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Abstract

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Changes in Listing's Plane after Sustained Vertical Fusion

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

PURPOSE. To determine whether prolonged fusion of an imposed vertical disparity leads to a change in the orientation of Listing's plane, even when measured during monocular viewing.

METHODS. Four normal subjects (age range, 24–37 years) wore Fresnel prisms of increasing power for 72 hours to produce a final left-over-right disparity (range, 7–11 prism diopters [~ 3.9 – 6.2°]) that was still fusible. Eye movements were measured binocularly, using three-axis search coils, as subjects fixated on an array of light-emitting diodes (LEDs) arranged on a flat screen, 124 cm away. A regression was used to fit the data points to a plane (Listing's plane) during monocular and binocular viewing. From each planar fit, the horizontal and vertical components of primary position (the direction of gaze that is perpendicular to Listing's plane) were calculated. Baseline data were collected in the unadapted state, either just before or at least 4 days after wearing the prisms.

RESULTS. After the period of viewing through the prisms, there was a change in vertical phoria (prism adaptation) ranging from 1.6° to 3.3° . There was a significant ($P < 0.01$) shift of the relative orientation of the vertical component of primary position between the two eyes of $6.3 \pm 1.7^\circ$ (right eye value minus left eye, up being positive, each measured during monocular viewing). There was no consistent pattern of change in the horizontal component of primary position.

CONCLUSIONS. Prolonged fusion of a vertical disparity is associated with a change in the orientation of Listing's plane that persists under monocular viewing. Possible mechanisms include phoria adaptation, the prolonged fusional effort itself, and the residual disparity that must be overcome by sensory mechanisms. (*Invest Ophthalmol Vis Sci.* 2002;43:668–672)

The effects of horizontal vergence on Listing's plane have been investigated extensively in the past decade. The most consistent finding is a convergence-evoked temporal rotation of Listing's plane of each eye.^{1–4} In contrast, only a few investigators have examined the effects of vertical vergence on Listing's plane and the results were conflicting.^{5,6} Each of these studies presents data after a relatively brief period of fusion of the imposed disparity. It is not known whether prolonged fusion of a disparity leads to changes in the orientation of Listing's plane, and if so, whether such changes would persist under monocular viewing conditions, thus becoming indepen-

dent of the fusion process itself. One factor could be phoria adaptation, which occurs with continuous exposure to displacing prisms that produce a sustained disparity.⁷ This is an adaptive mechanism, which drives the phoria in the direction of the alignment change required by the prism and so eases the load on the reflexive, immediate, disparity-driven, vertical fusional response. Another factor could be the sustained attempt at vertical fusion itself. In the present study, we investigated the effect of sustained (days) vertical fusion on the orientation of Listing's plane, and indeed found a change that persisted under conditions of monocular viewing.

METHODS

Subjects

Four subjects (age range, 24–37 years) participated in this study and provided informed written consent according to a protocol conforming to the Declaration of Helsinki and approved by the Johns Hopkins Joint Committee on Clinical Investigation. Two subjects (NH and VP) wore their habitual full-spectacle corrections (in sphere diopters, NH: -2.75 OD, -4.0 OS; VP: -3.0 , OU) during testing; the others wore no corrective lenses. All subjects were free of ocular abnormalities.

Visual Stimuli

Fixation points consisted of nine light-emitting diodes (LEDs), placed on a flat screen, 124 cm in front of the subject's eyes. 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. The room lights remained on during all experiments.

Recording of Eye Movements and Calibration Procedure

Three-dimensional eye movements were recorded using the magnetic field search coil method with dual-coil annuli.^{8,9} The field coil system consisted of a cubic coil frame producing three orthogonal magnetic fields (frequencies: 55.5, 83.3, 42.6 kHz; intensity: 0.088 Gauss). The dual search coils (Skalar, Delft, The Netherlands) yielded two sensitivity vectors, each being characterized by voltages induced in one of the two coils by the three orthogonal fields. An in vitro calibration was performed before each experiment, in which voltage offsets were nullified by placing the coils into a metallic tube that completely shielded the coil from the magnetic fields. The coil then was placed on a gimbal system that was in the center of the magnetic coil frame. Coil gains were determined by aligning the sensitivity vectors of each coil with each of the three magnetic fields. The output signals of the experiment were filtered with a bandwidth of 0 to 90 Hz and sampled at 500 Hz with 12-bit resolution. System noise was less than 0.1° . Data were stored on disc for later off-line analysis on computer (Matlab; Mathworks, Inc., Natick, MA). Further details of the calibration and recording procedures can be found in Bergamin et al.¹⁰

The annuli were placed on each eye after administration of a topical anesthetic (proparacaine HCl 0.5%, Alcaine; Alcon Laboratories, Fort Worth, TX). The subject's head was precisely centered in the field coils so that the center of the interpupillary line coincided with the center of the frame, and the interpupillary line was parallel to earth horizontal. This was accomplished by using space-fixed, horizontally and vertically oriented laser beams emanating from the location of the

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TABLE 1. Parameters of Vertical Eye Position before and after Prism Adaptation

Subject	Phoria _b (deg)	Prism (Δ)*		Total Prism _{power} (deg)	Phoria _a (mean deg)	ΔPhoria (deg)	Disp _{res}	Tropia _a (deg)
		RE	LE					
NH	-0.3 ± 0.2	4	6	-5.7	-3.6 ± 0.3	-3.3	-2.1 ± 0.3	-5.4 ± 0.1
HS	0.3 ± 0.2	4	4	-4.6	-1.3 ± 0.2	-1.6	-3.3 ± 0.2	-4.2 ± 0.2
VP	-0.9 ± 0.3	6	5	-6.3	-2.6 ± 0.2	-1.7	-3.7 ± 0.2	-4.6 ± 0.2
MS	-0.2 ± 0.2	7	—	-4.0	-2.1 ± 0.2	-1.9	-1.9 ± 0.2	-3.9 ± 0.2

Phoria_b, baseline vertical phoria in the unadapted state; prism_{power}, total power of the pasted prisms; phoria_a, vertical phoria in the prism-adapted state; Δphoria, prism-induced change in phoria; (Δphoria) = (phoria_b) - (phoria_a); disp_{res}, (prism_{power}) - (phoria_a), residual disparity in the adapted state. tropia_a, vertical tropia in the adapted state, which is the difference between right-eye vertical and left-eye vertical with binocular viewing in the adapted state.

*Prism power in diopters; prisms were always pasted so as to induce a left-over-right disparity.

zero-position LED. The head was immobilized with an earth-horizontal bite bar made of dental impression material.

Experimental Protocol

A vertical disparity was introduced by placing vertically oriented prisms in front of one eye (one subject) or both eyes (three subjects). The Fresnel prisms were pasted on a pair of spectacles that contained plano lenses (subjects HS and MS) or on the fully corrected, habitually worn refraction (subjects NH and VP). Spectacle frames contained no metal. The prisms were always placed base-up in front of the right eye and base-down in front of the left eye, thus inducing a left-over-right disparity in all subjects. The prisms were oriented as close as possible to vertical. Measures of horizontal eye position indicated that no more than 0.2° of horizontal disparity could have been introduced with the prism. The power of the prisms was gradually increased over a period of 3 days, depending on whether fusion occurred without asthenopia. For the 10 hours preceding the postadaptation recordings, the power of the vertical prisms was constant. All subjects performed their natural daily activities, including, for example, working in front of a computer for at least several hours a day.

The final power of the vertical prisms in each subject is indicated in Table 1. Recordings were made in two separate sessions: (1) in the unadapted state, just before (subjects NH, VP, and HS) or 4 days after wearing the prisms (subject MS) and (2) in the adapted state after wearing the prisms for 72 hours (all subjects). Data in the adapted state were collected with the prisms in place.

Target stimuli were presented as follows. After initial fixation at the center LED, 0,0, the LEDs at the eight eccentric positions were lit consecutively, beginning with the rightward LED and moving in a counterclockwise direction. Before the appearance of each eccentric LED, the center LED was illuminated so that subjects always made consecutive centrifugal and centripetal shifts of eye position. At each position, the LED was illuminated for 3 seconds. The entire series of eight eccentric LED fixations was usually repeated three times. Data were collected under monocular (with one eye covered) and binocular viewing conditions.

The order of the paradigms in the unadapted state (without prisms) was monocular right-eye viewing, monocular left-eye viewing, and both eyes viewing. In the adapted state (with prisms on) the order was both eyes viewing, monocular right-eye viewing, and monocular left-eye viewing. The reason for starting the protocol with a both-eyes-viewing condition in the adapted state was to minimize deadadaptation during the recording sessions.

Data Analysis

Coil signals were used to calculate rotation vectors¹¹ representing three-dimensional angular eye position relative to the fixed coil frame and thus to the immobilized head. Rotation vectors were converted to degrees and expressed with the following convention: Positive values describe upward, rightward, and clockwise rotations from the subject's viewpoint. A first-order linear regression was used to fit data

points to a plane. The goodness of the fit was expressed as the SD of the torsional eye positions—the so-called thickness of the plane. From each planar fit, we computed directly the horizontal and vertical component of primary position in degrees from the slopes of the regression,^{10,11} recalling that the primary position is defined when the line of sight is along an axis that is perpendicular to Listing's plane.

All trials were visualized off-line. For the analysis, all data points during a fixation period of 250 ms immediately before the switch from the reference position 0,0 to an eccentric position or back from the eccentric position to the reference position were taken. Both the torsional position of each eye and the vergence angle were calculated for this period of fixation. Less than 10% of data points had to be deleted due to blinks or loss of fixation.

From the fixation data, the alignment of the eyes was calculated in the different viewing conditions. In the adapted state, the alignment was measured with the prisms on. The vertical *phoria* is defined as the right eye-minus-left eye vertical position (up is positive) during monocular viewing of the straight-ahead LED. The vertical *tropia* is defined as the right eye-minus-left eye vertical position during binocular viewing. For the phoria, the mean and the SD were calculated from a total of 20 values obtained from each return to the straight-ahead position from each eccentric position, with 10 values for left-eye viewing and 10 values for right-eye viewing.

RESULTS

Effect of Sustained Fusion on Vertical Phoria

We will first present the amount of phoria adaptation in each subject for later comparison with the changes in the orientation of Listing's plane. The important data are in Table 1. The difference between the baseline vertical phoria (phoria_b) in the unadapted state and the power of the prisms yields the prism-induced disparity that drives vertical fusion when the prisms are first put on. The difference between the vertical phoria in the adapted state (phoria_a) and the baseline vertical phoria (phoria_b) yields the change in vertical phoria (Δphoria), which ranged from -1.6° to -3.3°.

The phoria in the adapted state only partially compensated for the prism-induced disparity. The residual disparity (disp_{res}) is the disparity that drives vertical fusion in the adapted state and is the difference between the power of the prisms and the phoria in the adapted state (phoria_a).

Effect of Prolonged Vertical Fusion on the Thickness and Orientation of Listing's Plane

We examined the effect of prolonged fusion on the thickness of Listing's plane, as reflected in the SD of torsional eye position. Looking at all subjects and all eyes and across all monocular viewing paradigms, the mean thickness (i.e., the mean of the SDs) in the unadapted state was 0.75 ± 0.22° (SD). In the

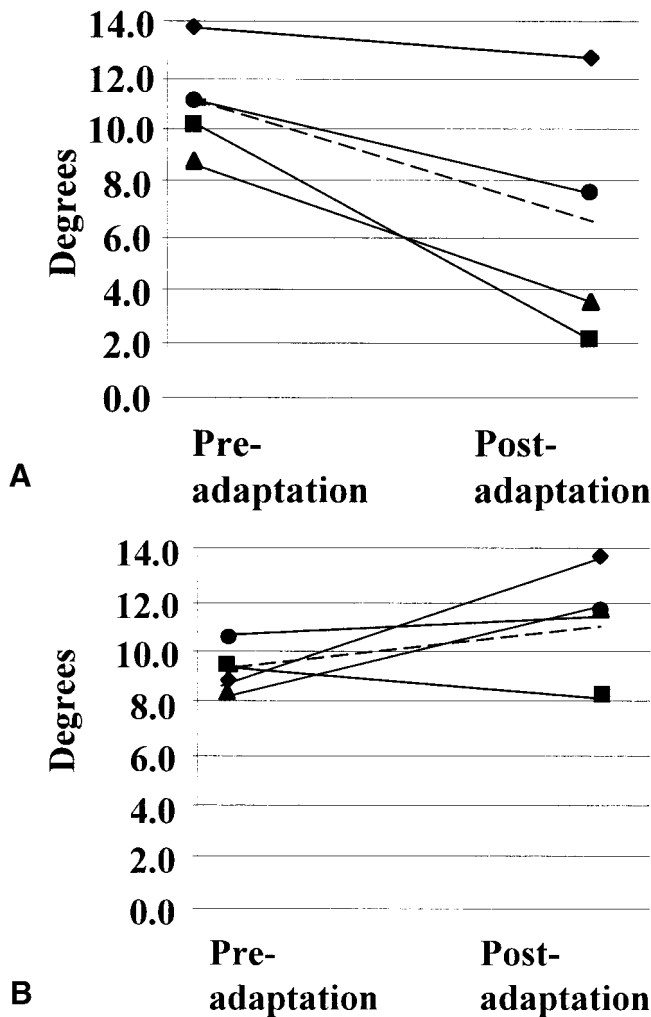


FIGURE 1. vPPs in the unadapted and adapted states (monocular viewing) of the right (A) and the left (B) eyes. Symbols represent subjects as follows: (●) MS, (■) HS, (▲) VP, and (◆) NH. Dashed line: mean value. The vPP of the right eye moved down in all subjects, the vPP of the left eye moved up in three subjects.

prism-adapted state the mean thickness was $0.90 \pm 0.39^\circ$. The thicknesses of the planes in the unadapted and the prism-adapted states were not statistically different ($P = 0.15$, paired t -test).

After prolonged vertical fusion, there was a relatively consistent pattern of shift of the vertical component of primary position (vPP; Fig. 1A). As measured during monocular viewing, the vPP of the right eye moved down in all subjects a mean of $4.3 \pm 2.9^\circ$ ($P = 0.02$, paired t -test). The vPP of the left eye moved up in three subjects and down in one subject (Fig. 1B, HS filled squares) a mean of $2.0 \pm 2.8^\circ$ ($P = 0.12$).

We also calculated the difference (vPP_{diff}) between the vertical component of primary positions of the right and left eyes (measured under monocular viewing conditions) in the adapted and unadapted states. Figure 2 shows vPP_{diff} for each subject in the unadapted and in the adapted state. Before wearing the prism the vPPs of the two eyes in each subject were similar, with the exception of subject NH in whom the vPP of the right eye was approximately 5° higher than that of the left eye. The main effect of prolonged wearing of the prism was a shift of the vPP_{diff} from $1.3 \pm 3.1^\circ$ in the unadapted state to $-5.0 \pm 4.0^\circ$ in the adapted state. This corresponded to a net shift of $-6.3 \pm 1.7^\circ$ ($P < 0.01$, paired t -test) with the primary

position of the left eye moving higher, relative to that of the right eye.

In contrast to the changes in vPP, there was no consistent direction or size of change in the horizontal (h)PPs after wearing the prism, although the changes in two subjects were large. In subject NH the horizontal components of the primary positions of the two eyes diverged by 8.8° (a net relative temporal rotation) and in subject VP they converged by 11.1° (a net relative nasal rotation). In the other two subjects, the changes were smaller (HS, 1.6° of divergence and MS, 4.0° of convergence).

Control Experiments for the Changes in vPP

In the adapted state, vPP and, consequently, vPP_{diff} were calculated using eye positions that were from 2.5° to 4.0° different from those used to calculate vPP in the unadapted state, because of the prisms. To exclude any artifact from using slightly different eye positions to calculate Listing's planes, we performed a control experiment in subject HS. During monocular viewing, primary positions were measured first with the usual LED display and then compared with those obtained when looking through a vertical prism of 4 prism diopters, base-up or base-down. The shift of the vPP_{diff} using these two displays was -1.2° , with the prism base-up in front of the right eye and base-down in front of the left eye. With the prisms reversed (base-down in front of the right eye and base-up in front of the left eye) the vPP_{diff} shifted by 0.4° . These shifts in primary position were much less than the shift of the vPP_{diff} of approximately 8° measured in HS after prolonged wearing of the prism. Thus, it is unlikely that the relatively small difference in fixation positions used to compare primary positions in the unadapted and adapted states were responsible for the shifts in the orientation of Listing's plane after prolonged wearing of the prism.

We also considered that the changes in Listing's plane associated with wearing a prism for 3 days may reflect day-to-day fluctuations in the orientation of Listing's plane. In three of our subjects (NH, HS, MS) we had measures of Listing's plane

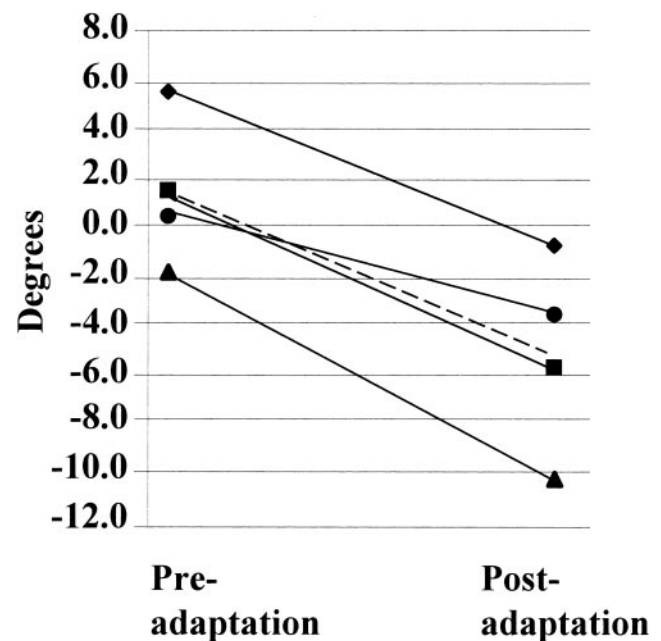


FIGURE 2. Relative orientation of the vPPs: vPP_{diff} = vPP of the right eye minus vPP of the left eye in unadapted and adapted states (monocular viewing). Dashed line: mean value. Symbols refer to the same subjects as in Figure 1.

at least several months apart. The differences between the values of vPP_{diff} measured on those two occasions were 2.1° , 1.5° , and 0.6° , respectively, which in each case was less than the shift associated with wearing the prism. The differences between the values of hPP_{diff} measured on two different occasions were 2.4° , 2.9° , and 0.6° , respectively.

Effect of Vertical Fusion on Listing's Plane after Adaptation

So far, we have considered the orientation of Listing's planes obtained under monocular viewing conditions, before and after adaptation. There is also a question of whether vertical fusion influences the orientation of Listing's plane when changing from monocular to binocular viewing. After 3 days of sustained vertical fusion, the phoria adaptation of our subjects was incomplete. During viewing with both eyes, however, some of the residual prism-induced disparity was removed with the motor component of the fusional process. We therefore compared primary positions under monocular viewing (one eye on target, no fusion) and binocular viewing (both eyes on target during fusion) in the adapted state. We found no significant changes in the vPPs of individual eyes with fusion ($P = 0.40$, paired t -test), although there was a trend for the relative orientation of the vPPs to change with fusion ($-4.3 \pm 4.4^\circ$, $P = 0.07$). We found no significant shifts of either the hPP of each eye ($P = 0.19$, paired t -test) or of the hPP_{diff} between the two eyes ($P = 0.28$, paired t -test). It must be remembered that the absolute values of the motor responses to the vertical $disp_{res}$ in our subjects were relatively small, with mean values ranging from 1.7° to 2.9° , when looking at the straight-ahead LED. In the unadapted state, without prisms (i.e., with no imposed vertical disparity to fuse) neither hPP nor vPP changed significantly when comparing monocular and binocular viewing conditions (for the hPP_{diff} $P = 0.29$; for the vPP $P = 0.20$, paired t -test).

DISCUSSION

The main result of the present study is that a prolonged attempt at vertical fusion is accompanied by a change in the orientation of Listing's plane that persists under monocular viewing conditions. After 3 days of binocular viewing through a vertical disparity prism combination, there was a relative shift in the vertical component of the primary positions of the two eyes (measured during monocular viewing), so that the vPP of the relatively higher eye moved up and that of the lower eye moved down. We will first compare our results with those of previous investigators who studied the effects of wearing prisms on the orientation of Listing's plane, and then we will discuss our findings in the context of what factors, sensory or motor, may be causing the shift in the orientation of Listing's plane.

Shift of Primary Position Associated with Fusion of a Prism-Induced Vertical Disparity: Comparison with Previous Studies

Our results are consistent with a previous study by Mikhael et al.⁵ in which prism-induced vertical vergence was associated with a shift of the vPP in the same direction as the verging eye (e.g., a base-up prism induces a downward movement of the eye and a downward shift of the vPP). Their results were based on data from five normal subjects who wore vertical prisms in a range of 1.5 to 7 prism diopters in front of each eye. Overall, they found that, during fusion, the vPP of either eye rotated by approximately 2.7° per degree of vertical vergence. Because in their study, training sessions of 30 to 60 minutes were necessary for the subjects to fuse the induced vertical disparity,

it is not clear whether the shift of the vPP was entirely related to the reflexive vergence that immediately followed the disparity demand or to any phoria adaptation that may have taken place during the training sessions, as a delayed adaptive response. Furthermore, they did not report values for primary position during monocular viewing, and we therefore do not know whether there were any non-disparity-driven changes in the orientation of Listing's plane. Indeed, the major finding of our study is that after wearing of the prism for several days, there was a consistent pattern of long-term change in the vertical component of primary position, independent of any immediate attempt to fuse disparity.

The effect of wearing vertical prisms on Listing's plane was also studied by Straumann and Müller.⁶ They tested three subjects in whom vertical fusion was elicited after a brief period of wearing vertical prisms with an overall power of 1.5 prism diopters. They found a small tendency for inward (nasal) rotation of Listing's plane associated with vertical fusion and no change in the plane's vertical orientation. Mikhael et al.⁵ also reported changes in the horizontal component of primary position; a temporal rotation with the prism base-up and a nasal rotation with the prism base-down. We found no consistent direction of a shift of the horizontal component of primary position, either after adaptation or during vertical fusion in the adapted state. However, we found a large shift of the horizontal component of primary position in two subjects after adaptation, although in opposite directions. The reason for this striking variability among our subjects is unclear. There was no change in the horizontal phoria in any of our subjects after wearing the vertical prisms. The different patterns of change in the horizontal component of primary position, however, imply different patterns and different degrees of change in the gradient of torsion along the vertical meridian. The direction of torsion that occurs with the vertical vergence associated with vertical fusion is known to be idiosyncratic from person to person.¹² If this were reflected in a variable pattern of change in torsion with up-and-down gaze, it might contribute to the variable pattern of change in the horizontal component of primary position. Overall, the reason for the discrepancies among the results of Mikhael et al.,⁵ Straumann and Müller,⁶ and ourselves is unknown, although the experimental protocols were quite different.

Functional Implications of a Shift in vPP

Our results seemingly agree with a prediction of the visual-motor theory of Tweed¹³ about the changes in torsion associated with optimal binocular control. Tweed relates the behavior of Listing's plane under binocular viewing conditions to preventing changes in cyclodisparity that would otherwise complicate neural processing of visual information. His theory includes the prediction that the direction of the tilt of Listing's plane during vertical vergence would be in the same direction as the movement of the verging eye, whereas the tilt of the plane during horizontal vergence would be in the opposite direction of the movement of the verging eye. These tilts of Listing's plane would minimize changes in cyclodisparity by equalizing the torsional orientation of both eyes in the visual plane (defined as the plane containing the gaze lines of both eyes).

In our experiments, the vertical vergence was induced by optical means, so that if vertical eye alignment were readjusted to meet the demands of the prism without a superimposed change in torsion, there would be no change in cyclodisparity and hence no visual drive to alter torsion. However, because primary position is not normally coincident with straight ahead gaze, there could be a change in torsional disparity with vertical realignment of the eyes, which might serve as a stimulus

to torsional phoria adaptation,¹⁴ as well as to a change in the orientation of Listing's plane. These considerations, along with the discrepancies between the results of our study and those of previous investigators, raise the issue of a potential role of vertical and torsional phoria adaptation in the elaboration of Listing's law. Sensory factors related to mechanisms underlying the sensory components of vertical and cyclofusion or changes in the sense of visual direction (which could be altered by prolonged viewing through a prism) may be important. Clearly, more subjects and recordings at more frequent intervals and after complete phoria adaptation are necessary to determine the relationship between phoria adaptation, sensory factors, and the shifts in the orientation of Listing's plane.

Regardless of the actual mechanisms, our results indicate that Listing's law is mutable. Schor et al.¹⁵ also have shown recently that the orientation of Listing's plane can be modified by altering cyclofusional demands. A capability for modifying Listing's plane could help to optimize binocular function in the setting of strabismus and its surgical or optical correction. What parts of the brain mediate the adaptability of Listing's law and how it is elaborated (through central or peripheral factors) still remain to be discovered.

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References

- Mok D, Ro A, Cadera W, Crawford JD, Vilis T. Rotation of Listing's plane during vergence. *Vision Res.* 1992;32:2055-2064.
- Kapoula Z, Bernotas M, Haslwanter T. Listing's plane rotation with convergence: role of disparity, accommodation, and depth perception. *Exp Brain Res.* 1999;126:175-186.
- Porrill J, Ivins JP, Friby JP. The variation of torsion with vergence and elevation. *Vision Res.* 1999;39:3934-3950.
- Steffen H, Walker MF, Zee DS. Rotation of Listing's plane with convergence: independence from eye position. *Invest Ophthalmol Vis Sci.* 2000;41:715-721.
- Mikhael S, Nicolle D, Vilis T. Rotation of Listing's plane by horizontal, vertical and oblique prism-induced vergence. *Vision Res.* 1995;35:3242-3254.
- Straumann D, Müller E. Is Listing's law preserved in the vertical fusional reflex? In: Fuchs AF, Brandt T, Büttner U, Zee D, eds. *Contemporary Ocular Motor and Vestibular Research: A tribute to David A. Robinson.* Stuttgart, Germany: Georg Thieme Verlag; 1994:336-338.
- Schor CM. Fixation disparity and vergence adaptation. In: Schor CM, Ciuffreda KJ, eds. *Vergence eye Movements: Basic and Clinical Aspects.* London: Butterworths; 1983:465-516.
- Robinson DA. A method of measuring eye movement using a scleral search coil in a magnetic field. *IEEE Trans Biomed Eng.* 1963;10:137-145.
- Collewijn H, Van der Mark F, Jansen TC. Precise recording of human eye movements. *Vision Res.* 1975;15:447-450.
- Bergamin O, Zee DS, Roberts DC, et al. Three-dimensional Hess screen test with binocular dual search coils in a three-field magnetic system. *Invest Ophthalmol Vis Sci.* 2001;42:660-667.
- Haustein W. Considerations on Listing's law and the primary position by means of a matrix description of eye position control. *Biol Cybern.* 1989;60:411-420.
- Hara N, Steffen H, Roberts DC, Zee DS. Effect of horizontal vergence on the motor and sensory components of vertical fusion. *Invest Ophthalmol Vis Sci.* 1998;39:2268-2276.
- Tweed D. Visual optimization in binocular control. *Vision Res.* 1997;37:1939-1951.
- Taylor MJ, Roberts DC, Zee DS. Effect of sustained cyclovergence on eye alignment: rapid torsional phoria adaptation. *Invest Ophthalmol Vis Sci.* 2000;41:1076-1083.
- Schor CM, Maxwell JS, Graf EW. Plasticity of convergence-dependent variations of cyclovergence with vertical gaze. *Vision Res.* 2001;41:3353-3369.