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Effects of the Linear Vestibulo-ocular Reflex on Accommodative Vergence Eye Movements

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Abstract

The aim of the study was to determine whether accommodation to the relative motion of a target along the visual axis of one eye during fore–aft movement of the head could induce accurate vergence over a wide range of viewing distances and frequencies of oscillation, despite lack of vision in the second eye. This was compared to the vergence when both eyes viewed the target. Two rhesus monkeys were trained to fixate a visual target located 216–336 mm in front and along the visual axis of one eye, while being sinusoidally translated in the fore–aft direction. There was no movement of the seeing eye while the other eye converged, regardless of whether there was vision in the converged eye. Gain and phase of the convergence were determined based on the ratio of actual versus expected eye position if the target was accurately fixated. During translation at frequencies from 0.05 to 2 Hz, the eye converged on the target with an eye position gain of ≈ 1 , and a phase close to zero. When vision was occluded in the converging eye, gains of convergence were 0.6–0.8 Hz up to 2 Hz, and the phases remained close to zero. At low frequencies of fore–aft movement, when the acceleration was negligible, convergence was driven by accommodation in the seeing eye. At higher frequencies, vergence could also be driven by the linear vestibulo-ocular reflex (IVOR). Thus, vision in one nonmoving eye and the IVOR combine to generate convergence over a wide range of frequencies and viewing distances.

Keywords

vergence; linear vestibulo-ocular reflex; accommodation

Introduction

It has been known that vergence and versional eye movements subserve different oculomotor functions and are independently controlled.¹ Version occurs when the two eyes rotate in the same direction to acquire a target. Vergence is rotations of the two eyes in opposite

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Conflicts of Interest

The authors declare no conflicts of interest.

directions to obtain or maintain a single binocular fixation point, which is at the approximate intersection of the visual axes of two eyes.² Vergence is essentially driven by two components: fusional and accommodative. Fusional vergence arises due to the interocular distance, which constrains each eye to view a target from a different perspective and the image is fused by the visual system to produce a single image.³ Accommodative vergence occurs when a target is moved toward or away from a subject and the eyes must change their relative angle to fixate the target binocularly. In both fusional and accommodative vergence, the visual axes of the eyes are driven to intersect at the target location in space relative to the observer.

Because of the demand that a single fused image be seen clearly while moving, the visual system activates the vergence system through pursuit and other compensatory systems, including the angular and linear vestibuloocular reflexes (aVOR, IVOR). In addition to generating vergence, the aVOR and IVOR have built-in mechanisms to adjust their gains as a function of viewing distance and vergence so that the eyes can appropriately compensate when viewing near and far targets. The IVOR gain when viewing near targets requires more substantial movements of the eyes in response to linear translation, and the gain is accordingly higher.^{4–9}

An important behavioral condition, which requires fairly exact vergence, occurs when a target approaches a subject during fore–aft translation. This condition requires not only accommodative vergence, which responds to a clarifying blur as targets move closer and further from the eyes, but also fusional vergence, so that a single image is observed at the intersection of the visual axes.¹⁰ While a number of studies have examined version and vergence responses induced by the IVOR,^{11–13} this has either been done in darkness or when fixating a target binocularly. Fore–aft translation at high frequencies has been shown to activate the IVOR and vergence,^{11–13} in accordance with the necessity to maintain binocular fixation. At low frequencies, convergence is primarily controlled by the visual system.¹³ Thus, together, vision and the IVOR maintain vergence so that there is accurate binocular fixation over a wide range of frequencies.¹³

The relative contribution of accommodative vergence to maintenance of binocular fixation while moving is not known. Previous studies that have examined accommodative vergence were done with targets moving sinusoidally fore–aft along the visual axis of one eye while the other eye was occluded.^{14–16} In general, the dynamic vergence responses have an approximate 3-dB fall off at 1 Hz, although the gain and phase characteristic have been inconsistent.^{10, 14, 16} In this study, we examined how accurately monocular vision and fore–aft translation, interact while viewing a target along its visual axis, to generate vergence responses to maintain binocular fixation points.

Methods

During experiments, animals sat in a primate chair with the head fixed in the stereotaxic horizontal plane. The chair was mounted on top of the linear sled with the naso-occipital axis of the head aligned with the axis of sled motion. Eye movements were recorded with a rotating magnetic-field coil system.¹³ Two search coils were implanted in each eye: one coil

(frontal) was used to record horizontal (yaw) and vertical (pitch) components of the eye movements. Another coil, which was placed on the top of the eye, was used to record roll eye movements. Eye position was calibrated by having animals look at a target located in front of the eye being calibrated while the other eye was covered.¹³

A computer monitor was placed 216, 276, or 336 mm in front of the animal. The animal was in darkness while a single 1° dot was presented in front of one eye while the other eye remained open or was occluded. The eye in front of the was remained stationary during fore–aft translation, while the second eye rotated to implement the convergence. Animals were translated fore–aft along the naso-occipital axis at frequencies ranging from 0.05 Hz to 2 Hz. Amplitude of translation was adjusted as a function of frequency (± 50 mm at 0.05 Hz [Fig. 1A], ± 47 mm at 0.25 Hz, ± 41 mm at 0.5 Hz, ± 29 mm at 1 Hz, and ± 17 mm at 2 Hz). The corresponding linear acceleration was negligible during oscillation at 0.05 Hz, but was 0.11 g at 1 Hz and 0.27g at 2 Hz.

Eye movements and expected target location for each eye were derived as Fick angles. Saccades were identified and marked for exclusion from analysis using a maximum-likelihood ratio criterion. The residual signals were visually inspected and eye positions were compared to actual visual target positions for the left and right eyes separately. Only yaw and pitch components were analyzed in this study.

The gain of each eye movement component was computed as the amplitude of the sinusoidal fit at the oscillation frequency through desaccaded positions of each eye divided by sinusoidal fit through the expected target location of the corresponding eye. A positive phase shift indicates that the peak eye position occurred after the peak stimulus position.

Results

Animals were translated fore–aft at 0.05 Hz, while fixating a target located along the visual axis of the left eye (Fig. 1A–1E, animal M0652). Pitch and yaw eye position of the left eye, whose visual axis was aligned with the target, were not modulated by the translation (Fig. 1B, 1C), regardless of whether the target was seen by both eyes (left column) or only by left eye (right column). The pitch component of the converging right eye was also negligible, regardless of whether vision in this eye was occluded (Fig. 1D). When both eyes saw the target, the yaw component of the converging eye was modulated and its position overlaid target position (Fig. 1E, left column; compare black and gray traces). When vision in the converging eye was occluded, there was a discrepancy of $\approx 2^\circ$ between yaw eye and target position (Fig. 1E, right column). Additionally, the amplitude of yaw eye oscillation was somewhat less than that of the target. This shows that when fore–aft linear acceleration is negligible, there is still substantial vergence when only one eye has vision. Results were similar for a second animal, M3082, where the average eye position was close to the average target position relative to the subject. The amplitude of modulation was still reduced, however (not shown).

Gains (amplitude of eye position change re computed target-position change) and phases of the eye position were computed when the animals were translated at various frequencies

while the visual target was presented at 276 mm in front of left or right eyes. This corresponded to an average vergence angle of 7° . Tests were repeated on three different experimental days to obtain an average gain (SD) and phase (Fig. 1F–1I). When the target $\pm$ was seen by both eyes the computed gains were close to unity for both animals (Fig. 1F, 1H, open symbol) while phase was close to zero (Fig. 1G, 1I). When the moving eye was occluded, so that it could not see the target, the gain was ≈ 0.8 or below at all tested frequencies for both animals (M0652 and M3082). Thus, the amplitude of eye oscillation was reduced by $24 \pm 5\%$ in M0652 ($P = 4 * 10^{-5}$) and $23 \pm 13\%$ in M3082 ($P = 6 * 10^{-4}$). The phase was close to zero for both animals ($P = .202$ for M0652, $P = .07$ for M3082).

The gain of the convergence was also examined when the target was located at 216 mm (average vergence $\approx 9^\circ$) and at 336 mm (average vergence $\approx 6^\circ$) (not shown) to determine whether average vergence angle affected the gain of the response. For binocular viewing, the convergence gain was ≈ 1 for all average vergence angles and all frequencies of oscillation. The average gain reductions for monocular viewing, across all frequencies of fore–aft oscillation in M3082, was $38 \pm 11\%$ ($P = .008$) for an average vergence of 9° and $19 \pm 6\%$ ($P = .045$) for an average vergence of $\approx 6^\circ$. Thus, changes in gain between monocular and binocular viewing for a 9° average vergence angle were only moderately reduced from those at 7° (38% vs. 33%). Changes in gain were significantly smaller at a vergence angle of 6° (19%, $P = .04$, ANOVA with the Bonferroni approach). Phases, however, were close to zero for all average vergence angles ($P = .380$). The changes in gain were smaller for average vergence angles of $\approx 6^\circ$ in animal M0652 (not shown). However, the reductions in average gain did not significantly depend on vergence angle ($P = .595$, ANOVA). The phase angle was close to 0° at all frequencies and vergence angles, as in M3082.

In addition to determining the average gain during oscillations, we also compared the average vergence angle when the target was viewed binocularly and monocularly (Fig. 2). For binocular viewing, the average vergence angle was close to the expected values across all frequencies and target positions for both animals (Fig. 2A–2F, open symbols). During monocular viewing in animal M3082, the eye verged about 2° less than expected if the eye would be on target (Fig. 2A–C, filled symbols). The error was $19 \pm 4\%$ ($P = 6 * 10^{-6}$) when the average convergence angle was $\approx 9^\circ$ (Fig. 2A), $20 \pm 3\%$ when the average vergence angle was $\approx 7^\circ$ ($P = 5 * 10^{-6}$), and $18 \pm 4\%$ ($P = 6 * 10^{-5}$) when the average vergence angle was $\approx 6^\circ$. Thus, although the inaccuracy of the vergence angle during monocular viewing was substantial, the values were comparable for all three target locations ($P = .580$, ANOVA). During monocular viewing, in animal M0652, the convergence was accurate across all frequencies when the average vergence angle was $\approx 9^\circ$ and $\approx 7^\circ$ ($P = .536$, $P = .234$, respectively; Fig. 2D, 2E). Although there a significant difference in average vergence angle between binocular and monocular viewing when the average vergence angle was $\approx 6^\circ$ ($P = .04$), the difference was only $4 \pm 4\%$.

Discussion

This study demonstrates that the IVOR activates accommodative vergence, so that monocular fixation of a visual target in front of a monkey along its visual axis during fore–aft motion induces convergence over a frequency range of 0.05–2 Hz, even if the seeing eye

does not move. This behavior is consistent with the findings of Mueller (nineteenth century) and has been reanalyzed by Alpern and colleagues,^{17, 18} who observed that when targets moved along the visual axis of one eye, the other eye moved as if to follow the moving target, even if it was occluded and could not see the target. Our findings extend these results, showing that the gain and average vergence angle during binocular viewing of the target is accurate across a frequency range of 0.05–2 Hz. The phases of the vergence were accurate (close to 0°), regardless of frequency, viewing distance, and whether the target was viewed binocularly or monocularly. However, the gain of vergence is substantially reduced when viewing monocularly across all frequencies. The gain reduction was greater when viewing close targets. This indicates that accommodative vergence has a substantial reduction in gain as the target moves closer to the subject and that fusional vergence may play a more important role at close distances.

Early studies of the system characteristics of convergence focused on fusional vergence in humans.^{1, 3, 10, 19} In these early studies, two targets equidistant from the eyes were brought together and moved apart and the convergence properties were examined. Fusional vergence in response to purely visual stimuli were capable of following the vergence stimulus, with a 3 dB point of approximately 2 Hz in humans.³ The IVOR appears to enhance this binocular vergence response when animals are moved fore–aft up to frequencies of 3 Hz and possibly higher.¹³ Thus, fore–aft movement enhances binocular vergence beyond just a superposition of pursuit. This is in contrast to a high frequency cutoff of approximately 1 Hz for accommodative vergence^{14–16} as referenced in Ref. 10. Thus, the IVOR interacting with accommodative and fusional vergence can generate substantial eye vergence with zero phase across a wide range of frequencies and viewing distances.

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Figure 1.

(A–E, *left panels*) Pitch and yaw eye-movement responses to fore–aft movement of the head sinusoidally, when binocularly viewing a space-fixed target, which was aligned with the visual axis of the left eye. (A–E, *right panels*), Pitch and yaw eye-movement responses when the right eye was covered. (B, C, *left and right panels*) Both for binocular and monocular viewing, the left eye, along which the target was located, had no pitch or yaw movement. (D, *right and left panels*) The eye whose visual axis was aligned with the target also did not move when viewing binocularly. (E) For both binocular and monocular viewing, the moving eye close to that of the fore–aft motion, although the gain was somewhat reduced for monocular viewing (E, *right panel*). (F, H) Gains and (G, I) phases of two monkeys (M0652 and M3082) as a function of frequency over a range 0.05–2 Hz. In both animals, the gain was 1 for binocular viewing of targets and ≈ 0.8 for when the converging eye was covered. The phases were 0° for both binocular and monocular viewing of the target.

Figure 2.

Eye-position change (degrees) of the moving eye during binocular (○) and monocular (●) viewing of the target, which lies along the visual axis of the left eye, as a function of the average distance of the target from the eye. In both monkeys (M3082 and M0652), the vergence angle declined from (A, E) 9° to (B, E) 7° to (C, F) 6° as the target distance was increased from (A, E) 216 mm to (B, E) 276 mm to (C, F) 336 mm. However, there was a significant difference in one monkey (M3082) between when the moving eye was covered (●) as compared to when viewing binocularly (○). In another monkey (M0652), there was no significant difference between binocular or monocular viewing.