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Rotation of Listing's Plane with Convergence: Independence from Eye Position

Heimo Steffen,^{1,2} Mark F. Walker,² and David S. Zee²

PURPOSE. To determine whether asymmetrical vergence results in a rotation of Listing's plane independent of vergence-associated changes of eye position in the orbit.

METHODS. Six normal subjects were required to fixate on a 3×3 array (40° on a side) of light-emitting diodes arranged on a flat screen 124 cm from the subject. Disparity-induced vergence was elicited with a horizontal Fresnel prism (30 cm/m, $\sim 17^\circ$) placed in front of one eye. In four subjects accommodative vergence (10° to 15°) was produced by placing a minus spherical lens in front of one eye while the other eye was covered. Eye position was measured binocularly using three-axis search coils. Control data were collected without prisms during monocular and binocular viewing. For all data a planar regression was used to fit torsional eye position as a function of horizontal and vertical position to calculate the horizontal and vertical primary positions that define the orientation of Listing's plane.

RESULTS. In the prism experiment, the horizontal primary position of the eye not wearing the prism rotated temporally by $3.9^\circ \pm 1.7^\circ$ compared with the both eyes viewing control condition. The rotation of the prism eye was in a similar range ($3.4^\circ \pm 2.0^\circ$). With accommodation, the horizontal primary position of the viewing eye rotated temporally by $4.4^\circ \pm 1.4^\circ$ compared with the monocular viewing control. In both the accommodation and the prism paradigms there was usually a rotation of vertical primary position downward.

CONCLUSIONS. Vergence-induced changes in Listing's plane can be independent of changes in orbital position associated with vergence. This finding supports a role for changes in central innervation in the elaboration of Listing's law. (*Invest Ophthalmol Vis Sci.* 2000;41:715-721)

The validity of Listing's law during convergence has been reinvestigated extensively in recent years.¹⁻⁷ It has been shown that during vergence, whether induced by a prism or by the viewing of near objects, the torsional position of the eye can be predicted, because a single plane—Listing's plane—can still be found that contains all the axes around which the eye is rotated from the primary position to any eccentric position. However, this plane is temporally (outwardly) rotated compared with the location of the plane during fixation of a target at distance. A consequence of this temporal rotation of Listing's plane is a relative extorsion in down gaze and a relative intorsion in up gaze.

In these recent reports the vergence stimulus caused both eyes to change their orbital position.¹⁻⁷ Thus, a potential confounding influence on the orientation of Listing's plane—the change in the horizontal position of the eyes in the orbit associated with the change in vergence—was not considered.

Here, we asked whether or not “position-independent” vergence leads to a similar rotation of Listing's plane. For example, with both eyes viewing, does vergence induced by placing a laterally-displacing prism in front of just one eye affect the Listing's plane of the other eye? Similarly, does vergence induced by accommodation during monocular viewing affect the Listing's plane of the viewing eye? In both examples, only 1 eye undergoes a change in its position in association with the change in vergence, although both eyes may receive a convergence command. The main result of this study is that the rotation of Listing's plane with convergence is independent of any vergence-induced change in eye position.

METHODS

Subjects

Six subjects participated in this study (24–54 years of age), and all provided their informed written consent according to a protocol conforming to the Declaration of Helsinki and approved by the Johns Hopkins Joint Committee on Clinical Investigation. One subject (SA) wore a full spectacle correction (-3.0 D, OU) during testing. The others wore no corrective lenses. All subjects were free of ocular and neurologic abnormalities, other than refractive errors. Among the subjects the maximum value of any esophoria was 3.0° and of any exophoria was 3.8° , when viewing a target at 124 cm.

Visual Stimuli

Fixation points consisted of nine light-emitting diodes (LEDs), placed on a flat screen, 124 cm in front of the subject's eye.

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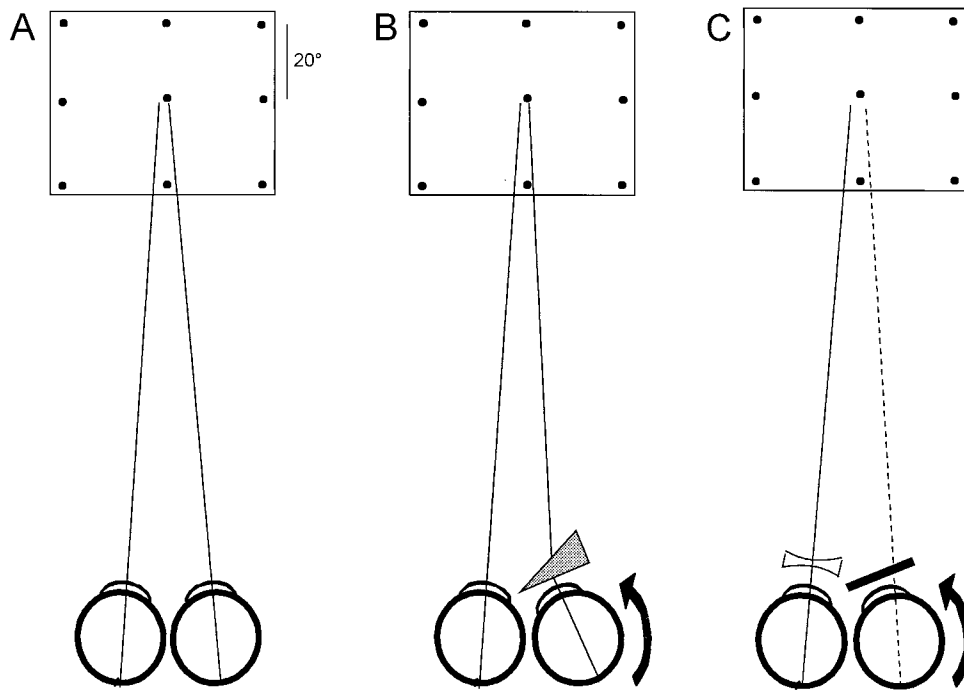


FIGURE 1. Experimental paradigms. In each case, the subject looks at the center target of a 3×3 LED array (40° on a side) at a distance of 124 cm. (A) Binocular control. (B) Prism-induced vergence: Fresnel prism placed base out over the right eye, which converges to fuse the target. (C) Accommodative vergence: -5.0 D spherical lens in front of the left eye induces accommodation. The associated vergence produces an adduction of the right eye, which is under cover. In both (B) and (C), the position of the left eye does not change.

They were arranged in a 3×3 array, 40° on a side, with the center LED (0,0) located at the straight-ahead reference position. For the accommodation paradigm (see below), small numbers, which could only be discerned with a visual acuity of at least 20/25, were placed just under each LED to provide an accommodative target. The room lights remained on during all experiments.

Recording of Eye Movements and Calibration Procedure

Movements of both eyes were recorded around all three axes of rotation (horizontal, vertical, and torsional) using the magnetic field search coil method with dual annuli. The output signals from the frequency detectors were filtered with a bandwidth of 0 to 90 Hz and sampled with a digital computer at 500 Hz with 12-bit resolution. The accuracy of the measurements was to at least 0.1° with noise levels less than 0.05° . Data were stored on disc for later off-line analysis using Matlab (Mathworks). Further details of the calibration and recording procedures can be found in Straumann et al.⁸

The annuli were placed on each eye after administration of a topical anesthetic (proparacaine HCl 0.5%, Alcaine). The subject's head (orbits) was precisely centered in the field coils using space-fixed horizontally and vertically-oriented laser beams emanating from immediately next to the center LED. The head was immobilized with a bite-bar made of dental impression material. The head orientation in the field coil system was not explicitly measured, but in most subjects in our setup the head is oriented such that Reid's line makes an angle of 20° upward.

Experimental Protocol

Two types of stimuli were used to elicit vergence: a Fresnel prism oriented horizontally in front of 1 eye, to elicit disparity-linked convergence, and a negative diopter spherical lens placed in front of one eye (the other eye was covered) to elicit

accommodative-linked convergence. The Fresnel prisms were pasted onto a pair of spectacles that contained plano lenses. The spectacles were entirely made of nonmetal material and therefore did not affect the coil signals.

The general pattern of presentation of target stimuli was as follows. After initial fixation at the center LED (0,0), LEDs at the eight eccentric positions were lit consecutively in the counterclockwise direction. Before the appearance of the LED at each eccentric stimulus, however, the center LED was illuminated, so that subjects always made consecutive centrifugal and centripetal shifts of eye position. Each LED position was illuminated for 3 seconds. The entire series of eight eccentric LED fixations was usually repeated three times. We verified for every fixation point that the horizontal and vertical positions were correct for that LED.

Prism-Induced Vergence Paradigm. The prism-induced vergence paradigms were performed on all six subjects. First, control data were collected with both eyes viewing without prisms (Fig. 1A). Then the same paradigm was performed with both eyes viewing but with a horizontal Fresnel prism placed base out ($30 \text{ cm/m} = \sim 17.1^\circ$) in front of the right eye (Fig. 1B). The left eye wore no prism. Subjects were asked to fuse the images of the LED. The vergence angle was calculated and displayed. Next, there was a second control experiment with both eyes viewing without prisms (BE_2 paradigm). Then the prism was positioned in front of the left eye (BE_{LP} paradigm). Finally, another set of data with both eyes viewing without prisms was collected (BE_3 paradigm). To summarize, the disparity paradigm order was as follows: BE_1 (both eyes viewing, no prisms, first control), BE_{RP} (both eyes viewing, right eye wearing prism), BE_2 (both eyes viewing, no prisms, second control), BE_{LP} (both eyes viewing, left eye wearing prism), and BE_3 (both eyes viewing, no prisms, third control).

It should be emphasized that in the BE_{RP} and BE_{LP} paradigms, the eye that is looking through the prism is converging to fuse the prism-induced disparity. The eye that is not looking

through the prism does not change its horizontal or vertical position within the orbit, relative to the target positions, even though the other eye is converging.

Because of the depth of their globes in the orbits and the relative location of their nasal bridges, four subjects could not reliably see the targets with the eye with the prism, when the targets were located in some of the nasal positions, which corresponded to the most temporal positions of the nonprism eye. Because fusion was lost in these positions, they were not used for analysis of either eye. Accordingly, analysis of the nonprism eye was based on the six nasal positions, and analysis of the prism eye on the six temporal-most positions, in which fusion was maintained by all subjects at all times. However, because of the change in orbital position of the prism eye during convergence, temporal positions with the prism in place were approximately 15° more nasal than the temporal positions of the control paradigm. Therefore, calculations of Listing's plane in the control paradigm were based on the six nasal positions for all eyes.

In the binocular and monocular control paradigms, in which all subjects could see all nine LEDs, we determined the effects of choosing a subset of points (relatively nasal or temporal) on the calculated orientation of Listing's plane. There was a small but consistent apparent "temporal rotation" (mean $2.4^\circ \pm 0.6^\circ$ RE- and LE-paradigm, mean $2.0^\circ \pm 0.8^\circ$ in the BE₁-paradigm) of the horizontal primary position, when the six nasal-most LEDs were selected instead of all nine LEDs. Selecting the six temporal-most LEDs for the calculation (instead of all nine LEDs) led to an apparent "nasal rotation" of the horizontal primary position of a similar magnitude (mean $1.7^\circ \pm 0.9^\circ$ in the RE- and LE-paradigms, mean $1.9^\circ \pm 0.5^\circ$ in the BE₁-paradigm). Thus, there is a small but consistent influence on the calculation of horizontal primary position, which depends on the LEDs selected; using relatively nasal eye positions leads to more temporal rotation of the primary position, and vice versa. Our data, as has been reported previously,⁹ indicate that Listing's "plane" is not a true plane but is curved and that the departures from a planar surface may be greater for more eccentric eye positions. This feature emphasizes the importance of matching, as closely as possible, the orbital positions used to calculate Listing's planes in the corresponding control and vergence paradigms.

Accommodation-Vergence Paradigm. Four of the subjects underwent the accommodation-vergence paradigm. Two presbyopic subjects were excluded. For this paradigm the subjects were encouraged to look at the small numbers placed next to the LEDs. The pattern of target presentation was otherwise as above. The subjects looked at the targets under monocular viewing conditions, first without and then with a minus lens of -5.0 D that called for accommodation (Fig. 1C). To summarize, the accommodation paradigm order was as follows: RE, monocular, right eye viewing with no minus lens (left eye covered); RE_L, monocular, right eye viewing with minus lens (left eye covered); LE, monocular, left eye viewing with no minus lens (right eye covered); and LE_L, monocular, left eye viewing with minus lens (right eye covered).

Data Analysis

The three-dimensional angular eye positions, relative to the fixed coil frame and hence to the immobilized head, were analyzed as rotation vectors and converted to gaze positions.¹⁰ Vergence angles were calculated as the difference in the hor-

izontal gaze positions of the 2 eyes, with convergence being positive.

All trials were visualized offline. For the analysis, all data points during an eccentric fixation period of 250 msec immediately before the return to the straight-ahead (0,0) reference position were taken. Thus, there was plenty of time for each subject to acquire the peripheral target, and the accuracy of fixation was also verified. Both the torsion value of each eye and the vergence angle were calculated for this period of fixation. Because each eccentric trial was both preceded and followed by a return to the reference position, any coil slip (as reflected in a sudden jump in the torsional eye signal) could be detected and corrected for by updating the reference position. This was not possible for the eye wearing the prism. When coil slips were observed in prism eyes, the affected data were excluded from the analysis. This occurred in 3 eyes of two subjects in which consistent coil slip happened in some positions of gaze. Overall, less than 5% of data points had to be deleted because of blinks or subjects not looking at the target.

Fixation data were combined from circling the entire array three times. A regression was used to fit the data points to a plane. The goodness of the fit was expressed as the standard deviation of the torsional eye positions, the so-called "thickness of the plane." From each planar fit, horizontal and vertical primary positions were calculated.¹¹ The shift in primary position was calculated as the difference between the primary position during vergence and the primary position during the corresponding control condition. For the prism experiment, data were compared to the immediately preceding control (i.e., BE_{RP} to BE₁ and BE_{LP} to BE₂). Likewise, primary positions during accommodation were compared with those of the immediately preceding monocular control. For convenience and to facilitate pooling of data, horizontal primary positions of the left eye were mirrored to the right by reversing the sign of the left eye value: Positive values describe upward and temporal rotations of either eye.

RESULTS

Prism-Induced Vergence

Control Data. Looking at all subjects, for all eyes, across all BE paradigms, the mean thickness (i.e., the mean of the standard deviations) was 0.5° with a SD of this value of 0.15°.

The mean horizontal primary position (hPP) was $4.80^\circ \pm 5.13^\circ$ for the right eye and $4.91^\circ \pm 6.58^\circ$ for the left eye. Vertical primary positions (vPP) were $8.54^\circ \pm 5.94^\circ$ for the right eye and $8.63^\circ \pm 5.82^\circ$ for the left eye. Thus, although there was a wide variation, on average the hPPs were temporal to and the vPPs above the straight-ahead reference position. These findings are similar to those reported by previous investigators.¹⁻⁷

Shift of Horizontal Primary Position. We next analyzed the effects of prism-induced vergence on the orientation of Listing's plane. We verified that the subjects were fusing the targets by monitoring the horizontal vergence angle. The values were in the 15° to 16° range as predicted from the power of the prism, except for the one subject (SA) who wore his spectacles. For this subject the vergence angle was several degrees smaller and commensurate with the minus power (about -3.0 D) of his spectacles. Figure 2A demonstrates the shift of the horizontal primary position of the eye not wearing

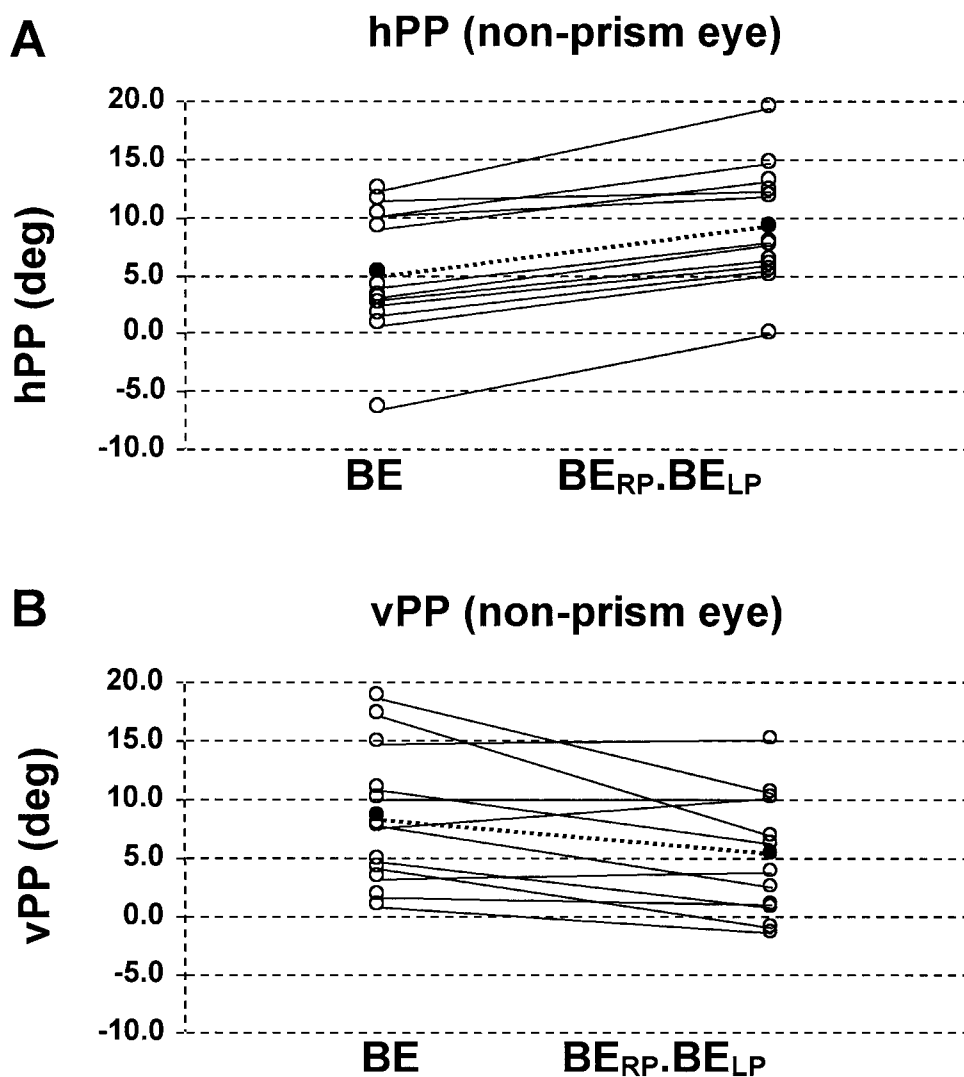


FIGURE 2. Shift of primary position of the nonprism eye in the asymmetrical vergence paradigm. (A) Horizontal primary position (hPP). (B) Vertical primary position (vPP). BE = both eyes viewing control paradigm without prisms. BE_{RP}, BE_{LP} = both eyes viewing paradigm with prism in front of the right (BE_{RP}) or the left (BE_{LP}) eye. For all eyes, positive values are temporal rotations and negative values are nasal rotations. (●), mean.

the prism (nonprism eye) for all subjects. Although individual hPPs varied across subjects, the shift of the hPP showed a uniform pattern. The hPP of the left eye (BE_{RP} paradigm) shifted temporally by $3.4^\circ \pm 2.1^\circ$ ($P = 0.01$, paired t -test), and the hPP of the right eye (BE_{LP} paradigm) shifted temporally by $4.1^\circ \pm 1.3^\circ$ ($P < 0.01$, paired t -test). The difference between the two eyes was not significant ($P = 0.08$). Combining right and left eyes, the average temporal rotation of the hPP was $3.9^\circ \pm 1.7^\circ$.

In four of the six subjects, we also examined the shift in the primary position of the eye wearing the prism (the eye that is converging). Data from two patients (DW and LC) could not be analyzed due to coil slippage. As described in the Methods section, we based the calculation of Listing's plane of the prism eye on the six temporal points. Because the motor response of horizontal vergence was approximately 15° , and because our LEDs were separated by 20° , temporal eye positions of the prism eye were approximately 5° more temporal than the nasal positions of the same eye during the control paradigm. The mean value of the temporal shift in the hPP of the prism eye for the four subjects was $3.0^\circ \pm 1.5^\circ$ in the BE_{RP} paradigm and $3.7^\circ \pm 2.4^\circ$ in the BE_{LP} paradigm. When all eyes were combined, the temporal shift was $3.4^\circ \pm 2.0^\circ$. There was no significant

difference in the shift of the hPP between the prism and the nonprism fellow eye ($P = 0.27$), or in an individual eye when it was or was not wearing the prism (e.g., right eye in BE_{RP} and BE_{LP}; $P = 0.44$).

A "gain" for vergence-induced changes in primary position can be calculated by dividing the shift of hPP by the amount of prism-induced change in horizontal vergence. For the right eye in the BE_{LP} paradigm the calculated gain was 0.23 ± 0.16 and for the left eye (BE_{RP} paradigm) the gain was 0.29 ± 0.13 . The gains of the converging eyes were similar, 0.22 ± 0.14 for the right eye (BE_{RP} paradigm) and 0.26 ± 0.22 for the left eye (BE_{LP} paradigm).

Shift of Vertical Primary Position. The shift of the vPP of the nonprism eye is depicted in Figure 2B. For most subjects, the vPP was displaced downward. In one subject (DZ), there was a slight upward shift of the vPP of whichever eye was the nonprism eye. In another subject (LG), the vPP of one eye did not change and the other shifted downward. On average, for all subjects, there was a downward shift of the vPP in both the nonprism and prism eyes. The mean shift for the nonprism eye was $-3.18^\circ \pm 3.84^\circ$ ($P < 0.01$) and for the prism eye $-5.19^\circ \pm 5.37^\circ$ ($P < 0.01$). As for the temporal rotation of the hPP, no difference was observed in the shift of vPP of an

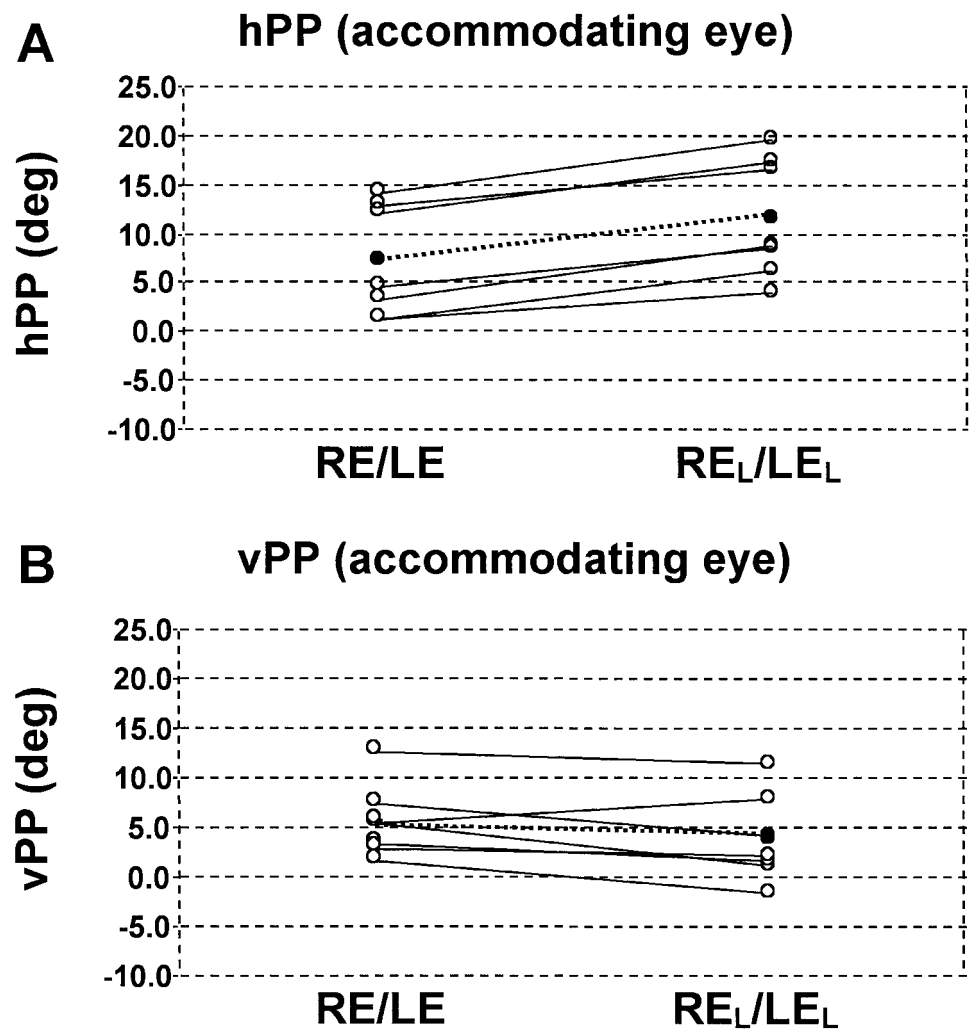


FIGURE 3. Shift of primary position of the viewing eye when accommodating -5.0 D during monocular viewing (RE_L/LE_L paradigms). (A) Shift of horizontal primary position (Δ hPP). (B) Shift of vertical primary position (Δ vPP). RE/LE refers to the values for the monocular viewing paradigms before wearing the minus lens. RE_L/LE_L refer to which eye is wearing the minus lens. For all eyes, positive values are temporal rotations and negative values are nasal rotations. (●), mean.

individual eye, whether it was the one looking through the prism or not ($P = 0.44$). Likewise, no significant difference was found in the change of vPP between the prism eye and its fellow eye ($P = 0.34$). There was also no significant correlation between temporal shifts of hPP and downward shifts of the vPP for either the nonprism eyes (correlation coefficient = 0.29) or the prism eyes (correlation coefficient = 0.05).

Accommodation-Induced Vergence

In a second set of experiments, which was possible in the four subjects without presbyopia, we used accommodation and accommodative vergence as the stimulus for a rotation of Listing's plane. We used the amount of convergence of the covered eye in the monocular viewing condition as a rough measure of accommodation. During the monocular viewing paradigm with the minus lens in front of the viewing eye the mean values of the associated change in vergence ranged from 9.9° to 15.4° . These values are reasonable for accommodative vergence; they correspond to AC/A ratios ranging from 1.9 to 3.1, which is within the range of normal.¹²

As for the both eye viewing paradigms, there was a large intersubject variability in the hPP and vPP in the accommodation paradigms. However, accommodation consistently led to a

temporal rotation of the hPP and to a downward rotation of the vPP. Figure 3 demonstrates the changes of the horizontal and vertical primary positions associated with accommodation-induced vergence. Only 7 eyes (instead of 8) are shown, because 1 subject (SA) developed an "accommodative spasm" after accommodating with the left eye and could not "relax" for the subsequent control paradigm. The mean temporal shift of the hPP was $4.4^\circ \pm 1.4^\circ$. Based on the accommodation-induced vergence change of the covered eye, the mean gain for the temporal rotation of the hPP associated with accommodation was 0.35 ± 0.13 for all 7 eyes.

DISCUSSION

Vergence-Induced Rotation of Listing's Plane

The main finding of this study is that both prism-induced and accommodative vergence lead to shifts in the primary positions of the eyes even if the horizontal and vertical orbital positions remain constant. Horizontal primary position was shifted temporally, and vertical primary position was usually shifted downward. The gain of temporal rotation of the horizontal primary position (~ 0.25 to 0.35) was in the range of rotations in

Listing's plane reported previously by Mok et al.¹ and Bruno and Van den Berg⁵ during convergence in which both eyes viewed a near target.

Our study showed no consistent difference in the magnitude of hPP shift between the converging and nonconverging eye. Recently, Porrill et al.,¹³ recording smooth tracking in-depth with the target aligned along the visual axis of one eye, found a greater change in relative torsion on up versus down gaze in the eye that was converging. The discrepancy between our study and theirs remains unexplained, although the experimental stimuli and the method of analyzing eye movements were different.

In another recent study, Kapoula et al.¹⁴ showed that not only the vergence itself but also the stimulus driving the vergence influence the amount of rotation of Listing's plane associated with near viewing. Although disparity-driven vergence alone led to a strong temporal rotation of Listing's plane in both eyes, albeit sometimes asymmetrical, accommodation-induced vergence led to variable results, with no apparent correlation between the tilt in Listing's plane and the change of vergence. In our study, however, the effects of vergence on the shift of primary position induced by disparity or by blur were similar, perhaps reflecting the facts that the visual stimuli used in our study were simpler than those used by Kapoula et al.¹⁴ and also that there was no associated disparity with our accommodative stimulus. Nevertheless, the results of Kapoula et al. argue for a "sensory" as well as a "motor" component to the shift of Listing's plane produced by near viewing.

The rotation of vertical primary position downward was a consistent finding in our paradigms but showed no difference between the prism and the nonprism eye.

Perhaps, because near viewing is usually associated with down gaze, there might be an advantage in rotating Listing's plane in the same direction to which both the eyes themselves rotate. On the other hand, the explanation may lie in the proposed changes in the innervation to the superior oblique muscle that accompany changes in vergence, as discussed below.

Listing's Law and the Ocular Motor Periphery

A controversial issue in ocular motor physiology is the role of peripheral versus central factors in the elaboration of Listing's law.¹⁶ The discovery of ocular motor "pulleys" in the orbital periphery, which could in themselves constrain eye rotations to a specific plane, has focused interest on the contributions of orbital mechanics to Listing's law and has challenged prior assumptions about the nature of the central contribution to the elaboration of Listing's law.^{17,18} Although vergence has been long known to produce changes in the orientation of Listing's plane,¹⁻⁷ our experimental paradigms removed one potentially confounding factor in the studies of the effect of convergence on Listing's law: the interaction between the position of the eye in the orbit and the changing command for convergence. The horizontal and vertical orbital positions of the nonprism and the accommodating eyes were unaltered by the change in vergence state, whether accommodative- or disparity-induced. The finding of a rotation of Listing's plane in the nonprism or in the accommodating eye in our paradigm thus provides even stronger evidence for a central contribution to Listing's law.

There are at least two mechanisms by which vergence might induce a change in the orientation of Listing's plane. First, it is possible that a change in the central innervation to

the smooth muscle of the orbital pulleys under conditions of convergence might lead to a change in the way that the pulleys alter the axis of eye rotation. It seems unlikely, however, that simply altering smooth muscle tone could lead to such precise and consistent changes in the axis of eye rotation associated with disparity- or accommodative-induced convergence. Alternatively, and more likely, convergence might lead to a change in the central pattern of innervation to the ocular muscles that would alter the axis around which the eyes rotate.

The reasons for rotation of Listing's plane with convergence have been argued extensively; both motor and sensory explanations have been invoked.¹⁸ The changes in primary position with convergence are similar to those that occur with a paralysis of the superior oblique muscle (producing a gradation of relative extorsion increasing from up to down gaze and a relative shift of the vertical primary position of the paretic eye downward).¹⁹ These changes may relate to relaxation of the superior oblique muscle during convergence. This is supported by the finding that trochlear motor unit activity decreases with convergence to a greater degree than with an equivalent conjugate adduction.²⁰ Relaxation of the superior oblique during convergence might facilitate adduction by decreasing its presumed tertiary action, abduction.²⁰ Alternatively, the horizontal consequences of superior oblique relaxation might not be a direct effect but rather due to changes in the pulling directions of other muscles in the setting of excyclotorsion.²¹ A greater degree of excyclotorsion in down gaze, and thus a temporal rotation of Listing's plane, is consistent with the finding of increased trochlear unit sensitivity to convergence with decreasing elevation.²⁰

In our experiments of asymmetrical prism-induced vergence, the amount of temporal rotation of Listing's plane was the same in the prism and nonprism eyes, even though only the prism eye was adducted. This suggests that an equal "convergence signal," including perhaps superior oblique relaxation, is sent to the two eyes, even when convergence is asymmetrical. A superimposed versional command could correct the horizontal position of the nonprism eye, while maintaining excyclotorsion, consistent with the limited effect of horizontal version (relative to vergence) on trochlear unit activity.²⁰

In conclusion, our results using an asymmetrical convergence paradigm argue for a central contribution to the convergence-evoked rotation of Listing's plane. Furthermore, the finding that there was no difference in the amount of rotation of the horizontal primary position of the prism and the nonprism eye suggests that convergence commands are distributed symmetrically between the two eyes even in asymmetrical stimulus conditions.

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