central target jump. Latency, amplitude at 150 ms, and average amplitude over 1 to 2 seconds after vergence onset; peak velocity; and the main-sequence relationship of the initial vergence response were calculated. How far the central target appeared to jump was scored subjectively.

Results. In half of the subjects, there was a clear effect of the peripheral disparity on the dynamics of the vergence response to the central disparity. The amplitude of vergence at 150 ms, as an index of open-loop gain, was significantly greater when the peripheral target moved closer, but steady state amplitude (average during 1–2 seconds) did not change, and the vergence latency was significantly greater when the peripheral target jumped away. There was no obvious relationship between the perceived amount of movement of the central target and the parameters of the dynamic properties of the vergence response.

Conclusions. Peripheral disparity can modulate the dynamics of the initial vergence response to a central disparity and is probably independent of the perception of motion in depth. (Invest Ophthalmol Vis Sci. 2004;45:1132–1138) DOI: 10.1167/iovs.03-0669

Visual Stimuli

The subjects wore glass-formed crossed polarizers and faced a large (45.6°×35.0°) translucent tangent screen placed at 2 m distance, on which a two-frame movie was back-projected from two liquid crystal display (LCD) projectors through crossed polarizers. Visual stimuli were controlled by a personal computer through an image-processing board (model CT-3000A; Cybertec, Osaka, Japan). The room was dark except for the target lights. The central disparity target was a vertical bar (2.5° high × 1.4° wide), which always jumped from a distance of 2 to 1 m, but the interval between target jumps was randomized between 1.5 and 3.5 seconds. The peripheral disparity target was a random-dot pattern, with density textured blobs subtending 0.4° at 2 m that were correlated between two eyes and with a luminance that ranged from 20 cd/m² (white dots) to 0.1 cd/m² (blank area). The peripheral disparity target contained a central blank square that was 10°×10°, 20°×20°, or 30°×30°. The central disparity was embedded within the central blank square (Fig. 1A). The random dots expanded or shrunk as they appeared to approach or recede—simulating optic flow—with a corresponding change in horizontal disparity and a change in size of the dots. There were no changes in cues, such
as blur, that might stimulate accommodation. The peripheral target jumped from the 2-m frontal plane at the same time as the central target moved, but to one of five distances, 0.75, 1, or 1.5 m (forward jump), 2 m (stationary), or 3 m (backward jump; Fig. 1B). For an interpupillary separation of 64 mm, a target distance of 3.0, 2.0, 1.5, 1.0, and 0.75 m called for 1.2°, 1.8°, 2.4°, 3.7°, or 4.9° of vergence angle, respectively. Eight trials for each type of the 15 paradigms were recorded (120 trials in total). Every 3 minutes subjects rested for about 1 minute with the total testing time being approximately 30 minutes. The effect of movement of the peripheral stimulus on the perception of motion of the central target (which always jumped by the same amount) was assessed qualitatively by asking the subjects to report how much they thought the central target moved compared with the condition when the peripheral target stayed stationary. The subject used a five-rank scale: 1, much smaller; 2, a little smaller; 3, the same; 4, a little greater; 5, much greater.

Eye Movement Recording and Data Analysis

Eye movements were monitored with an infrared limbus tracker (prototype; Handaya, Osaka, Japan). The apparatus was calibrated about every 10 minutes during the experiment, when the subject was asked to fix on targets on the center, right and left 5° positions. Analogue voltage signals encoding the horizontal position of both eyes were digitized and stored on a hard disc at a sampling rate of 1 kHz for further analysis. Overall noise was approximately 0.1°. The vergence angle was obtained by subtracting the eye position of the left eye from that of the right. Traces were analyzed by a computer-assisted procedure in which individual trials were displayed on a video monitor. The vergence angle was then filtered with a single-pole analogue filter with a cutoff frequency of 15 Hz and then differentiated with a two-point difference algorithm to get vergence velocity. Trials were rejected if eye traces were disturbed by blinks or if saccades occurred within 150 ms after vergence began (<5% of trials had to be rejected). A linear regression line was fit to the vergence trajectory between 20 ms before and 20 ms after the point at which the vergence angle first exceeded 0.1° from the baseline level. The time at which the regression line intercepted the baseline level defined the response latency. The experimenter verified the accuracy of this point by inspection for each

Figure 1. (A) Schematic illustration of the configuration of the visual target, which consisted of central and peripheral disparities. The central disparity was a vertical bar, 2.5° high × 1.4° wide. The peripheral disparity was a random-dot pattern, but there was a central, square, blank area of 10° × 10° (a), 20° × 20° (b), or 50° × 50° (c), containing the smaller central disparity target. (B) Both the central and peripheral targets were initially at a 2-m distance. The central target always jumped to a 1-m distance at a random time interval. Simultaneously, the peripheral target jumped forward to a distance of 0.75, 1, or 1.5 m, stayed at 2 m, or jumped backward to 3 m distance.

Figure 2. Representative traces from subjects 6 (left column) and 8 (right column) to show the effect of different amplitudes of movement of the peripheral target on the vergence response induced by the central target. From the top, panels are for peripheral target destinations of 0.75, 1, and 1.5 m (forward movement), 2 m (no movement), or 3 m (backward). The size of the central blank area containing the central target was 10° × 10°. Eight traces are aligned with the onset of the movement of the target. The y-axis indicates vergence angle (downward deflection indicates convergence). The x-axis indicates time after target onset. Note that when the peripheral target jumped closer, convergence velocities increased (solid arrows) but when the target jumped backward they decreased (dashed arrows).
Two measures of the vergence response were calculated: the vergence amplitude 150 ms after vergence onset to estimate the open-loop gain before visual feedback can modify the initial response, and the average vergence amplitude over the period 1 to 2 seconds after the onset of vergence to estimate the closed-loop gain during steady state fixation on the central target at 1 m. The peak vergence velocity and the main-sequence ratio ($\text{peak velocity}/\text{vergence amplitude}$) were also calculated. All analyses were performed on computer (MatLab; The MathWorks Inc., Natick, MA).

RESULTS

Representative traces from subjects 6 and 8 are shown in Figure 2. The vergence responses were markedly stereotypical for each set of stimulus parameters. Regardless of the size of the movement of the peripheral target, the vergence angle after 1 second was approximately 1.5°. Although the movement of the central target was always the same, convergence velocities were smaller when the peripheral target jumped backward and larger when it jumped closer; this can be seen in the slope of the response. The distributions of the convergence latencies for the different stimulus patterns are compared in Figure 3. When the peripheral disparity jumped backward against the central target, vergence latencies were usually greater. The significance of the difference in the distribution among the five types of peripheral target movement was tested using the Kruskal-Wallis one-way analysis of variance on ranks. When there was a significant difference, the distributions were compared with each other using the Dunn method.

When the peripheral disparity stimulus was larger—that is, the square blank area between the central and peripheral targets was small ($10^\circ \times 10^\circ$; left column), in five of eight subjects, the latencies were greater when the peripheral target moved backward. The same was true for two of the subjects when the blank area was $20^\circ \times 20^\circ$. When the blank area was $30^\circ \times 30^\circ$, there were no differences in latencies.

Four other parameters of the vergence response, (1) steady state amplitude (average vergence angle during 1 to 2 seconds after the vergence onset), (2) open-loop amplitude (vergence angle 150 ms after the vergence onset), (3) peak velocity (in degrees per second), and (4) main-sequence ratio, ($\text{peak velocity}/\text{verage amplitude}$), were calculated. A representative example of results from subject 8 is shown in Figure 4. The vergence amplitude 150 ms after onset and vergence peak velocity increased as the peripheral target jumped closer. Correlation coefficients between the values of these parameters and the size of the peripheral target jump were calculated.
for each case (usually, n = 40). In the subject shown in Figure 4, the amplitude of the movement of the peripheral target did not affect the steady state, closed-loop gain of the vergence response, but did affect the open-loop gain significantly with all three sizes of the blank area. There also was a significant correlation between peak velocity and peripheral target jump. For the main-sequence ratio, however, there was a weak correlation only when the central blank area was small (10° × 10°)—that is, when the peripheral disparity occupied the largest area.

The significance of the correlation coefficients for all the parameters of the dynamic response were tested in the same way for all subjects, and the results are shown in Table 1. Closed-loop vergence gain was unaffected by the amplitude of the jump of the peripheral disparity, except for one case (subject 1, when the central blank area was 10° × 10°) in which the correlation was unexpectedly negative. In contrast, open-loop vergence gain correlated significantly with the amplitude of the jump of the peripheral disparity in approximately half the cases: three (10 × 10 condition) and five (20 × 20 condition) of eight subjects (positive correlation indicates that the amplitude was larger when peripheral target moved closer). The vergence amplitude at 150 ms after the onset of movement was directly related to the average vergence velocity in the first 150 ms. The effect was weak when the blank area was 30° × 30°. Peak velocity was also related to the amplitude of the jump of the peripheral disparity, but weakly, in three of eight subjects (positive correlation indicates that the peak velocity was greater when the peripheral target moved closer). The main-sequence ratio had a significant correlation only in subject 8 and only when the central blank area was 10° × 10°. Thus, movement of the peripheral target had a clear effect on the initial open-loop portion of the response, by virtue of increasing convergence velocity, but had little effect on the steady state, closed-loop gain or on the main sequence ratio.

Further analysis of the dynamics of the convergence response is shown in Figure 5. The average velocity profile during vergence initiation and the phase planes (average traces of the vergence angle versus vergence velocity of the first 1.6 seconds of the vergence response) are shown, comparing the condition in which the peripheral target jumped forward (1 m)
with the condition in which it jumped backward (3 m). The effect of the peripheral target was the greatest in the phase planes of 5, 6, and 8. In accord with the results shown in Figure 3 and Table 1, in which six subjects showed a significant difference in amplitude at 150 ms and/or in peak velocity, the dynamic traces were different, including the point 150 ms after the onset of the response (Fig. 5; arrows). The most notable change was the smaller slope in the initial vergence velocity profile in subjects 2, 5, 6, and 8 when the peripheral target jumped back, which indicates that vergence acceleration was affected by the peripheral disparity motion.

Finally, we asked whether the jump of the peripheral target influences the perception of the size of the jump of the central target. The correlations between the subjective scores (1–5) of the subjects and the size of the jump of the peripheral disparity are shown in Table 2 (perceived motion). Negative correlations were seen in six of eight subjects. In other words, the size of motion perception was related to the relative disparity between the central and the peripheral stimuli. There was little correlation, however, between the subjective scores and the dynamic parameters of the vergence response (Table 2, motor parameters), suggesting that stereomotion perception did not reflect the motor characteristics.

**DISCUSSION**

In general, the vergence response to disparity stimuli presented on or near the fovea is more robust than the response to disparity presented in the periphery.\(^6\) Peripheral disparity in the absence of foveal stimuli, however, can still induce a vergence response.\(^7\) When the area of peripheral disparity is large, it can even break central fusion.\(^5,6,12\) Although many studies have reported the dynamic characteristics of the vergence response to various types of disparity stimuli, there has been little systematic comparison of the initial vergence response induced by relative amounts and directions of peripheral and central disparity stimuli.\(^3,8\)

Recent experiments suggest that the vergence response to an abrupt change in disparity consists of two components: a transient component associated with the initiation of vergence and a sustained (or tonic) component associated with steady fixation that allows binocular fusion of similar images.\(^15–17\) The initial, first 150 ms or so, portion of the vergence response is functionally open-loop—that is, during this period, there is insufficient time for the vergence (motor) response to have been influenced by the reafferent reduction in disparity.\(^18,19\) Several studies\(^20–25\) suggest that the transient and sustained components are differently tuned for retinal disparity, with the former being broadly sensitive to a wide range of disparities and the latter being narrowly tuned to small disparities. Based on this schema, it is hypothesized that the transient component is driven by the amplitude and/or the speed of the disparity of the larger field stimulus, whereas the sustained component uses closed-loop disparity feedback for accurate foveal fixation with a small residual error.\(^8\)

The main finding of our study is that when the peripheral disparity jumped closer (additive to the change in the central disparity), the speed of the initial open-loop portion of the vergence response increased. Not surprisingly, the larger the peripheral disparity area, the larger the effect, as seen in Table 1. In contrast, when the peripheral disparity jumped backward (subtractive), the latency of the vergence response increased. Furthermore, except for one subject and in only one condition, the steady state vergence gain did not vary significantly with the different spatial patterns of peripheral stimulus presentation. Analogous findings have been reported for the onset of another type of visual tracking eye movement, smooth pursuit.\(^24,25\) With a textured background moving in the same direction as the target, initial pursuit eye velocity increased, and vice versa, but there was much less effect on steady state pursuit tracking. In our stimulus setup, the peripheral target contained not only retinal disparity but also optic flow information and monocular cues, though the last is not likely to contribute to the vergence response.\(^20\) Optic flow information, however, could be a factor influencing the initial part of the vergence response, though, at the target distances used in this study, the effect would probably be small.\(^27\)

These results on the dynamics of the vergence response were different from those based on the subjects’ perceptions of target movement, which was related to relative disparity, implying that the perception of depth motion and the synthesis of the vergence motor command are processed differently in the brain. Such dissociation between stereomotion perception and vergence eye movement has been discussed in several recent studies.\(^28–30\)

Where in the brain does peripheral disparity modify the initial vergence response? In our study, the open-loop vergence amplitude and the peak velocity were affected by move-
ment of the peripheral target, but the effect on the main sequence ratio was much smaller. This corresponds to the smaller slope of the initial vergence velocity trace, which indicates a change in acceleration as the cause of the change in the dynamic properties of the initial vergence response. Brainstem premotor circuits and probably the cerebellum determine the dynamic pattern of vergence eye movement.1-33 In our current results, however, the main sequence ratio was little affected, suggesting that the effect of the peripheral disparity reflects a change in activity upstream from the brainstem circuits that generate the premotor vergence responses.

To attain static stereopsis, disparities have to be reduced beforehand by vergence eye movements. The data in our study support the idea that peripheral and central disparities have different roles in controlling vergence. Likewise, the contributions of central and peripheral disparity to visual analysis are different: Stimulation of the central retina leads to the activation of the ventral stream directed to the inferior temporal cortex and stimulation of the peripheral retina leads to the activation of the dorsal stream directed to the posterior parietal cortex.34 Such as V5. Indeed, fast visual motion stimuli activate area V5 simultaneously with, or earlier than area V1.35-37 Thus, it can be hypothesized that peripheral disparity facilitates the initial open-loop component through a more direct pathway in higher visuomotor integrating areas.38

When the peripheral target jumped backward, the latency of responses increased. Generally, latencies of approximately 150 ms are reported for vergence eye movements.1 However, when an object (a distractor) moving in a direction different from that of the target of interest is presented, latencies of other types of eye movement, saccades39 and pursuit,40 increase. Although Ferrera and Lisberger41 found that neither the higher visuomotor integrating areas.38

References


