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Rotation of Listing's Plane During Vergence

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When visually fixating targets on an isovergence surface, the position of each eye was constrained to a plane. Thus, Listing's law holds during vergence. The planes were, however, rotated temporally with respect to those when viewing distant targets. The effect of this rotation was to produce a torsion which depended on eye elevation; extorsion of the two eyes for downward gaze and intorsion for upward gaze. The saccadic velocity command was relatively unaffected during vergence. Computer simulations suggest that the saccadic tonic command and the vergence command interact multiplicatively in three dimensions.

Listing's plane Oculomotor Torsion Vergence

INTRODUCTION

It is generally assumed that because the eye rotates about the line of sight during vergence (Enright, 1980; Nakayama, 1983), Listing's law holds only for gaze at distant targets. This need not be the case. The change in torsion may simply reflect a shift or a tilt of Listing's plane. Thus, the axes of rotation to and from primary position could remain confined to a plane, as in the original definition of Listing's law, but the orientation of this plane may change during vergence. The purpose of this study was to examine this possibility.

As reviewed by Allen and Carter (1967), this question is complicated by a lack of consensus on a definition of ocular torsion. The definition depends on the coordinate system adopted. In Fick or Helmholtz coordinates, torsion is defined as rotation around the line of sight. We have recently argued (Tweed, Cadera & Vilis, 1990) that because the pulling directions of the extraocular muscles are fixed in the head, a head fixed coordinate system would be more appropriate. The problem then is to place an appropriate torsional axis on the head. One could draw a line relative to some arbitrary anatomical landmarks on the head; for example a line orthogonal to the interaural axis and through the centre of the orbit. If a subject were examined whose head was rotated upwards, the defined torsional and vertical axes would also rotate. In this position, a rotation of the eye about a purely vertical axis in the head would be a rotation about a torsional and vertical axis relative to space. Thus, the amount and direction of torsion is clearly dependent on where we locate the axes relative to the head.

The above choice of anatomical landmarks is clearly arbitrary. A less arbitrary choice is to use primary position to define the direction of the torsional axis. As originally defined, primary position is specific and unique. Primary position is that position adopted by the eye when the gaze direction is perpendicular to Listing's plane [Fig. 1(A)] (Tweed & Vilis, 1990).

Recent studies have suggested that this coordinate system, defined by Listing's plane and primary position, is one adopted by the saccadic generator (Crawford & Vilis, 1992) and the vestibular–ocular reflex (Crawford & Vilis, 1991). It does not appear to be based on any external head coordinates or landmarks such as those of the canals or extraocular muscles. Rather, it appears to be implemented neurally and thus is a coordinate system that can shift its location. Evidence for such a shift has been observed for vestibularly driven quick phases (Crawford & Vilis, 1991). It is therefore possible that Listing's coordinates undergo a similar shift during vergence.

The results described here show that the eye positions during vergence remain restricted to a planar surface. This surface is however rotated relative to that observed for far targets. The rotation is such that during convergence both eyes undergo extorsion during downward gaze shifts and intorsion during upward gaze shifts.

METHODS

Experimental paradigm

Results were obtained from eight human subjects, none of whom had any pre-existing ocular pathology, apart from a mild refractive error.

In order to determine whether Listing's law holds during vergence, the three-dimensional angular position of the eye was examined for various gaze directions. To ensure that convergence was the same at each gaze direction, a fibreglass isovergence mask (Collewijn, Erkelens & Steinman, 1988) was constructed for each subject based on individual interpupillary distances [Fig. 1(B–D)]. Interpupillary distances (*pd*), at far, were measured for each subject using an Essilor analogue

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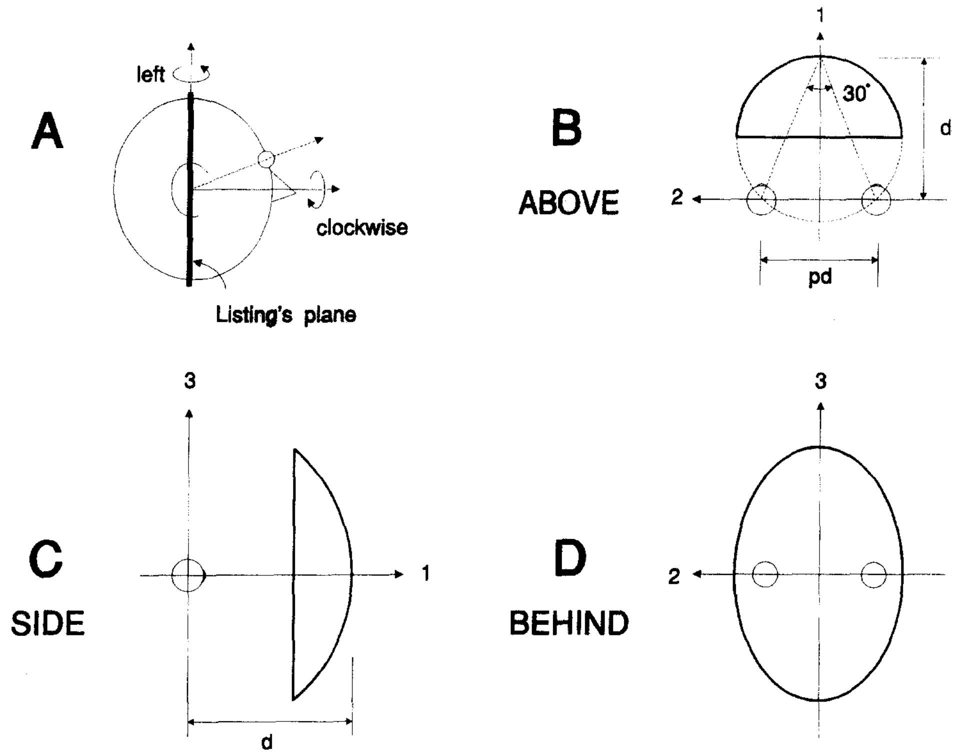

FIGURE 1. (A) A coordinate system based on Listing's plane. The torsional axis is collinear with primary position which, in turn, is perpendicular to Listing's plane. (B–D) Three views of the isovergence mask: (B) above, (C) side and (D) behind views. *pd* is the interpupillary distance when looking far. *d* is the distance from the centre of the eye to the isovergence mask.

pupillometer. An isovergence angle of 30 deg was chosen in the creation of each mask. The value, *d*, represented in Fig. 1 was calculated by the equation, $d = (0.5 \times pd)/\tan 15$ deg. In order to create the vertical dimensions of the isovergence mask, the bold semicircle represented in Fig. 1(B) was pivoted about axis 2 [see Fig. 1(C)]. Since each mask was mounted on a separate plexiglass frame, it was possible to quickly insert and remove the mask during the course of the experiment thus allowing a rapid comparison under vergence conditions (with mask in place) and nonvergence conditions (see below).

It was assumed that half the eye's axial length was a reasonable estimate of the centre of rotation of the eye (Parks, 1982). Each mask was placed a distance $d' = d - (\text{axial length})/2$ in front of each subject's cornea. The axial length of each subject's eyes was measured using an A-scan ultrasound (Ophthascan-s). Where the left and right axial lengths differed, an average was taken and used for that subject. None of the subjects showed a difference > 1 mm.

In order to obtain eye position data under nonvergence conditions, subjects were positioned at a distance of 2 m from a flat target surface, a distance which requires insignificant change in vergence (< 0.4 deg over a ± 30 deg horizontal and vertical range). The support apparatus for the isovergence mask was designed so that when the mask was not in place, the subject would have full view of the target surface. Fixed target positions, indicated by a 0.2 deg red dot and placed on a green background for enhanced contrast, covered a range of eccentricities of ± 30 deg. In addition, two pairs of targets were arranged at 15 deg to the left and right of a central target. One of each pair was placed 15 deg above and below centre. A similar configuration of red dots was used in demarcating target sites on each isovergence mask. Prior to obtaining eye position data, each subject was positioned such that the central target of both the mask and target board would be at a height level to the subject's eyes while looking straight ahead.

The subject sat in a magnetic field device with his head stabilized by a chin rest and by a supporting strap around his head. Two tasks were used. In the first, designed to determine whether eye position was confined to a plane, each subject looked randomly at the target surface (nonvergence) followed by a trial looking randomly around the inner surface of the isovergence mask (vergence). In both cases, the subject was asked to fixate randomly on the visual targets over the ± 30 deg range. The second task, designed to determine the axes of rotation during saccades, involved looking up and down alternately between the left target pairs on the far target surface (nonvergence trial) and on the mask (vergence trial). This was repeated for the right target pairs.

Recording of eye movements

Binocular recordings were made using a three-dimensional implementation search coil technique described by Tweed *et al.* (1990). The computer sampling rate was 100 Hz per channel during each random saccade task and 500 Hz per channel during each vertical saccade task. Data was rejected for one subject in each of the tasks because of slippage of the search coils. This slippage was noted by a change in the torsional value of eye position when viewing the distant central target and confirmed by a visual inspection of the location of the exit point of the lead wires relative to ocular landmarks.

Data analysis

Coil signals were reexpressed as unit quaternions, the sum of a scalar and vector, $q = q_0 + \mathbf{q}$. The vector part of this equation $\mathbf{q}$ specifies the direction and magnitude of rotation from the central distant target (Tweed *et al.*, 1990). The quaternions were then used to determine the axis about which the eye spins during a saccade and the magnitude of the instantaneous angular velocity (Crawford & Vilis, 1991).

RESULTS

Angular position of the eye during vergence

As predicted by Listing's law and confirmed recently (Ferman, Collewijn & Van den Berg, 1987a, b; Tweed & Vilis, 1990), eye position was restricted in the torsional direction to a flat pancake. The distribution of eye positions, as viewed from above, is illustrated in Fig. 2(A). During a 100 sec time period, subjects were required to fixate distant targets over a ±30 deg horizontal and vertical range. The data includes eye positions during and between saccades. When viewing near targets, eye positions remained restricted to a planar surface [Fig. 2(A)] but this surface was rotated temporally in each eye. To quantify these changes a plane was fit to the data in Fig. 2(A). The resulting fit demonstrates that the main change going from far to near is a temporal rotation of the planes [Fig. 2(B)]. To determine whether the near surface was any less planar, the width of this surface, as measured by the variability of the data about the fitted plane, was compared to that of the far targets. Figure 3 shows that little change was observed in the standard deviations of the data to a planar surface for each of the subjects. The means for the left and right eyes were 1.3 and 1.1 deg across subjects respectively for far conditions and 1.3 and 1.2 deg across subjects respectively during vergence. The Student's t-test for correlated groups revealed no significant difference between nonvergence and vergence conditions in the left ($t_6 = -0.51$, $P > 0.01$) and right ($t_6 = 1.51$, $P > 0.01$) eyes. Thus, because eye position remains equally constrained to a plane, Listing's law appears to hold during vergence.

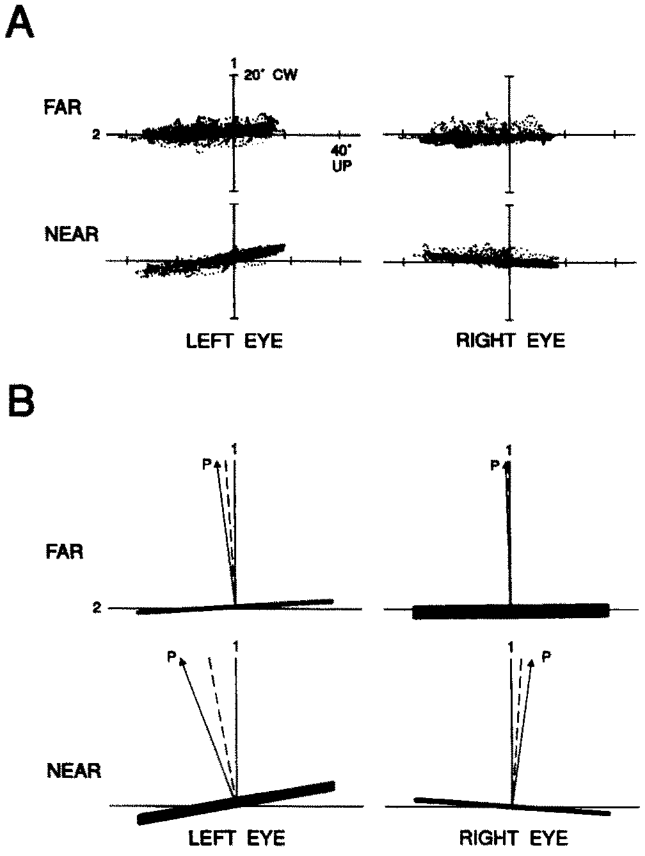

FIGURE 2. Eye position is confined to a plane when gaze is directed at various distant targets (far) and when gaze is directed to the isovergence mask (near) constructed to require a total of 30 deg vergence in the two eyes. (A) Above view of eye position expressed as quaternion vectors. (B) Above view of the planar fits to the data. The thicker surface in the right eye at far and the left eye at near indicates that the fitted plane is rotated slightly about axis 2. The dashed line is perpendicular to the fitted plane. *P* denotes the computed primary position. Axis 1 denotes clockwise rotations of the eye from the point of view of the subject. Subject TV.

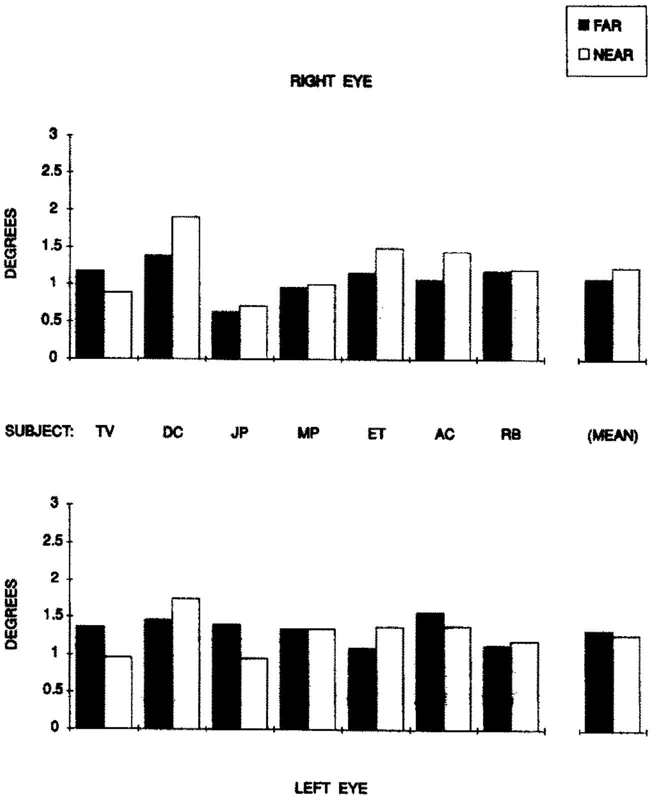

FIGURE 3. Surfaces are equally planar for near and far targets. Bars denote standard deviations of the torsional component of eye position about the fitted planes in both the far and near conditions for each of the subjects.

We next quantified the temporal rotation of the planes during vergence for each subject. A complicating factor, illustrated in Fig. 2(B), was that the fitted planes for the far targets did not have the same orientation in the two eyes. In this case, the left eye showed a small temporal rotation. Presumably, this is because the frontal plane of the head was rotated slightly to the left in our field coordinates. After correcting for this asymmetry, the fitted planes for the two eyes did not align with the frontal plane. Rather, the planes exhibited a rotation ranging from 1 deg temporal to 2 deg nasal in our seven subjects. This suggests that Listing's plane need not align with the frontal plane while viewing distant targets.

In order to avoid these assumptions, we examined the effects of vergence by measuring the change in orientation of the fitted planes. In particular, we determined whether the plane, fitted to the data, shifted in the torsion direction (Δa), rotated about the vertical axis (Δb) or rotated about the horizontal axis (Δc) when viewing near targets as compared to far targets (Fig. 4). The main change in the orientation of this plane, as observed in the raw data, was a rotation about the vertical axis (Δb) (Fig. 4). The plane of the left eye was rotated to the left (positive values) about the vertical axis while that of the right eye was rotated to the right (negative values) consistently in each subject (i.e. they both rotated temporally). Small changes were also observed in Δa and Δc.

The mean temporal rotation of the planes was -4.6 and 4.9 deg for the right and left eye respectively. As outlined in the discussion, these planes are the displacement planes with respect to the central reference position. Listing's plane and primary position rotate by twice the angle of these displacement planes (-9.2 and 9.8 deg for the right and left eye respectively). The theoretical vergence required of each eye for the 30 deg isovergence surfaces used was 15 deg [Fig. 1(B)]. The actual measured vergence was slightly smaller, 14.4 deg. The data thus suggests that during convergence, primary position is rotated temporally by approximately two-thirds the angle of vergence.

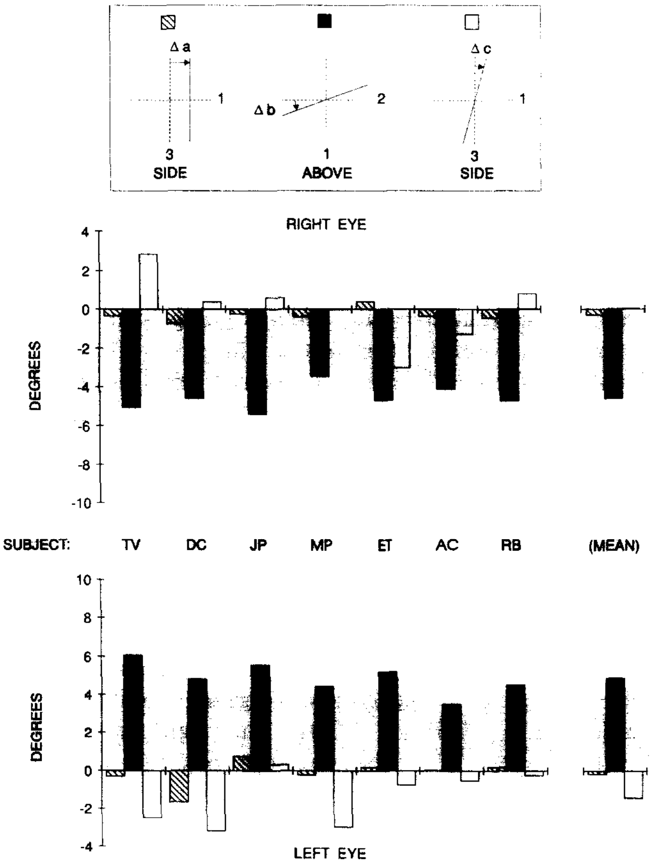

FIGURE 4. Changes in orientation and shifts of the planar fits while viewing distant targets and during 30 deg of convergence. Δa (hatched), forward or backward shifts. Shifts in the clockwise direction are positive. Δb (dark), rotation of the plane about the vertical axis. Positive values denote a leftward rotation. Δc (open), rotation of the plane about a horizontal axis. Positive values denote an upward rotation.

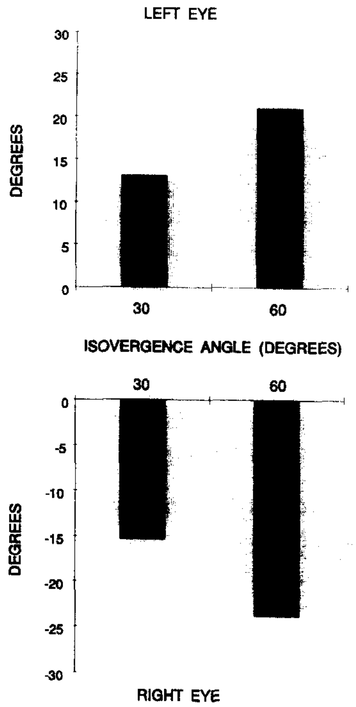

FIGURE 5. Rotation of Listing's plane and primary position about the vertical axis ($2\Delta b$) in one subject (TV) during vergence trials using masks with isovergence angles of 30 and 60 deg.

The temporal rotation of primary position increased if greater vergence was required. This is illustrated for one subject in Fig. 5 for isovergence surfaces that required 15 and 30 deg of vergence in each eye (combined vergences of 30 and 60 deg respectively). Doubling the required vergence almost doubled the observed temporal rotation of primary position. The finding that the change was less than double may be due to the fact that a 60 deg vergence was difficult to maintain over the entire isovergence surface. The subject's fusion was frequently broken and the eyes diverged.

Angular velocity of the eye during vergence

Having determined that the torsional eye position changes during vergence, we next examined whether the same was true for the torsional component of eye velocity during saccades. Each dot in Fig. 6 is the instantaneous angular velocity vector during vertical saccades of 30 deg amplitude as viewed from above. The axis of rotation during saccades is fairly constant, increasing to a peak of approx. 400 deg/sec and then decreasing. In some cases, for example left eye, far left target, the axes varied during acceleration and deceleration and were thus somewhat sigmoidal. For this reason, the axis at peak velocity was measured. When gaze is

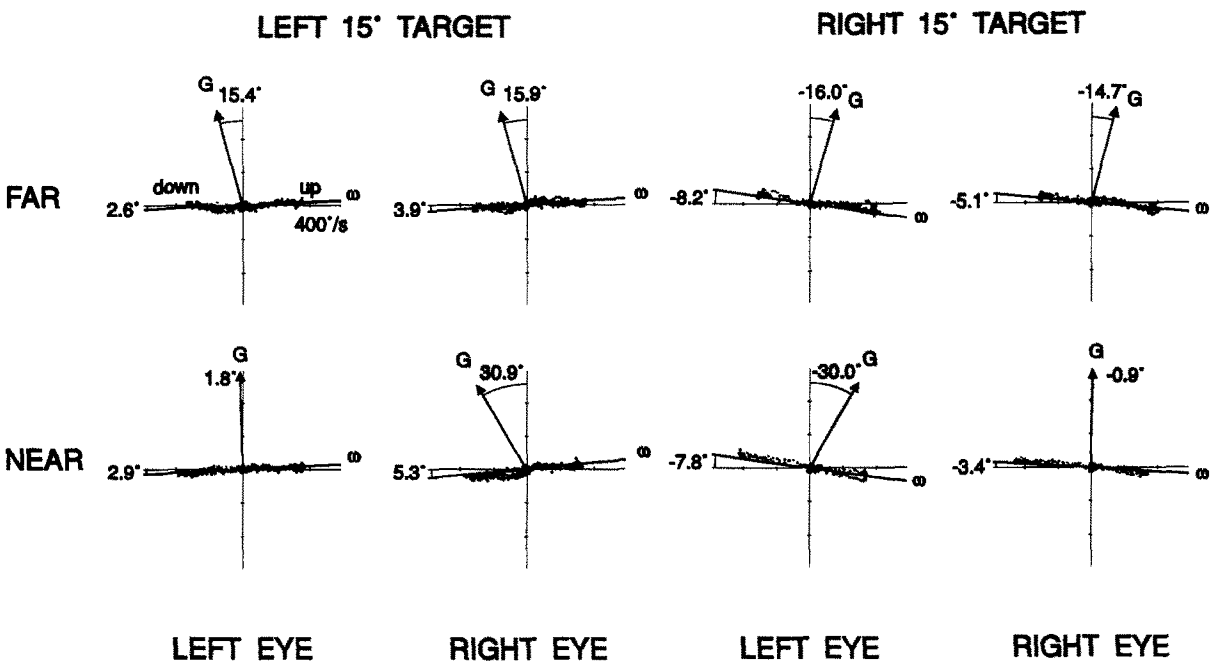

FIGURE 6. Instantaneous axes of rotation during far and near viewing conditions. Each dot denotes the instantaneous angular velocity during 30 deg vertical saccades between targets located 15 deg to the left (left half of figure) and between targets located 15 deg to the right (right half of figure). ω denotes the average axis computed from the mean peak velocity vector of approx. 10 saccades. G denotes the mean gaze direction of each eye. Subject ET.

directed between the far targets located 15 deg to the left, the velocity axes of both eyes are rotated slightly to the left. The opposite occurs for saccades between the far targets 15 deg to the right. This is expected since, as shown in Tweed and Vilis (1990), the velocity vectors rotate out of Listing's plane as the eye's eccentricity from primary position increases.

During vergence, the gaze direction of each eye also changes. For vertical saccades between targets on the left side, that of the left eye becomes less eccentric while that of the right eye becomes more eccentric (Fig. 6). If the rotation of the velocity vector out of Listing's plane is dependent on the actual gaze eccentricity in the same way as for distant targets (Tweed & Vilis, 1990), the rotation of the left eye's velocity vector should decrease while that of the right eye should increase. Consider the right eye. For targets to the left, the actual gaze direction shifts 15 deg further to the left during vergence. Such an increase in gaze eccentricity would for distant targets, rotate the axes of vertical saccades temporally by 7.5 deg [i.e. the half angle rule observed by Tweed and Vilis (1990)]. The change observed was only 5.3 − 3.9 deg = 1.4 deg. In general, the half angle rule predicts that for the right targets the rotation of these axes should increase by about 7.5 deg in the left eye and decrease by 7.5 deg in the right eye. The opposite should occur for saccades between the left targets. To quantify the changes that were actually observed, the peak saccade velocity was determined and averaged across about ten saccades between the same targets. These average axes are indicated by the lines labelled ω in Fig. 6. For saccades between the left targets, the left eye showed a mean increase of 0.3 deg and the right eye a mean increase of 1.4 deg. Changes of 0.4 deg decrease in the left eye and 1.7 deg decrease in the right eye were observed for the right targets (Fig. 6).

The effect of vergence on the velocity axes was examined in all subjects by comparing these average axes in far and near conditions. Figure 7 shows that during vertical saccades between far targets 15 deg to the left, the velocity axes of both eyes were consistently positive, i.e. rotated to the left. With one exception, the same was true during vergence (Fig. 7). In the right eye, the gaze direction increased from about 15 to 30 deg left. The velocity axes for that eye rotated by a mean of 1.8 deg to the left across subjects. In the left eye, the gaze direction decreased from about 15 to 0 deg. The velocity axes for that eye decreased by only 1.0 deg. Vertical saccades between the far targets to the right had negative axes (Fig. 7). During vergence, the mean rotation of the right eye's axes decreased by 2.6 deg while that of the left eye increased by 0.7 deg. In three of the subjects, a large change in rotation was observed in the right eye. An analysis of variance revealed no significant differences between the velocity axes in the far and near conditions for both eyes when viewing the left ($F_{3,24} = 3.80$, $P > 0.01$) or right ($F_{3,24} = 1.62$, $P > 0.01$) targets. Thus, in spite of large changes in the gaze direction during vergence, the axes of rotation remained relatively collinear. In summary, some small rotation of the axes was observed in the direction of the actual gaze shift during vergence. However, this rotation was, in most subjects, smaller than that of the actual gaze shift of 15 deg and also smaller than that predicted by the half angle rule (7.5 deg) (Tweed & Vilis, 1990).

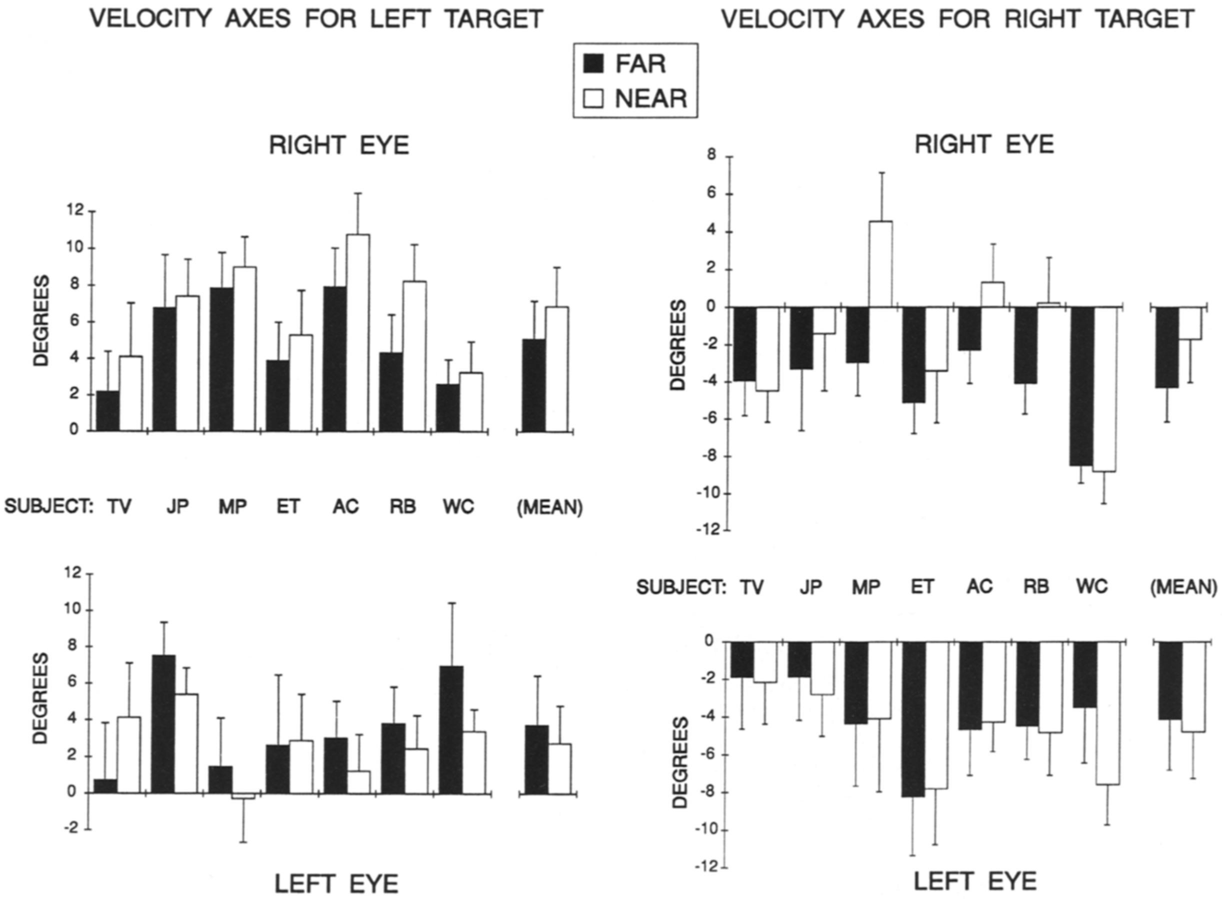

FIGURE 7. Quantitative comparison of the velocity axes for far and near viewing conditions. Bars denote the amount of rotation about the vertical axis. Positive values denote rotations to the left. Each bar is the average axis computed from the mean peak velocity vector of approx. 10 saccades as indicated by ω in Fig. 6.

DISCUSSION

The results of these experiments show that eye position, both between and during saccades, remains constrained to a planar surface when viewing near targets. The variability in torsional eye position about this plane remains the same whether viewing distant or near targets. Thus, contrary to the prevailing view, Listing's law holds during vergence. The orientation of this plane does not remain constant during vergence. Rather, it rotates temporally in each eye, that is, in a direction opposite to the vergence mediated nasal change in gaze. This suggests that a new primary position is neurally defined by the act of vergence.

To understand how the location of primary position is determined, consider the hypothetical Listing's plane of each eye when viewing distant targets [Fig. 8(A)]. By definition, the primary gaze direction is perpendicular to Listing's plane. If vergence has no effect on primary position, the Listing's planes of each eye should remain the same [Fig. 8(B)]. The plane plotted in our data (i.e. Fig. 2) was the displacement plane (DP) not Listing's plane (LP). This plane describes the eye position relative to the position observed when the eye fixated on the far central target (in this example, the far primary position). Suppose that during vergence, this plane rotates temporally by Δb [Fig. 8(C)]. As shown by Tweed and Vilis (1990), this means that Listing's plane rotates temporally by twice this angle, $2\Delta b$. The new primary gaze direction is perpendicular to Listing's plane. Thus, the primary gaze direction rotates temporally by $2\Delta b$.

By examining the changes in orientation of the displacement planes in our subjects (Fig. 4) we were able to determine whether vergence altered the location of primary position. The most prominent change was a temporal rotation. For isovergence surfaces which required 15 deg of convergence in each eye, this mean temporal rotation was 4.7 deg. Thus, Listing's plane and primary position rotated by twice this amount, 9.4 deg, an angle somewhat less than the change in vergence.

Let us now consider the torsional changes in eye position that would be expected during convergence. As illustrated in Fig. 4, the forward shift (Δa) and downward rotation (Δc) of the fitted plane is, on the average, small and variable. Thus, the change in the torsional position of the eye which occurs when verging on a central target, or one to the left or right is also small and variable. The largest change is the temporal rotation of the plane (Δb). The largest changes in torsion are therefore those observed during saccades between vertically displaced targets on the near isovergence surface, the amount of torsion increasing with the vertical eccentricity. When looking up or down, eye position moves left and right along the temporally rotated DP [Fig. 8(C)]. When looking up, the left eye rotates about a horizontal axis with a clockwise component. Thus the left eye intorts relative to its position when looking at the far target [Fig. 8(A)]. The opposite axes are used during downward gaze shifts and the left eye extorts. The extorsion observed during downward gaze is in agreement with that of Nakayama (1983). However, Nakayama also observed extorsion, albeit much smaller, for upward gaze. Two factors may reconcile these differences. The first is the shift of the plane in the torsional direction observed in some subjects (Δa in Fig. 4). When this shift is large and counterclockwise, as in the case of subject DC, it can overcome the intorsion produced by the temporal rotation of LP. Thus, such a subject shows a small extorsion when verging upwards. However, the temporal rotation of Listing's plane produces a systematic increase of ocular extorsion when looking down as observed by Allen and Carter (1967) and Nakayama (1983). The second factor may be a misinterpretation of the primary position. If the zero elevation point was, for some reason, estimated to be below centre, i.e. to the left of centre in Fig. 8(C), the measured values for all positions would become more extorted. The mean measured temporal rotation of the DP was 4.7 deg during 30 deg of convergence. When the eye is elevated by 30 deg this translates into 30 deg × tan 4.7 deg = 2.5 deg of intorsion in each eye and 2.5 deg of extorsion when the eye is depressed by 30 deg. The average change in torsion between 30 deg up and 30 deg down is thus about 5.0 deg. An extrapolation of Nakayama's data to these same conditions produces a comparable torsional change of 4.5 deg.

What are the implications of the observed rotation of Listing's plane on the activity of oculomotor neurons? Assuming that muscle axes are fixed in the head, the rotation of Listing's plane cannot be simply the result of coactivation of the medial recti. This can be best seen by considering the left eye in Fig. 8(C). The displacement plane is rotated to the left by Δb. This means that when the eye looks above primary position, the eye is torted clockwise (i.e. intorted). The right eye is torted counterclockwise and is thus also intorted. The opposite occurs when both eyes look down. Both eyes become extorted. This change in torsion requires a different coactivation of the vertical recti. Such a change has indeed been observed. Mays, Zhang, Thorstad and Gamlin (1991) have observed a decrease in the tonic firing rate of superior oblique motoneurons of the left eye during

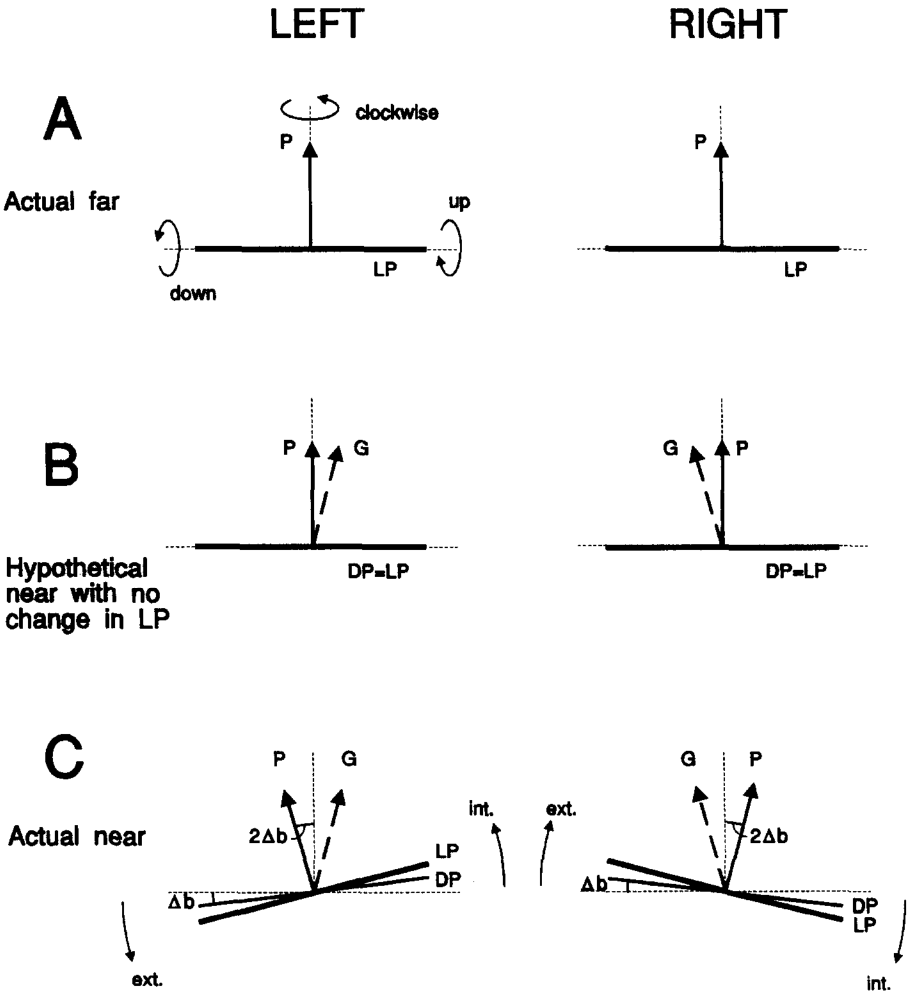

FIGURE 8. Theoretical changes in eye position during vergence. (A) Far viewing conditions. (B) Near viewing condition assuming no change in Listing's plane. (C) Near viewing conditions assuming that Listing's plane rotates temporally by an amount equal to vergence. LP, Listing's plane; DP, displacement plane; P, primary position; G, gaze direction; ext, extorsion; int, intorsion.

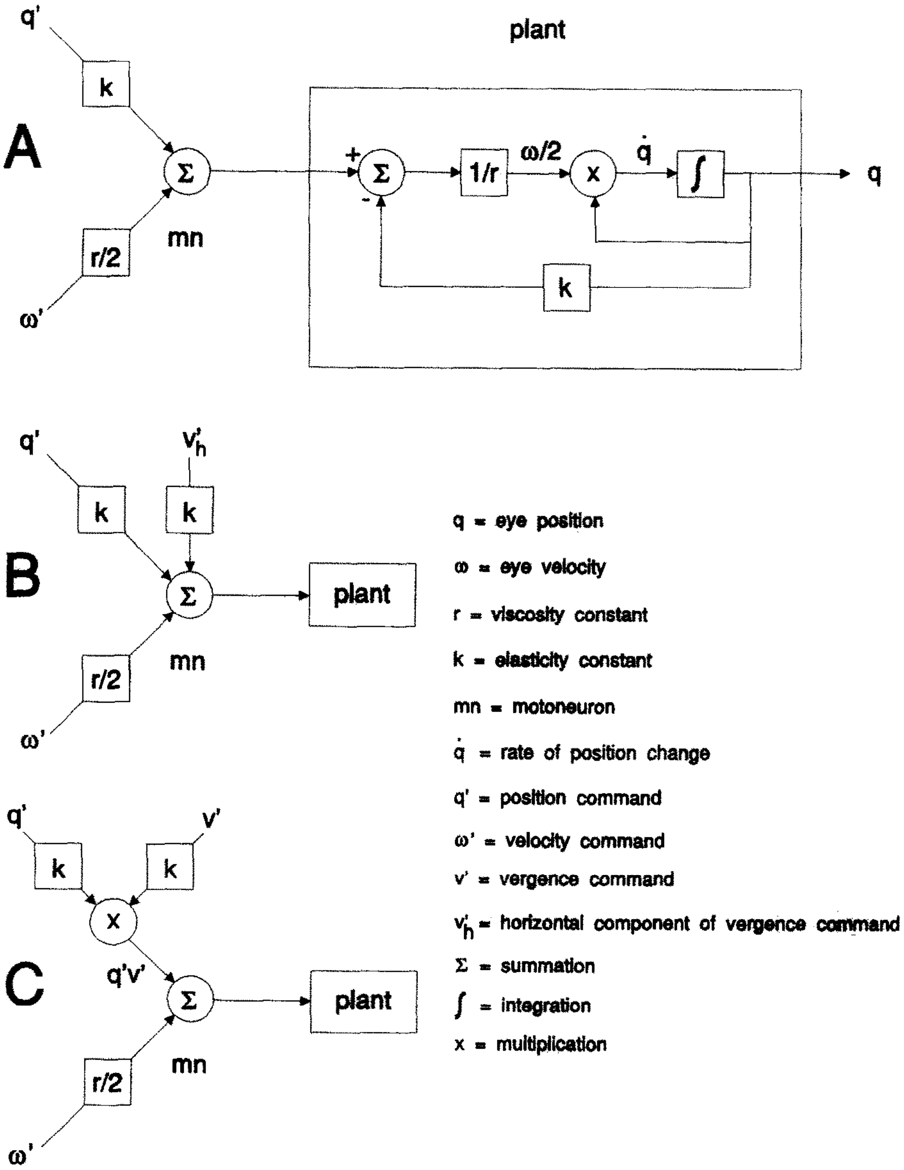

FIGURE 9. A model of the possible neural control of Listing's plane. (A) The saccadic commands to a three-dimensional model of the oculomotor plant. (B) The horizontal component of the vergence command v'_h, a scalar, is added to the saccadic eye position command. (C) The vergence command, v', is multiplied by the saccadic eye position command, q', a quaternion vector, to yield $q'v'$.

vergence. This decrease was most prominent for downward gaze as expected from our observed increase in extorsion.

To examine how Listing's plane can be rotated neurally during vergence, we explored various possible configurations using computer simulations (Figs 9 and 10). Figure 10(A) [generated by the model depicted in Fig. 9(A)] shows the change in position of the right eye for vertical saccades from primary position without vergence. As expected, eye position is confined to Listing's plane. In Fig. 9(B), the sole action of the vergence system is the addition of tone to the motoneurons of the medial recti muscles. The amount of tone selected was that which would produce a convergence of 30 deg in each eye. In this situation, the same purely vertical saccadic command produces saccades which initially drive the eye out of Listing's plane. The initial trajectories of this right eye are rotated temporally as observed in the data. This temporal rotation is purely the result of rotational kinematics; i.e. it is the expected change in position for a rotation about a horizontal axis when the eye is converged. This is then followed by postsacccadic drift back to Listing's plane [Fig. 10(B)]. The tonic signal, generated by the saccade integrator, is ineffective in maintaining eye position in its new rotated position.

To correct for this, the tonic component of the saccadic command must be altered. Figure 9(C) illustrates the effect of multiplying this tonic saccadic command by the tonic vergence command. If v' and q' are considered as rotations, the combined rotation is $q'v'$. In this case, postsaccadic drift is eliminated and the correct rotated position is maintained [Fig. 10(C)]. This suggests that the vergence command serves two functions. The first is to converge the eyes. The second is to rotate the tonic command.

Qualitatively, the changes observed in our data during vergence are reflected in the model. First, convergence produces a temporal rotation of Listing's plane, the

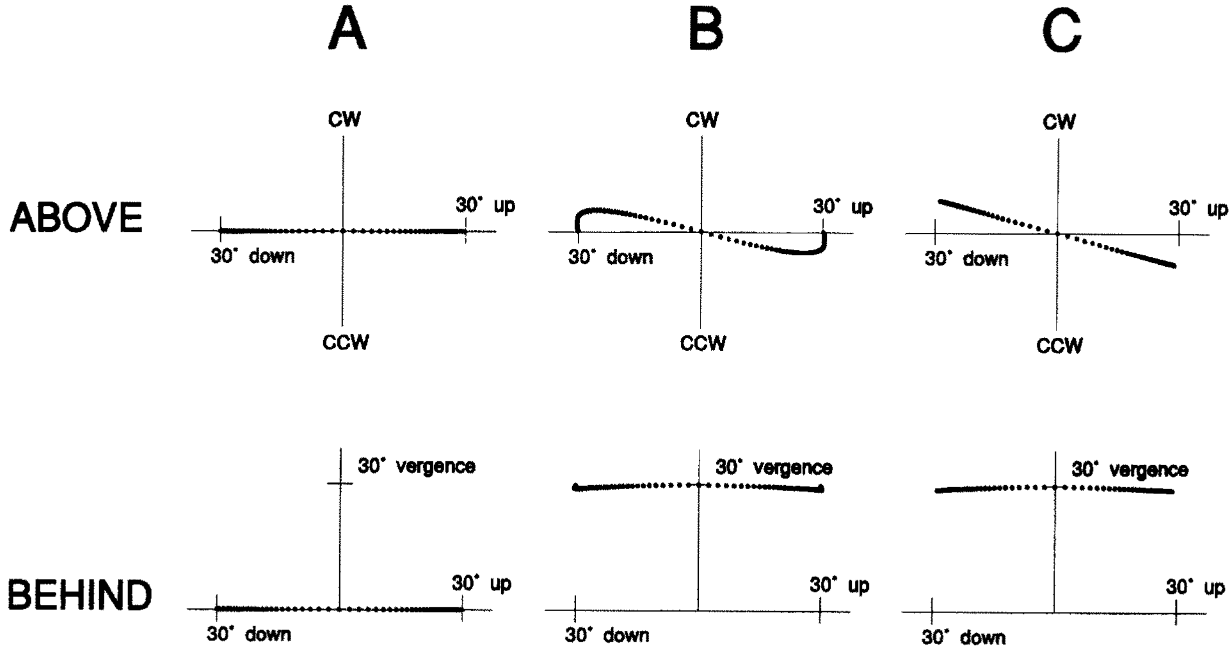

FIGURE 10. Computer simulations of the models depicted in Fig. 9. Each figure shows the position, q, of the right eye for 30 deg upward and downward vertical saccades. The top row shows the view of position from above and the bottom row shows that from behind. (A) Far viewing conditions. (B) A 30 deg vergence command, v'_h, is added to the saccadic eye position command as in Fig. 9(B). (C) The vergence command is multiplied by the saccadic eye position command as in Fig. 9(C). CW, clockwise; CCW, counterclockwise.

amount of rotation being dependent on the degree of convergence. Secondly, the vergence has little effect on the saccadic velocity command. Quantitatively, there are some differences. First, the model produces a temporal rotation of Listing's plane that is equal to the angle of convergence. The mean measured temporal rotation across all subjects was less, 9.8 and −9.2 deg for the left and right eye respectively for 15 deg of convergence. Why this was so is not clear. Second, the actual gaze direction during vergence had some effect on the saccadic velocity command (Fig. 6). On average, the effect is small, 6% of the actual, vergence induced, change in gaze direction. This is in contrast to the effect of gaze eccentricity on saccades between distant targets. Here, the velocity axes rotate by 50% of the change in gaze eccentricity (Tweed & Vilis, 1990).

The functional consequence of the shift in Listing's plane is not clear. Nakayama (1983) has suggested that extorsion would increase the horizontal tilt of the vertical horopter. This could be useful in fusing a line in the sagittal plane that is directed towards one's feet. Another possible benefit is to assist the action of the vestibulo-ocular reflex (VOR). Assume that the head rotates up and down about a horizontal axis. To keep the eye stable in space, the VOR must rotate the eye about the same axes but in the opposite direction. This same axis should also be used in the verged state. Rotating the tonic component q' but not the velocity command ω' would achieve this.

In summary, this study shows that Listing's law holds during vergence. Eye position is still confined to a plane but this plane rotates temporally as the eyes converge nasally. The effect of this rotation is to produce extorsion of the two eyes for downward gaze. At the same time, collinearity in the axes of rotation of each eye in far and near viewing conditions is maintained for saccades. The functional significance of the latter may be to maintain congruency with the action of the VOR while that of the former may be perceptual.

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