

Dynamic Asymmetries in Convergence Eye Movements Under Natural Viewing Conditions

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Purpose: To clarify differences in the dynamics of convergence eye movements in response to symmetrical stimuli between the dominant eye and the nondominant eye under natural viewing conditions.

Methods: This study was conducted in 11 normal volunteers (age range, 22–30 years). The subject was seated on a chair, and the head was fixed using a bite-block. The dominant eye was determined with the "hole-in-the-card" test. Horizontal positions of the eyes were recorded using an infrared reflection device. Recordings of right eye movements were subtracted from left eye movements to obtain the vergence response. The fixation target was moved toward the center of both eyes from 50 to 20 cm in front of the face at a constant velocity in five steps (20, 30, 40, 50, and 60 cm/s). The target was moved by a pulse motor controlled by a microcomputer. The dynamic properties of each eye movement and the vergence components were analyzed.

Results: At velocities ≤ 40 cm/s, convergence responses consisted of two components: the fusion-initiating component and the fusion-sustaining component. The fusion-initiating component drove the initial faster dynamic portion of the response, and the fusion-sustaining component maintained the latter slower dynamic portion of the response. The mean peak velocity of the fusion-initiating component was significantly greater in the dominant eye than in the nondominant eye. The mean peak latency of the catch-up component was significantly shorter in the dominant eye than in the nondominant eye.

Conclusions: The present study indicated that the trajectory of convergence eye movement under natural viewing conditions consists of two components, the fusion-initiating component and the fusion-sustaining component, and that the convergence response to symmetric stimuli was asymmetric between the dominant eye and the nondominant eye during the fusion-initiating phase. The neural control system of convergence eye movements preferentially drives the dominant eye during the fusion-initiating phase of the response. **Jpn J Ophthalmol 2001;45:437–444** © 2001 Japanese Ophthalmological Society

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Introduction

In vergence eye movements, the eyes are rotated simultaneously in opposite directions in response to motion in depth. In conjugate eye movements, such as saccadic eye movements or smooth pursuit eye movements, a single generator symmetrically drives the two eyes by identical amounts of innervation (Hering's law of equal innervation). However, vergence eye movements are often asymmetric, because targets will never be located along the mid-sagittal plane in the natural world. Therefore, the vergence generator should control the movement of each eye independently, depending on the arrangement of the target. Previous studies in man and the monkey actually indicated that during convergence eye movements, each eye can respond independently to that eye's view of the target.^{1,2} Another study indicated that large dynamic asymmetries in disparity ver-

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gence often occur, even if eye movements are produced by symmetrical stimuli.³ These dynamic properties of convergence eye movements are thought to represent the properties of the vergence system in the central nervous system. However, the control system of vergence eye movements is less established in contrast to that of conjugate eye movements.

Recently, neurophysiological studies have revealed the neuronal substrate for vergence eye movements in the central nervous system. Vergence eye movements are evoked by electrical stimulation of the frontal and parieto-occipital cortices in the monkey and the cat.^{4,5} Neuronal activities associated with vergence eye movements have been found in the posterior parietal and parieto-occipital cortices in the monkey and the cat.^{5–7} Vergence eye movements evoked by stimulation of the parieto-occipital cortex and the posteromedial lateral suprasylvian (PMLS) area, showed asymmetry of amplitude between both eyes.⁸ These findings suggest that the cortex predominantly controls the contralateral eye during vergence eye movements.

Under natural viewing conditions, there is ocular motor dominance in humans.^{9,10} Usually, one of the eyes (dominant eye) plays a controlling role in binocular vision. Although neuronal mechanisms underlying ocular motor dominance are as yet unknown, it is possible that the dominant cortex predominantly controls the dominant eye through the asymmetric vergence system. Therefore, it is important to study differences in dynamic properties between the dominant eye and the nondominant eye during vergence eye movements to clarify the control mechanisms of vergence eye movements.

In the present study, we investigated the differences in the dynamics of the dominant eye and the nondominant eye in convergence eye movements in response to symmetrical stimuli under natural conditions, and attempted to clarify the control mechanisms underlying vergence eye movements.

Materials and Methods

Subjects

The experiment was conducted in 11 healthy volunteers (8 men and 3 women). Their ages ranged from 22 to 30 years, with a mean of 26.5 years. All had a corrected visual acuity of at least 1.0 in both eyes. The spherical equivalents of autorefractometry in all subjects were within ± 3.0 diopters, and differences in the spherical equivalents in left and right eyes were within 1.0 diopters. All subjects had normal binocular vision, and little phoria (<5°). The subject was seated on a



Figure 1. Scheme for theoretical calculation for angle of movement of 1 eye (θ) in ramp stimulation. L: half of interpupillary distance, M: distance from subject to starting point of target, Ψ : angle between visual axis and line M, V: velocity of target.

chair, and the head was fixed using a bite-block. The dominant eye was determined with the "hole-in-thecard test."⁹ Informed consent was obtained from all subjects after the nature of the procedure had been explained. Tenets of the Declaration of Helsinki were followed, and institutional human experimentation committee approval was obtained.

Eye Movement Recording

Horizontal positions of both eyes were recorded using an infrared reflection device (Takei, Model TKK 928; Tokyo). In this system, the linear range was 25° to either horizontal side of the primary position. This system has a resolution of 0.3° .

Measurements were calibrated based on 10° horizontal displacement before the experiment. A fixation target ("X" shape) was moved on a rail toward the center of both eyes from 50 to 20 cm in front of the face at a constant velocity in five steps (20, 30, 40, 50, and 60 cm/s). The target was moved by a pulse motor controlled by a microcomputer. The subject was instructed to fixate on the center of the target.

Throughout the experiment, the subject was seated on a chair in a semi-dark room and the head was fixed using a bite-block. This extent of head im-



Figure 2. Recordings of vergence changes and velocities (black lines) with theoretical vergence changes and velocities (blue lines) at various stimulus velocities in one subject (27-year-old man). Upward deflections represent convergence. Each trace consists of five responses.

mobilization was sufficient to prevent drifts in recordings generated by head movement.

Data Analysis

Target and eye position signals were recorded using a data recorder for later analysis. Data were digitized using a computer with a sampling rate of 400 Hz. Recordings of right eye movements were subtracted from left eye movements to obtain the vergence response. We analyzed the parameters of each eye movement and

vergence eye movement with respect to onset latency, peak latency of the velocity, and peak velocity. The parameters of the dominant and nondominant eyes were compared. For calculating the onset latency, we considered the moment when the eye velocity reached 1°/s as the onset of movements. Theoretically, the angle of the movement of 1 eye (θ). and the velocity (θ') were calculated as a function of the time from the onset of target movement (Figure 1) by the formulae:

$$\theta(T) = \Psi - \pi/2 + tan^{-1} + (L/(M - TV))$$



Figure 3. Plot of mean peak velocity of fusion-initiating component in 11 subjects versus target velocity (\mathbf{A}), and plot of mean peak velocity of fusion-sustaining component in 11 subjects versus target velocity (\mathbf{B}). Error bars represent standard deviations.

$$\theta'(T) = VL/((M - TV)^2 + L^2)$$

where L, M, T, V, and Ψ are half of the interpupillary distance, distance from the subject to the starting point of the target, time from the onset of target movement, velocity of the target and the angle between visual axis and line M, respectively. In this experiment, stimulus was symmetrical for both eyes. Therefore, the vergence angle and the vergence velocity were defined as 2ϑ and $2\vartheta'$, respectively. Actual and theoretical trajectories of vergence eye movements were compared.

Results

Trajectory of Convergence Response

The mean (\pm SD) onset-latency of convergence was 136.7 \pm 13.0 ms (n = 220). Figure 2 shows the trajectories of vergence eye movements at target velocities of 20, 30, 40, 50, and 60 cm/s in one subject. At velocities \leq 40 cm/s, two peaks of the velocity were seen. At velocities \leq 50 cm/s, the response was monophasic, and the eye positions did not catch up with the target position while the target was moving. These response patterns were observed in all the subjects. The early component and the late component were designated as the fusion-initiating component and the fusion-sustaining component, respectively. The monophasic component at velocities of 50 and 60 cm/s was determined to be the fusion-initiating component in this study. The mean (\pm SD) peak latencies of the fusion-initiating component were 305.6 ± 36.7 ms at 20 cm/s, 329 ± 34.6 ms at 30 cm/s, 345.2 ± 36.4 ms at 40 cm/s, 521.5 ± 47.9 ms at 50 cm/s, and 470.4 ± 32.8 ms at 60 cm/s. The peak velocities of both fusion-initiating and fusion-sustaining components correlated well with the target velocity (Figure 3). The peak velocities of the fusion-initiating components were always higher than stimulus velocities.

Differences Between Dominant and Nondominant Eyes

There were some differences in parameters of eye movements between the dominant eye and the nondominant eye. Figure 4 shows the trajectories of eye movements of the dominant and nondominant eyes. The mean peak latency of the fusion-initiating component was significantly shorter in the dominant eye than in the nondominant eye at all the target velocities (two-way repeated-measures analysis of variance [ANOVA], P < .01) (Figure 5A). The difference in the peak latency between the dominant eye and the nondominant eye ranged from 19.5 to 71.6 ms (mean = 37.5 ms). The mean peak velocity of the



Figure 4. Recordings of eye positions and velocities in dominant eye (red lines) and nondominant eye (black lines) at various target velocities in one subject (26-year-old man). Each trace consists of five responses.

fusion-initiating component was significantly higher in the dominant eye than in the nondominant eye at all target velocities (two-way repeated-measures ANOVA, P < .01) (Figure 5B). The difference in the peak velocity between dominant and nondominant eyes ranged from 1.1 to 2.4°/s (mean = 1.8°/s). The peak latency and the peak velocity of the fusionsustaining component were not significantly different between the dominant eye and the nondominant eye (Figure 6). These differences in responses between the dominant eye and the nondominant eye were observed in all the subjects.

Discussion

Trajectory of Convergence Response

The present study indicated that the trajectory of convergence eye movement under natural viewing conditions consists of two components: the fusioninitiating component and the fusion-sustaining com-



Figure 5. Plot of mean peak latency of fusion-initiating component in 11 subjects versus target velocity (\mathbf{A}), and plot of mean peak velocity of fusion-initiating component in 11 subjects versus target velocity (\mathbf{B}). Error bars represent standard deviations.

ponent. Previous studies also indicated that the convergence response is a "two-stage process" consisting of a transient fusion-initiating phase and a fusion-sustaining component.^{11–13} These studies showed responses of disparity vergence, while the present study showed vergence responses under nat-

ural viewing conditions. Dynamic properties of the two-stage process in disparity vergence are similar in both eyes in the present study. Semmlow et al¹³ indicated that slower ramps are tracked rather smoothly by the sustained component, while faster ramps bring out the transient component. Results of their



Figure 6. Plot of mean peak latency of fusion-sustaining component in 11 subjects versus target velocity (**A**), and plot of mean peak velocity of fusion-sustaining component in 11 subjects versus target velocity (**B**). Error bars represent standard deviations. \bullet : dominant eye, \bigcirc : nondominant eye.

study showed that the peak velocity of the transient component increased in association with the increase in the target velocity similar to those of our study. These findings suggest that the early component of the convergence response is not an open-loop response.

The early component of the convergence response is thought to be a catch-up response. The onset latency of the convergence response is about 140 milliseconds. The latency elicits a gap between an eye position and a target position in the early phase of the convergence response. Therefore, the vergence system should eliminate the gap by the transient fusioninitiating response. When the eye positions catch up with the target position by the fusion-initiating component, and binocular vision on the target is accomplished, the fusion is maintained by the fusion-sustaining component.

Dynamic Asymmetries of Convergence Eye Movements and Eye Dominance

The results of the present study indicated dynamic asymmetries of the fusion-initiating component between the dominant eye and the nondominant eye. The mean peak velocity of the fusion-initiating component was significantly higher in the dominant eye than in the nondominant eye. The mean peak latency of the fusion-initiating component was significantly shorter in the dominant eye than in the nondominant eye. In contrast, the fusion-sustaining component was symmetric between the dominant eye and the nondominant eye. These findings suggest that the neural control system of convergence eye movements drives the dominant eye preferentially during the fusion-initiating phase.

Han et al¹⁴ also indicated the difference in the gain of accommodative vergence between responses of the dominant eye and the nondominant eye. The gain was higher when the dominant eye was moved by accommodative stimuli to the nondominant eye. These findings suggest that there are variations between the left eye and the right eye in the processing of the visual input or in the processing of the motor control signal. Most neurons in the primary visual cortex equally receive visual inputs from both eyes.¹⁵ Therefore, it is probable that there is a difference in the processing of the motor signal of the vergence between the 2 eyes.

Recent neurophysiological studies have identified the neuronal substrate for vergence eye movements in the central nervous system. Vergence eye movements are evoked by electrical stimulation of the frontal and parieto-occipital cortices in the monkey and the cat.^{4,5} Neuronal activities in association with vergence eve movements have been found in the posterior parietal and parieto-occipital cortices in the monkey and the cat.^{3–5} The vergence center in the cortex does not control both eyes symmetrically, but drives the contralateral eye predominantly.^{5,7,8} Vergence eye movements evoked by stimulation of the PMLS in the cat showed asymmetry in amplitude between the left eye and the right eye.⁸ The amplitude of the contralateral components was significantly larger than that of the ipsilateral components. After a unilateral lesion in the PMLS, both amplitude and peak velocity of the contralateral components were significantly decreased as compared to those of the ipsilateral eye.⁸ Therefore, each cortex drives the contralateral eye preferentially. This system makes it possible to control independently the movement of each eye responding to that eye's view of the target.

Under natural viewing conditions, the amount of the gap between both eyes should always be different. If both eyes are driven symmetrically to a given amount of disparity, the target image on the retina will never reach the fovea. The vergence system in the cortex should adjust the gain of the vergence angle between both eyes. If the vergence system drives the dominant eye preferentially to eliminate the gap between eye positions and a target position, the target image on the retina of the dominant eye will precede that of the nondominant eye in reaching the fovea. Then the nondominant eye will be driven by the remaining gap, and the target image on the retina will reach the fovea. This must be one of the motor strategies for coordinating the movements of the 2 eyes.

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