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# Listing's plane rotation with convergence: role of disparity, accommodation, and depth perception

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**Abstract** Earlier studies have reported temporal rotation of Listing's plane with convergence of the eyes causing torsion, which is dependent on eye elevation. The amount by which the planes rotate differs from study to study. To gain insight into the functional significance of the temporal tilt of Listing's plane for vision, we examined whether the rotation of the plane depends on the visual conditions, namely on the stimuli driving vergence. In different conditions, accommodative vergence, disparity-vergence, combinations of disparity with accommodation or depth perception were used and the resulting rotation of Listing's plane was measured. Our findings show, for the first time, that the relationship between convergence and Listing's-plane temporal rotation depends on the stimuli driving vergence. When the stimulus contains only disparity cues, vergence and Listing's plane rotate immediately and consistently among subjects. Accommodative vergence, the mutual couplings between vergence and accommodation, can influence the orientation of Listing's plane, but they do so in a idiosyncratic way. The largest rotation was elicited by stereograms combining disparity-vergence with depth perception. These findings support the idea of a functional role of Listing's plane rotation for binocular vision, perhaps for depth perception.

**Key words** Listing's plane · Vergence · Binocular · Eye movements · Human

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## Introduction

According to Listing's law, all eye positions during fixation can be reached from a reference position by rotations about axes that lie in a plane, provided the head is stationary (Helmholtz 1866; Ruete 1853). Listing's law holds fairly well during voluntary saccades (e.g., Straumann et al. 1995), although this obedience is not perfect (Straumann et al. 1996). It is also known that, when the eyes converge upon proximal targets, Listing's law still holds, but Listing's plane rotates temporally. This causes elevation-dependent torsion: the eyes intort for up proximal gaze and extort for down proximal gaze (Mikhael et al. 1995; Minken and Van Gisbergen 1994; Mok et al. 1992; Van Rijn and Van den Berg 1993). All previous studies have reported a temporal rotation of Listing's plane with convergence of the eyes. In the following, we will label the tilt of Listing's plane as a function of vergence as Listing's Plane Vergence Tilt (LPVT). The amount of LPVT, however, is different in each study: the slope of the line relating the tilt angle of Listing's plane to vergence was 0.72° per degree of vergence for the studies of Mikhael et al. (1995) and Mok et al. (1992), about 1.0° for the study of Minken and Van Gisbergen (1994), and 1.6° for the study of Van Rijn and Van den Berg (1993). A direct comparison of the values between the four studies is difficult because of different methodological approaches and theoretical assumptions, and the discrepancy between the values of different studies is not understood. Minken and Van Gisbergen (1994) considered differences in visual conditions, but this was not supported by their control experiments, in which the luminosity of the target was decreased. The amount by which the planes tilt is important for the interpretation of this phenomenon. More recently, Tweed (1997) and Bruno and Van den Berg (1997) re-examined the differences between these studies. In his comprehensive study, Tweed (1997) gives several possible interpretations. A first hypothesis would be that LPVT is a strategy for motor efficiency, allowing the eyes to be kept in an eccentric position with minimal effort. A second hypothesis associates tilt with a functional role for binocular vision, e.g., in obtaining binocular single vision of lines orthogonal to Listing's plane or, more likely, to reduce the cyclodisparities of the visual planes themselves. A third hypothesis states that it might be both a strategy for motor efficiency as well as a strategy subserving binocular visual function. The experimental data obtained so far do not allow us to decide between these different hypotheses.

To gain insight on the functional significance for vision, we examined whether the LPVT depends on the visual conditions, namely on the stimuli driving convergence of the eyes. The main stimuli driving vergence are binocular disparity and blur-induced accommodation. Blur (disfocused images) induces accommodation, convergence, and pupil constriction (the well-known near triad; for a review, see Hung 1997; Semmlow and Hung 1983). The amount of accommodative convergence is described by the ratio accommodative convergence/accommodation (AC/A), which is about 3–4 in normal humans (see Von Noorden 1990). Mutually, convergence can influence accommodation; this coupling is known as the convergence accommodation/convergence ratio (CA/C). These reciprocal couplings are well integrated in current thinking and modeling of the vergence system (see Semmlow and Hung 1979; and reviews by Mays and Gamlin 1995; Schor and Kotulak 1986). In various conditions, accommodation and disparity were manipulated alone or together, and the orientation of Listing's plane was measured. We also studied the role of depth perception by using a stereogram instead of a flat image. If LPVT is the result of a motor strategy, the slope of the rotation (tilt of Listing's plane/change of convergence) should be the same, regardless of the stimulus driving convergence. We report here, however, that this is not the case. Disparity-vergence alone changes the orientation of Listing's plane powerfully and instantaneously; accommodative vergence, the interaction between vergence and accommodation, influences the orientation of Listing's plane, but it does so in a idiosyncratic way. When disparity-convergence is combined with depth perception (e.g., when using stereograms), the gain of the LPVT is almost doubled compared with the disparity-alone condition.

## Materials and methods

### Subjects

Eleven subjects (nine male and two female) were studied. Their ages ranged from 21 to 49 years (mean age: 28.1±9.7). Each subject underwent a complete neuro-ophthalmologic examination. Subject PB had a small hyperopia of +0.5 D in the left eye, which remained uncorrected during the experiment. Binocular vision of subjects was normal (the TNO random-dot stereoacuity test was 60 s arc or better). Subjects participated in the experiment after giving informed consent.

### Testing conditions

Subjects sat 1 m in front of a flat, translucent screen. The head was stabilized by a bite bar with an individually fitted dental impression of each subject's upper teeth. Two projectors were used to project an image to each eye. To separate the images for each eye, the polarization of the two beams differed by 90° and the subjects had an appropriate polarizer in front of each eye. The room was completely dark, the subject could see only the projected images. Two X-Y mirror-galvanometers (General Scanning CCX660) were used to position the images on the screen (see Kapoula et al. 1996).

In the "far 1 m, control" condition, identical grids (33×33°) were presented to each eye. Subjects fused them and saw a single grid (Fig. 1A). They were instructed to make vertical saccades (16°up, 16°down) to different grid nodes along the midline and along tertiary positions. The expected horizontal vergence angle was 3.4°, and the paradigm lasted about 2 min. In the four other conditions, closeness of the target was simulated artificially by manipulating one or more distance cues.

In the "close, accommodation-alone" condition, the screen was 1 m distant, and subjects viewed the same grids. To bring accommodation to 33 cm, a –3 diopter spherical lens was inserted in front of each eye. This caused blur of the grid and stimulated accommodative convergence. The normal AC/C ratio (Accommodative Convergence in prism Diopters / Accommodation in diopters) is 3–4 (see Von Noorden 1990). Therefore, for the –3 diopters lens we used, the expected accommodative convergence would be 10–12 prism diopters, which approximately corresponds to 5–6° (1 prism diopter = 0.57°).

In the "close, disparity-alone" condition, the screen was at 1 m, but the grids were cross-offset on the screen (Fig. 1B). The right-eye grid was shifted to the left and the left-eye grid was shifted to the right. This caused crossed disparity similar to that of a prism and called for convergence of the eyes. In most of the experiments, the grids were offset by an amount corresponding to a convergence angle of 13°, which corresponds to a simulated close distance of 26 cm. The exact amount by which the grids were crossed varied for different subjects; it was adjusted according to the ability of individual subjects to fuse the crossed grids rapidly and to keep the convergence angle stable. This was determined for each subject by preliminary testing just before the eye-movement recording session. The amount of vergence varied from 8.5° to 13°, corresponding to 40 or 26 cm simulated viewing distance.

In the disparity-alone condition, there was a conflict between vergence and accommodation, since accommodation could remain at approximately the distance of the screen (1 m), whereas the vergence corresponded to a more proximal target distance, e.g., 26 cm. In an effort to reduce this conflict, another condition was tested, the "close, disparity+accommodation" condition. The grids were also cross-offset on the screen (in most cases by 13°), and, in addition, a –3 diopters spherical lens was inserted in front of each eye to bring accommodation to the vergence angle.

In the "close, disparity+stereo" condition, the image viewed was a stereogram of black and white random-dot patterns (Fig. 1C). Each pattern consisted of 128×128 dots. The sizes of the dots were 0.1° at the center of the pattern and 0.3° at the upper and lower edges. The two random-dot patterns were superimposed on the screen. The patterns seen by the right and left eye were monocular projections of a virtual three-dimensional object onto the plane of the translucent screen. The object was a wedge-shaped tunnel, with the center being perceived at a distance of 1 m and the upper and lower edges at a distance of only 40 or 30 cm, depending on the subject. The disparity of the random-dot patterns simulated a disparity field that would have been present under natural viewing of the three-dimensional object. Subjects obtained a vivid depth perception. In this condition, subjects were instructed to saccade along the midline or to tertiary positions approximately 16° up and 16° down, avoiding fixation at the middle, eye-level positions, which were perceived at a different depth (that of the physical screen).

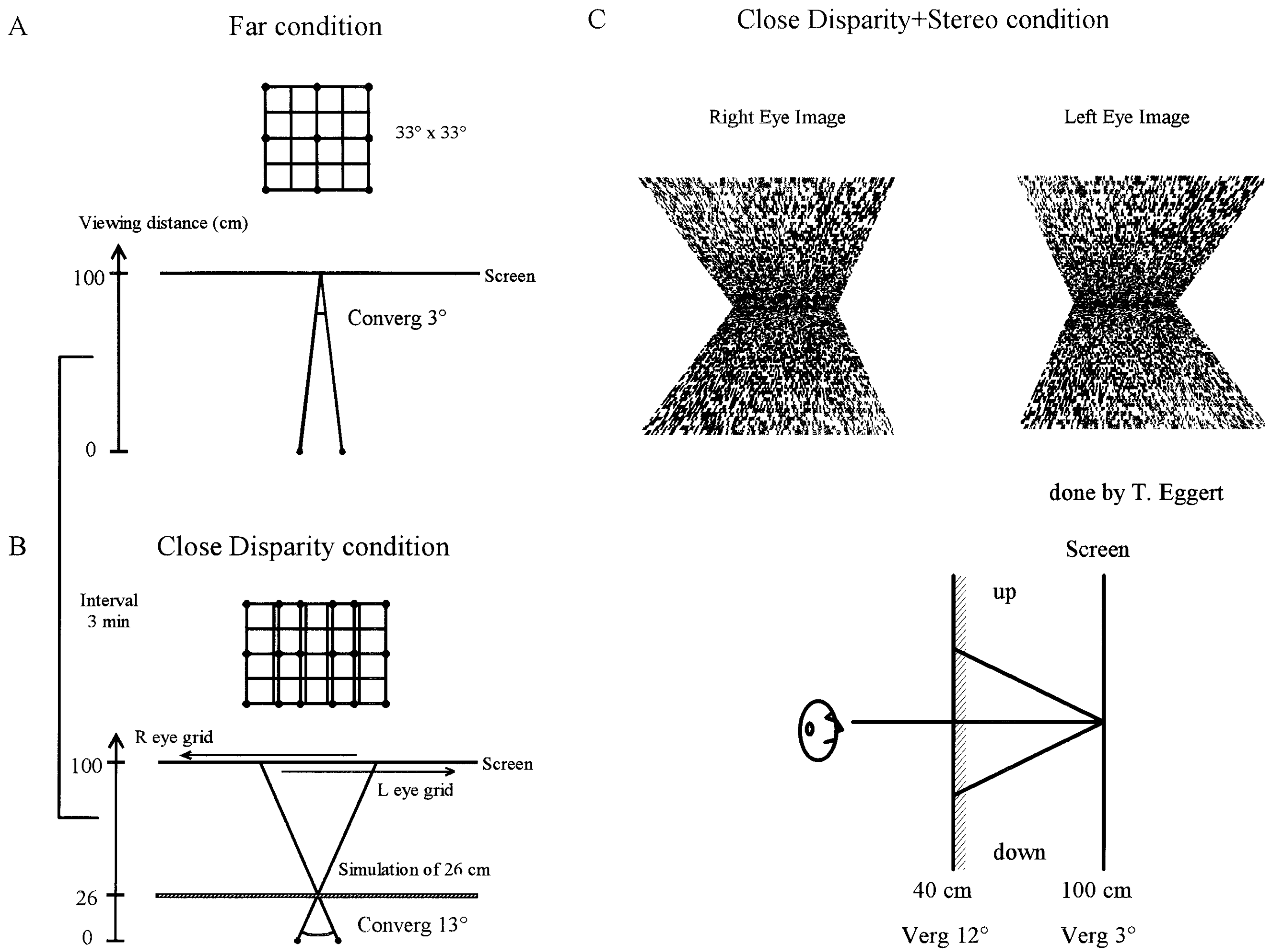


**Fig. 1A–C** The subjects' view was dichoptic due to polarizers (see text). **A** Two identical grids were superimposed on the screen. Subjects fused them and perceived a single grid. Viewing distance was 1 m, and the expected vergence angle was 3°. **B** In the following 3 min, the grids were cross-offset on the screen; this caused crossed-disparity similar to that induced by prisms. The eyes converged by about 13°. **C** Random dot patterns, creating a vivid 3D perception of a wedge whose upper and lower parts are more proximal to the observer (40 cm, corresponding to 12° of vergence) than the middle part (1 m, i.e., 3° of vergence)

In the "quasi-infinity" condition, the distance between the subject and the screen was 2 m. The polarizers were removed, and the subjects looked around at a nonpolarized random-dot pattern. This condition was run on two subjects only and aimed at providing an estimation of Listing's plane for natural binocular viewing at a distance, quasi-infinity. Vergence demand in this case was only about 1°.

Table 1 shows the expected vergence angle in each condition and the actually measured vergence angle for each individual subject. Not all subjects participated in all conditions. Furthermore, results from some conditions were discarded from one or both eyes because of slippage of the coil, as described below.

We took care to keep the order of the conditions different for different subjects, as indicated in Table 1. The disparity+stereo condition was run at the end of the session for six subjects (FK, PD, PB, SI, MI, SE) and at about the beginning of the session for subjects ER, FR, MB, and GD. The rationale for changing the order was to avoid eventual learning or fatigue effects. Because of the natural coupling and interactions between convergence and accommodation, the order was also particularly important for the conditions dissociating or combining disparity and accommodation. For instance, disparity-driven convergence could change accommodation; in such a case, subsequent addition of a negative lens could have no increasing effect on accommodation. To control for this, five subjects (FK, PD, ER, PB, FR) first performed the disparity-alone condition and then the combined disparity+accommodation condition. In contrast, MB, GD, SI, and MI first performed the accommodation-alone condition and then the combined accommodation+disparity condition.

The experimental session lasted about 30–35 min. Different conditions succeeded each other at the rate of 2–3 min and each condition lasted about 2 min. Thus, we studied instantaneous changes of the orientation of Listing's planes in conditions simulating artificially close viewing. During each condition, subjects made saccades at their natural rate; in some experiments, a metronome was used to slow-down the pace of saccading.

## Eye movement recording

Stimulus presentation and data collection were directed by a software developed under MS-DOS for real-time experiments (REX) and run on an Pentium PC. Three-dimensional eye movements were recorded from both eyes with the dual search-coil method (Skalar two magnetic fields; Collewijn et al. 1975; Robinson 1963). The eye-position signals were low-pass filtered with a cut-off frequency of 200 Hz and digitized with a 12-bit analog-to-digital converter. Each channel was sampled at 500 Hz. The data were stored on the disk for off-line analysis.

**Table 1** Measured vergence angle over expected vergence angle (indegrees) for each testing condition. In the far (*F*), control condition, viewing distance is 1 m and the expected vergence is 3.4°. In the close disparity (*D*) condition, simulated viewing distance is 26, 32, or 40 cm, corresponding to 13°, 10.5°, and 8.6°, respectively, of vergence. In the close accommodation (*A*, *accom*) condition, simulated viewing distance is 33 cm and the expected vergence is 5.5°. In the close disparity+accommodation condition (*DA*, *disp+accom*), the simulated viewing distance is the same as in the D condition. In the disparity+stereo condition (*DST*, *disp+stereo*), the simulated viewing distance is 30 or 40 cm for the up and down gaze, corresponding to 11.4° and 8.6° of vergence. Group mean gain is the average of individual gains (measured/expected vergence angle), together with standard deviation. *L*, *R* indicate the left or right eye from which data are reported; results from the other eye were discarded because of slippage of the coil. *Letters under the initials* of each subject indicate the order with which the different conditions were run

| Subjects | Age | Far | Close disparity | Close accom | Close disp+accom | Close disp+stereo |
|---|---|---|---|---|---|---|
| FK (1)<br>*F, D, DA, DST* | 20 | 3.3 / 3.4 | 13.3 / 13.0 | – | 13.2 / 13.0 | 11.8 / 11.4 |
| PD (2)<br>*F, D, DA, DST* | 38 | 2.4 / 3.4 | 11.8 / 13.0 | – | 12.3 / 13.0 | 11.4 / 11.4 |
| ER (3)<br>*DST, F, D, DA* | 21 | 5.8 / 3.4 | 13.9 / 13.0 | – | 13.4 / 13.0 | 9.4 / 8.6 |
| PB (4)<br>*F, D, DA, DST* | 32 | 3.7 / 3.4 | 8.5 / 8.6 | – | 8.6 / 8.6 | – |
| FR (5)<br>*F, DST, D, DA* | 22 | 2.4 / 3.4 | 12.8 / 13.0 | – | 12.8 / 13.0 | 4.8 / 4.3 R |
| MB (6)<br>*DST, F, A, DA* | 49 | 4.2 / 3.4 | – | 5.4 / 5.5 | 15.5 / 12.4 | 6.0 / 8.6 |
| GD (7)<br>*DST, F, A, DA* | 38 | 3.0 / 3.4 | – | 4.9 / 5.5 | 10.7 / 10.5 | 7.4 / 8.6 |
| SI (8)<br>*F, A, DA, D, DST* | 22 | 4.6 / 3.4 | 11.4 / 10.5 | 5.1 / 5.5 | 10.5 / 10.5 | 7.5 / 8.6 |
| MI (9)<br>*F, A, DA, D, DST* | 22 | 4.0 / 3.4 | 11.6 / 10.5 | 3.2 / 5.5 | 10.1 / 10.5 | 4.7 / 4.3 L |
| SE (10)<br>*F, A, DA, D, DST* | 22 | 1.3 / 3.4 | – | 5.8 / 5.5 | 4.0 / 5.3 R | 5.9 / 4.3 L |
| MA (11)<br>*D, F, DA* | 23 | 3.0 / 3.4 | 8.6 / 8.6 | – | 4.2 / 4.3 R | – |
| Mean gain | | 1.01±0.36 | 1.02±0.06 | 0.89±0.18 | 1.00±0.11 | 1.02±0.19 |

To determine the sensitivity of the search coils, an in-vitro (with a Fick gimbal) calibration was performed before each experiment. At the beginning of each experiment, we performed an in-vivo calibration, during which the subject monocularly fixated a pair of nonius-lines that stepped vertically in the mid-sagittal plane of the measured eye. The nonius-lines were aligned to the viewing eye, i.e. 3 cm from the center of the screen; the distance between the two parallel nonius-lines was 2 min of arc. The subjects were instructed to fixate as accurately as possible between these two lines. The same calibration procedure was repeated at the end of each experiment. Furthermore, at the beginning of some conditions, the reference position was re-determined by asking the subjects to fixate monocularly a marker that was aligned to the viewing eye. For the data calibration, we used the algorithm developed by Hess et al. (1992).

## Data analysis

Eye-position data were expressed as rotation vectors (Haustein 1989). For the data representation, we used the commonly employed Cartesian head-fixed coordinate system with the positive x-, y-, z-axis pointing forward, leftward, and upward, respectively. The x-component of the rotation vector indicates a torsional, the y-component a vertical, and the z-component a horizontal eye position, and positive eye movements are leftward, downward, and clockwise (CW). Since we mainly wanted to investigate the LPVT, the rotation vectors were displayed in top view (i.e., elevation versus torsion, see Fig. 2). We calculated the best-fit plane to the data, called "displacement plane", and its orientation by determining the coefficients offset, y and z, which minimize the mean square-root deviation of the rotation vectors from the plane described by:

$$r_x = \text{offset} + y * r_y + z * r_z$$

where ($r_x$, $r_y$, $r_z$) are the rotation vectors describing the eye positions. The normalized vector perpendicular to the plane is then given by:

$$n = (1, -y, -z)/\text{sqrt}(1 + y^2 + z^2)$$

The vector perpendicular to Listing's plane is tilted twice as far away from the straight-ahead direction (1, 0, 0). The *thickness* of Listing's plane is given by the standard deviation of the distance of the rotation vectors from this plane. Due to the geometry of three-dimensional rotations, the tilt of the primary position – and thus of Listing's plane – is twice the tilt of the displacement plane (Haslwanter 1995). From these plots and from the "thickness" of the Listing's planes (given by the standard deviation of eye positions from the best fit plane), the validity of Listing's law was judged. Slippage of the coil, particularly torsional slippage, was detected when a sudden change of the steady-state position of the torsional component occurred. Such results were discarded. The horizontal component of each rotation vector was expressed in degrees by:

$$\alpha = 2 * \arctan * (r_z) * 180/\pi \quad (1)$$

Subsequently, the vergence angle was calculated by subtracting the horizontal position of the right eye from the horizontal position of the left eye every 2 ms and averaging these differences for each condition. For each condition, the same data points were used to determine the vergence angle and the displacement planes. The reference position was usually taken from the initial calibration when the eyes looked at infinity. However, in some cases, close inspection of the data revealed some coil slippage. In these cases, a new reference position had to be chosen. We did so by selecting a point where the subject was looking straight ahead (in the respective close disparity-vergence condition) and compensated for the expected amount of vergence. As the gain of disparity-induced vergence is close to 1 [e.g., Mikhael et al. (1995) reported a gain of 0.86], this should yield a reference position that is very close to the original one: the largest vergence required in our experiments was 13° (see Table 1), and a possible overestimation of the vergence would be less than 2°. Therefore, any error in the orientation of Listing's Plane, which may have been induced by this re-determination of the reference position, should be less than 1°.

The horizontal and vertical orientation of Listing's plane was determined by calculating the angle between the vector perpendicular to Listing's plane and the midsagittal plane and the horizontal plane, respectively. Since we wanted to investigate the effects of vergence on Listing's plane, we concentrate below on the horizontal orientation of Listing's plane.

To determine the LPVT, we subtracted the value of the orientation of the plane for each close-viewing condition from the one in the far-control condition (1 m viewing distance). This was done for each eye individually (see Fig. 3). The gain of the tilt of Listing's plane was determined by:

$$\text{gain} = (\text{LPVT of the left eye} - \text{LPVT of the right eye}) / \text{change in vergence angle} \quad (2)$$

The change in vergence angle was the difference in vergence for each close viewing condition from the far-control condition. In cases where data from one eye had to be discarded, gain estimation was obtained by dividing the change in the orientation of Listing's plane by the change in vergence angle of this eye alone.

## Results

### Thickness of Listing's plane

In the quasi-infinity condition, the thickness of the Listing's planes was 0.7°and 0.9°for subject SI (left and right eye) and 0.9°for the right eye of subject MI. These observations confirm that Listing's law is applicable for distance viewing as well as that our measurement-analysis algorithms were correct.

Table 2 shows the thickness of Listing's plane for all individual eyes for the control far-viewing condition (1 m) and for the artificial conditions simulating close viewing. Group means were close to 1° for the far-control condition and for the close disparity-alone condition. These values are comparable to those reported in the literature, e.g., Mok et al. (1992). In contrast, in the accommodation, disparity+accommodation, and disparity+stereo conditions, the thickness was larger. Thus, the thickness of Listing's plane in our experiments varied with the testing condition.

**Table 2** Thickness of Listing's plane (in degrees). Each value is the standard deviation in degrees of the data points around the best fitted plane. Abbreviations as in Table 1

| Subject | | Far | Close disparity | Close accom | Close disp+accom | Close disp+stereo |
|---|---|---|---|---|---|---|
| FK | LE | 0.73 | 0.94 | – | 0.69 | 0.94 |
| | RE | 1.07 | 1.58 | | 1.29 | 1.42 |
| PD | LE | 0.95 | 1.51 | – | 1.48 | 1.22 |
| | RE | 1.85 | 1.67 | | 1.30 | 1.90 |
| ER | LE | 0.60 | 0.91 | – | 0.51 | 0.93 |
| | RE | 0.84 | 0.50 | | 0.72 | 0.75 |
| PB | LE | 0.60 | 0.86 | – | 0.47 | – |
| | RE | 0.41 | 0.75 | | 0.67 | |
| FR | LE | 0.94 | 0.55 | – | 1.01 | – |
| | RE | 0.39 | 0.31 | | 0.48 | 0.36 |
| MB | LE | 1.77 | – | 1.45 | 1.36 | 1.72 |
| | RE | 0.63 | | 0.66 | 0.60 | 0.82 |
| GD | LE | 1.11 | – | 1.48 | 1.59 | 1.96 |
| | RE | 1.54 | | 1.69 | 1.35 | 1.12 |
| SI | LE | 1.23 | 1.37 | 1.17 | 1.33 | 1.68 |
| | RE | 0.92 | 0.90 | 0.85 | 0.98 | 1.08 |
| MI | LE | 0.76 | 1.15 | 0.99 | 1.15 | 0.82 |
| | RE | 1.15 | 1.46 | 1.20 | 1.21 | – |
| SE | LE | 1.39 | – | 1.68 | – | 1.75 |
| | RE | 0.91 | | 1.34 | 1.98 | – |
| MA | LE | 0.47 | 0.39 | – | – | – |
| | RE | 0.63 | 0.61 | | 0.61 | |
| Means | LE | 0.96±0.39 | 0.96±0.38 | 1.35±0.27 | 1.07±0.42 | 1.38±0.45 |
| | RE | 0.94±0.45 | 0.97±0.53 | 1.15±0.41 | 1.02±0.45 | 1.06±0.50 |

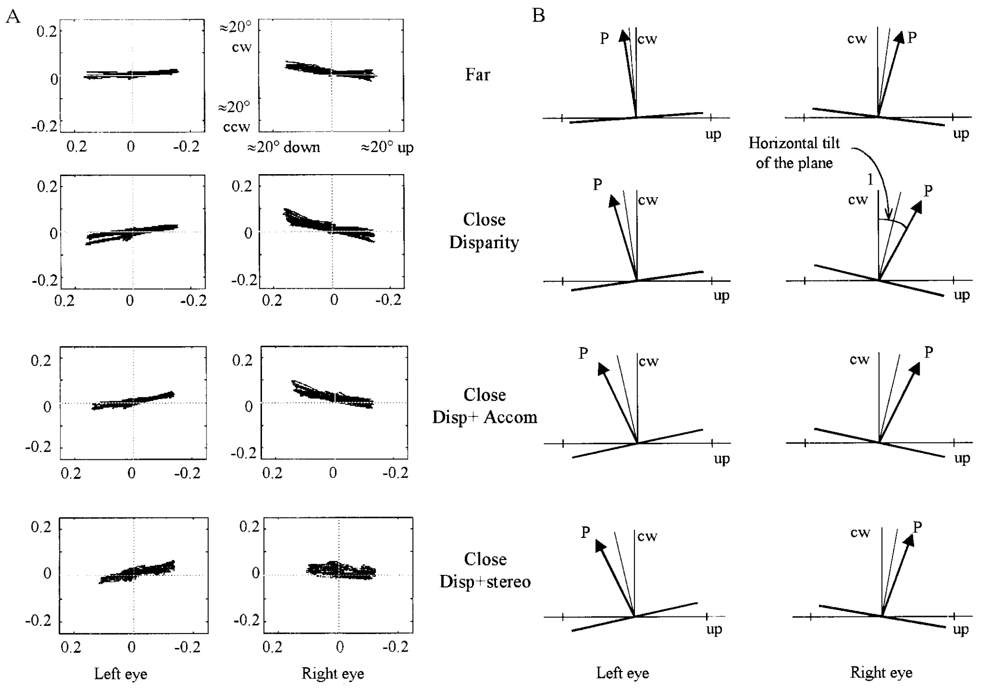


**Fig. 2** **A** View from above (torsional versus elevation) of left- and right-eye position in rotation vectors for subject FK and for each viewing condition in the order they were performed. **B** Shows the estimated best fit to the data. The *thin line* is perpendicular to the best fit and the *thick arrow*, *P*, is the calculated primary position, which is perpendicular to Listing's plane. The horizontal tilt of the plane is the angle between the vector perpendicular to Listing's plane and the midsagittal plane (axis 1)

## Vergence gain

The measured versus expected vergence angle (in degrees) is shown in Table 1. On average, the vergence gain was close to 1 in all but one condition. In the accommodation condition, the group gain was lower (0.89); this was due, however, to a single subject (MI), whose gain was very low (0.58). The variation of vergence, partially due to looking at different points on a flat screen, was below 2° for all subjects and for all conditions except the disparity+stereo condition. The group-mean variation of vergence was 0.85±0.31° ($n$=11) in the far condition, 0.91±0.51° ($n$=8) in the disparity-alone condition, 0.56±0.36° ($n$=5) in the accommodation condition, 0.91±0.48° ($n$=9) in the disparity+accommodation condition, and 1.83±0.97° ($n$=6) in the disparity+stereo condition. The thickness of Listing's plane was not correlated with the variation of vergence.

## Listing's plane orientation with vergence. Qualitative results

Figure 2 shows data from subject FK for four conditions, in the order they were run. In Fig. 2A, top views of the displacement plane are shown, i.e., torsion versus elevation for the left and for right eye. Figure 2B shows the corresponding planar fit for these data. The thin line is perpendicular to the best-fit data plane; the thick line, *P*, is the calculated primary position, which is perpendicular to Listing's plane; the horizontal tilt of the plane is indicated by the angle between *P* and the midsagittal plane, axis 1 (in Fig. 2B). For the control far-viewing condition, the vergence angle was 3.3°. The planes were already temporally tilted by 8°in the left eye and 15° in the right eye. In the following 2 min during the close-disparity condition, the vergence angle was 13.3° and was symmetrically distributed in the two eyes (6.7° and 6.6° for the left and right eye, respectively). Listing's planes rotated temporally in both eyes; the left-eye plane was tilted 16.3° to the left, the right eye plane 28° to the right. Thus, disparity vergence alone caused temporal rotation of Listing's plane immediately and without prior adaptation to the disparity. The tilt was asymmetric in the two eyes, even though vergence was symmetric.

In the subsequent condition, disparity+accommodation, the angle of convergence remained almost the same (6.2° and 7.0° for the left and right eye, respectively). Insertion of a –3 D spherical lens in front of each eye in this condition aimed at bringing accommodation from 1 m (distance of the screen) to 33 cm, which is close to the vergence angle and to the simulated viewing distance of 26 cm. The Listing's plane rotated more temporally in the left eye (from 16° to 25°), even though convergence of that eye was slightly reduced (from 6.7° to 6.2°). In contrast, the plane of the right eye shifted slightly nasally (became less temporal, from 28° to 26°), even though vergence of this eye increased (from 6.6° to 7.0°). Thus, the addition of an accommodative cue influenced the orientation of Listing's plane differently for the two eyes and regardless of the effect on the vergence itself.

The last two panels of Fig. 2B show the data from the disparity+stereo condition. It should be noted that the change from the disparity+accommodation condition to the disparity+stereo condition involved removal of the grid images from the projectors and replacement by the random-dot patterns of the stereogram. During this brief 1 min preparation interval, the subject fixated a blank

**Table 3** Horizontal orientation of Listing's plane in degrees (the angle between the line perpendicular to Listing's plane and the midsagittal plane). Positive values indicate temporal orientation for the left eye and nasal for the right eye; negative values indicate temporal orientation for the right eye and nasal for the left eye. Abbreviations as in Table 1

| Subject | | Far | Close disparity | Close accom | Close disp+accom | Close disp+stereo |
|---|---|---|---|---|---|---|
| | | L/R | L/R | L/R | L/R | L/R |
| FK | LE | 8.32 | 16.34 | – | 24.84 | 25.70 |
| | RE | –15.12 | –27.62 | | –25.72 | –19.84 |
| PD | LE | –11.88 | –7.04 | – | –5.52 | –9.92 |
| | RE | –5.40 | –13.59 | | –14.92 | –22.56 |
| ER | LE | –7.26 | –3.76 | – | –3.88 | –0.58 |
| | RE | 7.98 | 0.54 | | 4.44 | 1.10 |
| PB | LE | 9.42 | 14.78 | – | 10.26 | – |
| | RE | –1.56 | –4.14 | | –4.50 | |
| FR | LE | –13.18 | 2.10 | – | –7.92 | – |
| | RE | –10.78 | –12.36 | | –16.34 | –17.92 |
| MB | LE | 12.48 | – | 13.30 | 19.04 | 14.46 |
| | RE | 7.94 | | 5.52 | 7.60 | 6.60 |
| GD | LE | 4.50 | – | 7.46 | 14.62 | 5.28 |
| | RE | –6.18 | | –7.46 | –16.20 | –9.68 |
| SI | LE | 0.30 | 6.36 | 2.90 | 5.26 | 4.24 |
| | RE | –1.20 | –5.06 | –3.24 | –5.94 | –6.88 |
| MI | LE | 9.00 | 12.78 | 10.06 | 17.30 | 14.94 |
| | RE | 2.94 | –3.92 | 2.54 | 2.38 | – |
| SE | LE | 2.18 | – | 5.86 | – | 7.02 |
| | RE | 0.04 | | –1.12 | –3.80 | – |
| MA | LE | –0.32 | 7.80 | – | – | – |
| | RE | 5.40 | 4.38 | | 3.30 | |
| Means | LE | 1.23±8.78 | 6.17±8.57 | 7.92±3.97 | 8.22±11.86 | 7.64±10.82 |
| | RE | –1.45±7.47 | –7.72±10.01 | –0.75±5.04 | –6.34±10.66 | –9.88±11.00 |

screen located at 1 m viewing distance with a decreased convergence angle of about 3°. The disparity of the stereogram caused the eyes to reconverge rapidly, in addition to creating vivid depth perception. The mean vergence angle for up and down gaze fixations was 11.8° (6.8° and 4.9° for the left and right eye). The planes tilted temporally by 17° in the left eye and 5° in the right eye. Thus, the disparity+stereo condition produced an immediate strong tilt of Listing's plane. This was almost always the case, even when this condition was run at the very beginning of the experimental session. The high gains in this condition were not simply a training or cumulative effect. In summary, qualitatively, the data provide evidence for dependence of LPVT on the stimulus driving convergence of the eyes.

## Listing's plane orientation with vergence. Quantitative data

Table 3 shows the horizontal orientation of Listing's plane for each individual eye and for each condition. Noteworthy is the large intersubject variability in the orientation of Listing's planes in the far, control condition. For 50% of the individual eyes, Listing's plane was nasally oriented and was temporally oriented in the remaining cases. The amplitude of the tilt was also largely variable among the subjects. In the conditions artificially simulating proximal vision (disparity, accommodation, disparity+accommodation, disparity+stereo), the planes tilted temporally for all eyes; 72% of the individual eye planes were now temporally oriented.

Figure 3 shows, for each individual eye and for each simulated close-viewing condition, the change in the orientation of Listing's plane relative to the control far condition. The change was temporal in all cases: it was largely asymmetric in the two eyes in several cases. Also, the amount by which the planes tilted was subject-dependent, as shown by the large variability (vertical lines of group means). The sum of the tilt for the two eyes shown in the lower part of the graph also shows large intersubject variability, particularly in the combined conditions (disparity+accommodation, disparity+stereo). The group means are smaller for the accommodation condition. This, however, is due to the smaller change in vergence and will be better substantiated in

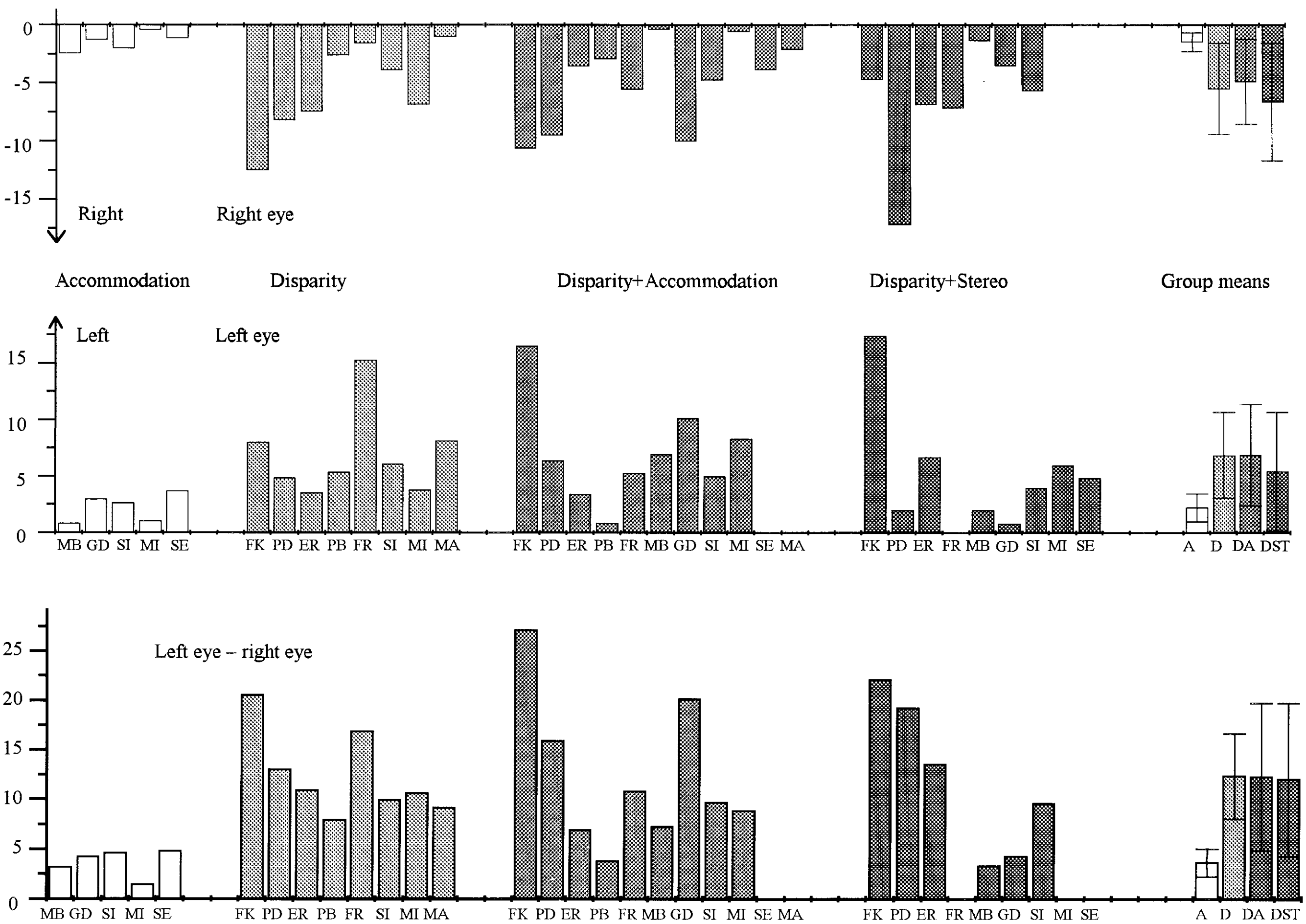


**Fig. 3** Change in the orientation of Listing's plane for each individual eye (orientation of plane in far, control condition – orientation of the plane in the close, simulated condition; in degrees). Temporal tilt is indicated by negative changes for the right eye, positive changes for the left eye. The tilt of the planes summed for the two eyes is shown at the bottom. *Initials* denote the individual subjects

Fig. 4, which displays the tilt of Listing's plane as a function of the change in vergence angle (LPVT).

Figure 4 shows scatter plots of individual gains of Listing's plane tilt with the change in vergence. The slope for each condition is a fit that goes through zero (this type of slope is appropriate for the data, since they show variability both in vergence and in the tilt of Listing's plane).

The accommodation condition produced highly variable results, and there was no correlation between the tilt of Listing's plane and the change in vergence. In fact, the tilt of the planes was decoupled from the change in vergence for two subjects: for subject SI, the planes tilted temporally by 4.64°, even though the change of the convergence was only 0.5°; more striking, for subject MI, the planes tilted temporally by 1.46°, even though the small change in vergence was divergent (–0.8°). The remaining three subjects showed a temporal tilt of the planes that was related to the change in vergence; the gain values for these subjects were high. Overall, this condition shows that the accommodative vergence can drive tilt of Listing's planes, but also that decoupling between vergence and the orientation of Listing's plane can occur when the accommodative demand is high.

For the three other conditions (disparity, disparity+accommodation, disparity+stereo), the slopes of individual gains were significantly different from 0 and were always above 1; the slopes were similar in the disparity and in the disparity+accommodation condition, but the data were more variable in the latter condition. Importantly, the slope almost doubled in the disparity+stereo condition. The group-mean gain of LPVT in the disparity condition (1.56±0.23, $n$=8) or in the disparity+accommodation condition (1.38±0.72, $n$=11) was significantly different from that in the disparity+stereo condition (2.3±0.98, $n$=8, Student's $t$-test comparing the group means, significant at $P$<0.056 and at $P$<0.03, respectively). The comparison between these conditions, based on the same subjects (paired $t$-test), also showed highly significant differences (disparity versus disparity+stereo condition: $t$=3.47, $n$=5, significant at $P$<0.003; disparity+accommodation versus disparity+stereo: $t$=2.78, significant at $P$<0.03). Thus, the disparity+stereo condition produced significantly higher gains from the other conditions. No other comparison between conditions was sta-

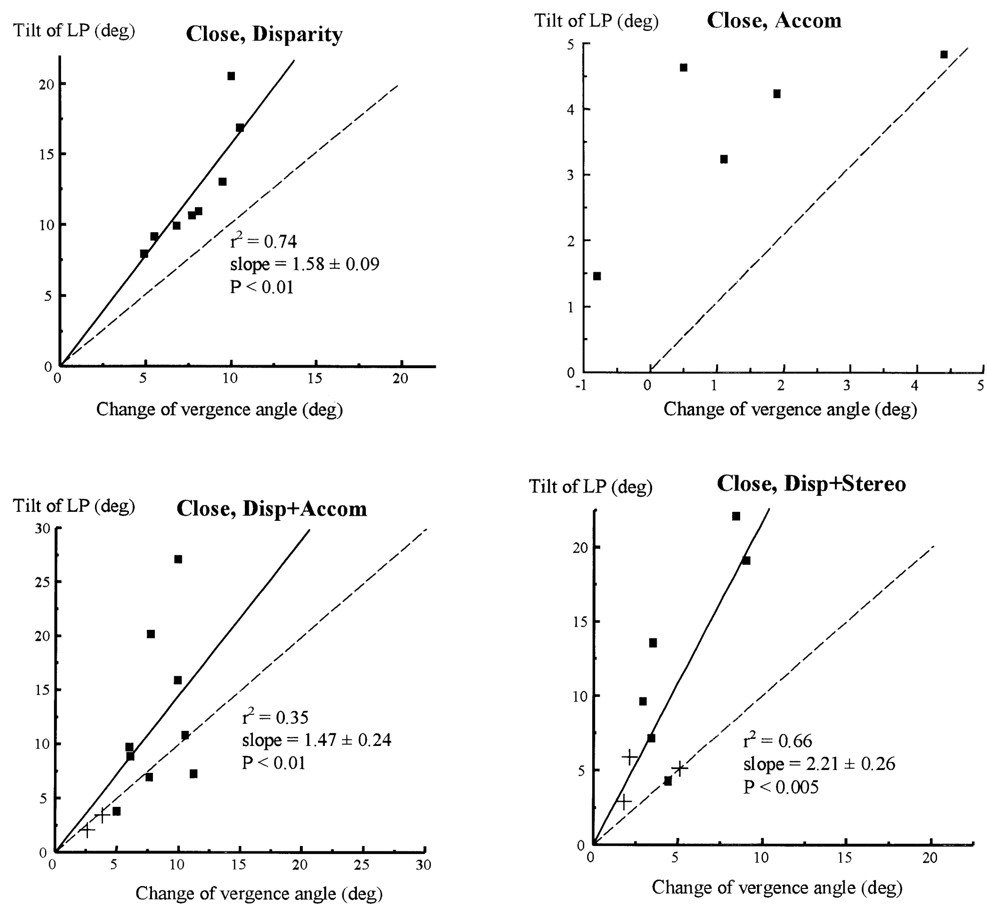


**Fig. 4** Each *square* is an individual value of the gain of Listing's plane vergence tilt (LPVT): rotation of Listing's plane as a function of the change of the horizontal vergence angle [tilt of the plane of the left eye – tilt of the plane of right eye in degrees / change of vergence (the left-right eye horizontal position, in degrees)]. *Crosses* indicate gains of LPVT for a single eye (see notation in Table 1, data from the other eye were discarded because of slippage of the coils). Results are shown for each testing condition. All individual gain estimations are based on the rotation of the planes relative to the far, control condition (1 m viewing distance). In each panel, the *thick line* is the least-squares estimate of the straight-line fit going through zero; the *dotted line* is the ideal fit line, slope of 1. The value of the slope of the gains and its significance is also shown in each panel together with the $r^2$ value. *LP* Listing's plane

tistically significant. In summary, the results in Fig. 4 show that the gain of LPVT were different for the different visual conditions; the gains were higher in the disparity+stereo condition.

## Discussion

### Idiosyncratic orientation of Listing's planes

This study confirms Listing's law obedience in normal subjects, since, in all our conditions, eye positions lay in a single plane. The orientation of the plane, however, was highly variable and individual idiosyncratic differences were observed: in the far, control condition, the planes were temporally or nasally oriented by as much as 15° (see Table 3). Our observations in this respect are partially consistent with the study of Haslwanter et al. (1994), which showed substantial temporal rotation of Listing's plane for distant viewing. They are consistent with the studies of Mikhael et al. (1995) and Bruno and van den Berg (1997), who reported large intersubject variability, temporal or nasal, in the orientation of the primary positions of the eyes for distant viewing.

### Thickness of Listing's plane

The thickness of Listing's planes (standard deviation of eye position around the best-fit plane) was, on average, about 1° in three of our experimental conditions (far, disparity-alone, and disparity+accommodation conditions); slightly larger values were observed in the accommodation-alone condition (1.35°) and in the disparity+stereo condition (1.38°). These values are comparable to those reported by Mok et al. (1992). DeSouza et al. (1995) reported that torsional variability and thickness of Listing's plane is larger when subjects make saccades frequently and is even larger when they make vertical saccades than when making horizontal saccades. In all our experiments, subjects exclusively made vertical saccades at a rapid, albeit self-determined pace. These aspects could account for some of the intersubject variability and thickness values. It should be also noted that our Listing's planes contain eye positions during and after the saccades. It is known that saccades are associated with small blips of torsion (Straumann et al. 1995). Despite this variability, there was an overall tendency for the thickness of Listing's plane to increase in the disparity+stereo condition and in the accommodation-alone condition. The thickness of the plane was not correlated with the variability of vergence. These observations are intriguing and suggest that obedience of Listing's law and Listing's plane is also influenced by the poorness or the strength of visual and perceptual cues controlling the positions of the eyes; this, however, deserves further investigation.

## Temporal tilt of Listing's plane with vergence

The most important finding of our study is the temporal rotation of Listing's plane with convergence in reduced-cue situations. All our conditions artificially involved various degrees of conflict between different cues for distance. We showed, for the first time, that LPVT occurs instantaneously in such artificial situations. The ability of isolated visual cues to alter the orientation of Listing's plane instantaneously suggests that this is a robust phenomenon, regardless of whether its function is for motor efficiency, for visual perception, or for both.

The gain of the tilt of Listing's plane with convergence was, however, highly variable for different subjects and depended on the testing conditions. The intersubject variability we observed even in the conditions where disparity-vergence was involved contrasts with prior studies (e.g. Mikhael et al. 1995; Minken and Van Gisbergen 1994; Mok et al. 1992; Van Rijn and Van den Berg 1993). It should be noted, however, that these studies examined a smaller number of subjects.

Other possible factors for the variability could be: (1) the artificial nature of our conditions, i.e., our use of reduced cue situations; (2) the high rate at which the different conditions succeeded each other; or (3) the relatively small range of vergence angle studied. The vergence in our different conditions varied from 3° to 13°; this range is smaller than that investigated in most other studies (from infinity to 30°: Minken and Van Gisbergen 1994; Mok et al. 1992). It is possible that, in the limited vergence range of 3–13°, the orientation of Listing's plane and the vergence are more loosely linked. Small numbers could also be more sensitive to errors, particularly when computing their ratio.

Another intriguing observation is that the amount by which the plane tilted was very different between the two eyes, even when the vergence was symmetric for the two eyes (see Fig. 3). For the three conditions involving disparity, the group gain of LPVT was always above 1 (see Fig. 4). This contrasts with prior studies (e.g., Minken and Van Gisbergen 1994; Mok et al. 1992). High gain values similar to ours were observed by Bruno and Van den Berg (1997) for three subjects when comparing the orientation of the planes between far and near natural binocular viewing relative to the change in vergence. Here, we emphasize that our conditions succeeded each other rapidly; they were all artificial and contained various degrees of conflict between different distance cues, binocular versus monocular, i.e., disparity versus blur-induced accommodation. Perhaps, for natural viewing where multiple cues are available that are in agreement between themselves, the gain is closer to 1, as found by other studies (e.g., Minken and Van Gisbergen 1994; Mok et al. 1992). It should be noted that the ideal gain for motor efficiency is 0, while that for binocular vision is 1. In the light of this, our gains, which were much greater than 1, are puzzling. The most important aspect of our findings is the difference in the gains of LPVT for the different visual conditions, providing new information on the relative importance of individual cues (see below).

## Dependency of LPVT on visual conditions: significance

### *Role of disparity*

Mikhael et al. (1995) have shown that prism-induced disparity alone can cause tilt of the planes. In that study, however, subjects wore prisms for about 1 h before eye movement was recorded, and adaptation effects may have been involved. Our study shows that disparity-driven vergence causes tilt of the planes instantaneously. The tilt is highly correlated with the change in vergence angle (see Fig. 4).

### *Role of depth*

The most important new finding is that the addition of a stereo cue and depth perception caused the gain of LPVT to double compared with the disparity alone or to the disparity+accommodation condition. The difference in the group-mean gains between the disparity+stereo condition and the disparity or the disparity+accommodation condition was statistically significant (at the level $P<0.05$, Student's *t*-test comparing the average gains for the two conditions). This finding strongly suggests that the tilt of Listing's plane is not entirely determined by the vergence itself, i.e., is not a pure motoric phenomenon. Our interpretation is that the increased sense of proximity created by the stereogram boosted the tilt of Listing's plane relative to the change in vergence angle. Bruno and Van den Berg (1997) discussed the hypothesis of Listing's plane being determined by the perceived distance, particularly in cases of conflict, rather than by the vergence itself. To our knowledge, our findings are the first to support this hypothesis directly. An interesting question is whether depth information from real 3-D objects provide similar boosting of LPVT, and this deserves further investigation.

### *Role of accommodation*

This study shows that accommodative vergence stimulated under binocular viewing with the use of negative lenses can also instantaneously drive temporal tilt of the planes. The ability of accommodative vergence to drive temporal tilt of Listing's plane was addressed by Bruno and Van den Berg (1997) for the following conditions: under monocular viewing (no disparity) of a closely located target configuration or under dichoptic viewing, where the left- and right-eye images were shifted by the interocular distance to simulate optical infinity; accommodation in the latter case was at screen distance (1.5 or 2 m, i.e., 0.67 and 0.5 diopters) and, thus, in conflict with optical infinity. In the present study, we stimulated accommodative vergence under binocular viewing and used powerful lenses of –3 diopters in front of each eye. For three of the subjects, we obtained accommodative vergence and high gains of LPVT (2.95 for subject MB, 2.23 for subject GD, and 1.1 for subject SE). Thus, our study confirms prior studies on the ability of accommodative vergence to drive LPVT and extends it for binocular viewing, where the interactions between accommodation and vergence are more complex. As discussed by Schor (1983), the AC/A ratio is larger under binocular than under monocular viewing. Ogle et al. (1967) attribute this to differences in the accommodative response itself, but Semmlow and Hung (1979) showed that convergence accommodation (the CA/C ratio involved under binocular viewing) may account for the differences. The intersubject variability in the gain of LPVT we observed was particularly important. For two subjects, the change in vergence was negligible, resulting in unreliable LPVT gain values. Perhaps, their AC/A ratio was abnormally low or, most likely, their accommodative ability was weak relative to the power of the stimulus used (–3 diopters). Yet, the planes tilted temporally even for these subjects. Possibly, accommodative effort itself is responsible for the tilt of Listing's plane. The results for these subjects show decoupling of vergence and Listing's plane orientation and are consistent with observations of Bruno and Van den Berg (1997).

### Vergence accommodation interaction

The disparity+accommodation condition did not produce higher gain than the disparity-alone condition. This suggests, indirectly, the major importance of disparity. For individual subjects, addition or removal of the accommodative cue did influence the orientation of Listing's plane, even though the vergence remained, on average, the same. There was, however, no common trend in this influence. The LPVT rotated more temporally for subjects FK and PD compared with the disparity-alone condition, but nasally for subject PB (see Table 3). The idiosyncratic nature of changes is most likely due to individual differences in the strength of mutual couplings between convergence and accommodation. For instance, the rotation of Listing's plane nasally for subject PB may have been caused by a strong CA/C ratio: convergence-driven disparity might have modified the accommodation substantially; subsequent insertion of a negative lens relaxed accommodation and perhaps created an additional conflict with vergence.

In summary, our findings show for the first time that, under artificial reduced-cue situations, the relationship between convergence and Listing's-plane temporal rotation depends on the stimuli driving convergence. Disparity alone drives vergence and Listing's plane immediately and consistently over subjects. Accommodative vergence, the mutual interaction between vergence and accommodation, can influence the orientation of Listing's plane, but they do so in a idiosyncratic way. Depth perception of stereograms enhances the gain of the tilt of Listing's plane with vergence. The present findings support the hypothesis that Listing's-plane rotation with convergence is not exclusively a strategy for motor efficiency. Rather it subserves binocular vision and perhaps depth perception.

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