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Orientation of Listing's plane during static tilt in young and older human subjects

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Abstract

Three-dimensional eye positions, when expressed as rotation vectors, are constrained to lie in a head-fixed Listing's plane. The offset and orientation of Listing's plane changes when the head is tilted. To assess the influence of age on this phenomenon, young (less than 30 years old) and older (>65 years old) human subjects were seated upright, pitched nose up and nose down, and rolled right ear down and left ear down. Listing's plane was computed from eye movements recorded using a dual scleral search coil while subjects scanned a complex visual scene. During pitch, Listing's plane counterpitched with respect to the head, while during roll, it translated in a manner consistent with "ocular counterrolling". There was no significant difference in this reorientation of Listing's plane between the young and older subjects. The only obvious difference between the two age groups was that the "thickness" of Listing's plane was greater in the older subjects. This suggests that aging has a small, but definite, influence on Listing's law.

Keywords: Aging; Human; Listing's law; Otolith; Vestibular

1. Introduction

To completely describe the position of the eye with respect to a fixed coordinate frame, for example eye-in-head or eye-in-world (gaze), requires three coordinates. One common coordinate system, Fick coordinates, describes eye position in terms of horizontal (deviation of the eye to the left or right of straight ahead), vertical (elevation of the eye above or below the horizontal plane), and torsional (rotation of the eye about the line of sight) coordinates. It has been known for some time, however, that eye movements are constrained so that eye positions appear to have two rather than three degrees of freedom. Donders' law states that the torsional coordinate of eye position seems to be a function of the horizontal and vertical components (Van Opstal, 1993). If eye positions are expressed as vectors representing the rotation of the eye away from a standard fixed reference position such as straight ahead gaze, this constraint takes on a particularly compact mathematical form known as Listing's law: all of the rotation vectors lie in a plane called the displacement plane (Haslwanter, 1995). The orientation of this plane with respect to the head depends upon the particular choice of a reference position. There is a unique reference position that is perpendicular to its associated displacement plane. This particular reference position is called Primary Position (Nakayama, 1978) and the associated displacement plane is called Listing's plane (Haslwanter, 1995).

For human or sub-human primates subjects seated with their head erect, Listing's plane tends to be near the subject's frontal plane (Haslwanter, Curthoys, Black, & Topple, 1994). When the subject is tilted however, the orientation of Listing's plane can change. For example, when Rhesus monkeys are pitched forward or backward, their Listing's plane tends to counterrotate with respect to the head so as to remain more earth-vertical (Cabungcal, Misslisch, Scherberger, Hepp, & Hess, 2001; Haslwanter, Straumann, Hess, & Henn, 1992). This phenomenon has also been reported to occur in humans (Bockisch & Haslwanter, 2001; Schor & Furman, 1999). Another example of a change in Listing's plane occurs when a subject is tilted (rolled) to the side; the eye tends to counterroll so that the vertical axis of the eyeball remains more earth-vertical (Diamond & Markham, 1983). This ocular counterroll is manifested

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by a translation of Listing's plane along the subject's fore–aft (X) axis (Bockisch & Haslwanter, 2001).

The purpose of this study was twofold. One was to examine, in normal human subjects, the influence of a modest change of orientation with respect to gravity on the orientation of Listing's plane. In particular, we hoped to confirm the observation made in rhesus monkeys (Cabungcal et al., 2001; Haslwanter et al., 1992) and humans (Bockisch & Haslwanter, 2001; Schor & Furman, 1999) that presumed vestibular input modulates the orientation of Listing's plane. The second was to examine the phenomenon of Listing's plane and its control in both young and older subjects, to better understand how aging affects ocular motor control and function. Aging is known to affect the vestibulo-ocular reflex (VOR) and the ocular motor control system; velocity storage is less effective (Paige, 1992; Peterka, Black, & Schoenhoff, 1990) and ocular pursuit is less accurate (Larsby, Thell, Moller, & Odkvist, 1988; Zackon & Sharpe, 1987). The influence of aging on otolithic responses is less well understood. Recent data suggest that aging can produce an alteration in otolith-ocular responses, semicircular canal–otolith interaction, and otolith-visual interaction (Furman & Redfern, 2001, 2002). However, the influence of aging on Listing's law, including any effects of gravity on the orientation of Listing's plane, is unknown.

Our results confirm that in both young and older humans, changing the orientation of the head with respect to gravity produces a compensatory alteration of the orientation of their Listing's plane. These results have been previously presented in abstract form (Schor & Furman, 1999).

2. Methods

This study was approved by the Institutional Review Board of the University of Pittsburgh. All subjects were naïve volunteers in good health with no history of balance disorders. Following receipt of informed consent, all subjects underwent vestibular and ocular motor testing. Inclusion criteria included normal ocular motor function, no positional nystagmus, normal caloric responses, and normal age-corrected hearing.

Subjects were seated on, and belted into, a turntable chair, with their head, immobilized by a helmet, oriented upright and with the plane of the infraorbital ridge and external auditory canal pitched down 15°. The chair and turntable, in turn, could be tilted away from an upright orientation by as much as 30°. By proper positioning of the turntable chair, nose-up pitch, nose-down pitch, right ear down roll, and left ear down roll could be delivered to the subject (Fig. 1).

Three-dimensional eye position was assessed for each subject by placing a dual scleral search coil (Skalar) in the left or right eye. Two sets of magnetic field coils, one producing a vertical field, the other a transverse horizontal field, were bolted to the turntable chair, with the subject's head near the center of the two fields. The four currents induced in the two coils by these fields were amplified and detected, resulting in a voltage proportional to the strength of the signal (CNC Engineering). Before or after each recording session, each dual eye coil assembly was calibrated by placing it on a fixture that permitted precise positioning of the coil.

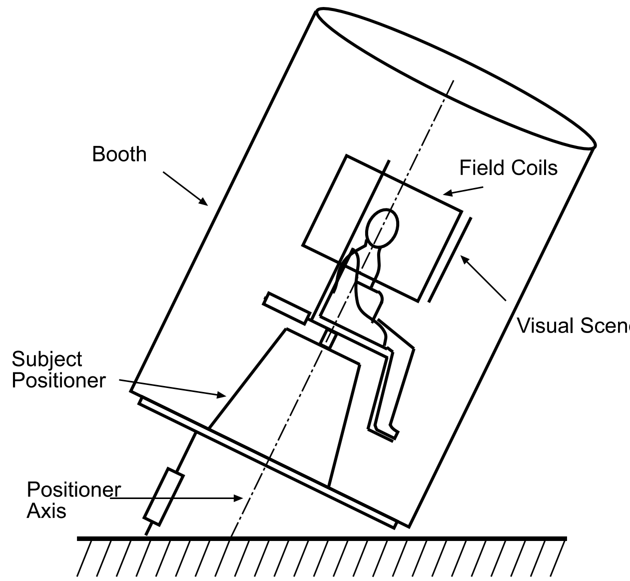

Fig. 1. Subjects are seated in a circular booth that can be tilted up to 30° from the vertical. Test positions included upright, nose-down pitch (illustrated), nose-up pitch, right ear down roll, and left ear down roll. The subject, field coils and visual scene moved together as a unit.

The experimental paradigm was as follows: Subjects were seated and comfortably restrained in the chair. The dual scleral search coil, embedded in a soft annulus, was placed on the eye following administration of a topical ophthalmic anesthetic. Testing always began with the subject and chair not tilted, i.e. earth-vertical. First, the subject was asked to gaze at a projected laser target one meter distant that was carefully positioned "straight ahead" of the eye in which the coil was placed; we used this particular target both to deduce the position of the coil on the eye (by recording the position of the coil in space when the subject looked at the target), and to serve as an initial reference position from which to compute eye position rotation vectors. In particular, we considered the eye to be at 0° in horizontal, vertical, and torsional position when gazing at this reference position.

Following recording of this reference position, the subject was asked to view a complex visual scene at a distance of 44 cm that subtended an angle of about 60° horizontally and 40° vertically. The scene was divided into nine sections (3×3); subjects were instructed to "Look around in Section 1" for from 5 to 10 s, then asked to look in the next section. No other instructions were given to the subject. Each such test accordingly took about 45–90 s, with enough communication between operator and subject (for example, to look at the next section) that alertness was maintained.

Following one such sequence of viewing the scene and recording eye positions while seated upright, the entire test chamber in which the subject was seated was tilted with respect to gravity by up to 30°. Before being tilted, the subject was positioned with respect to the tilt axis so as to deliver the appropriate (for example, nose-up) tilt. The subject, the chair and restraining helmet, the visual scene, and the magnetic field coils all moved together; thus from the subject's perspective, the only difference between an "upright" and "tilted" trial was the direction of gravity. Subjects were tilted at a rate of about 1°/s. Once in position for at least 30 s, the subject was again asked to view the scene, and eye positions were recorded. A typical experimental session would record the subject's eye movements in five orientations—upright, nose-up pitch, nose-down pitch, right ear down roll, left ear down roll—with several interspersed recordings while upright of the eye position while the subject looked at the straight ahead reference position. These additional reference determinations served to verify the location of the coil on the eye, and to thus allow us to correct for minor coil slippage over the course of the recording session.

The currents induced in the magnetic scleral coils were amplified, detected, converted into four voltages, sampled at 100 Hz and stored for off-line analysis. We use a right-handed Cartesian coordinate system, with the Z axis being earth-vertical, the X axis being aligned with the subject's nose, and the Y axis aligned with the subject's left ear. Since we were particularly interested in the control of eye position during fixation, we examined the recording of eye position during the "busy scene" task and, using both automatic and manual criteria, identified periods of fixation lasting a minimum of 0.1 s. The three-dimensional eye position corresponding to the average position of the eye during each fixation epoch was computed, and expressed as a rotation vector. The length of the vector, for computational and mathematical reasons, was expressed as the tangent of half the amount of rotation about the rotation vector axis to go from the reference position to the recorded eye position (Haustein, 1989; Schor & Furman, 2001). Once each fixation point was expressed as a single average rotation vector, we fit a displacement plane through the cloud of points representing the ends of these vectors. Knowing our initial reference position and its associated displacement plane, we then computed Primary Position and its associated Listing's plane using the defining criterion that Primary Position is perpendicular to its displacement (Listing's) plane (Schor & Furman, 2001).

We expressed the orientation of Listing's plane by describing the location of Primary Position, using the spherical polar coordinates of azimuth and elevation. By azimuth, we mean the projection of Primary Position into the XY plane; this corresponds to a "yaw" of Listing's Plane from a frontal orientation, with positive azimuth corresponding to yaw to the left (or a right-hand rotation about the $+Z$ axis). Elevation is the angle between Primary Position and the XY plane, with positive elevation corresponding to a positive Z component. For most of our subjects, the coil was placed in the left eye. For those trials in which the coil was in the right eye, we have reversed the sign of the azimuth value, so that all of the results are as though coming from a coil placed in the left eye.

Azimuth and elevation fully describe the orientation of Listing's plane. An additional characteristic of Listing's plane is its distance from the origin, which we will call the "offset" of Listing's plane. We define the sign of the offset as the sign of the X coordinate of Primary Position.

Two other quantities are of interest. One is a measure of how stable the eyes were during the epochs of visual fixation. We quantified this stability as follows: for each fixation, we computed the mean rotation vector (the "center" of gaze during the fixation epoch); next, we calculated how far each rotation vector was from this mean, and computed the standard deviation of these distances; finally, we averaged these "standard deviations from the mean" across all of the fixation epochs for the trial. Our final measure was to define a "thickness" of Listing's plane by computing the root-mean-square distance of each point from the plane (similar to a "standard deviation from the plane"). The units of both the stability and thickness are the rotation 'distance' in "half-radians". To express them in more familiar angular measurements, we used the inverse of the tangent-half-angle formula, which converts rotation vector lengths into the equivalent amount of rotation about the axis represented by the rotation vector.

3. Results

The subject population consisted of 18 healthy adults. Of these, eight (five males, three females) were between 19 and 30 years old; we will refer to this group as the "younger" subjects. The remaining 10 subjects (six males, four females) were between 66 and 75 years old; we will refer to them as the "older" subjects.

Fig. 2 illustrates data taken from a 69-year-old female subject. From the four voltages arising from the dual scleral search coil, eye position in Fick coordinates was computed and displayed off-line to allow identification of epochs representing fixation. Several such epochs are illustrated in Fig. 2A. Note that for purposes of defining

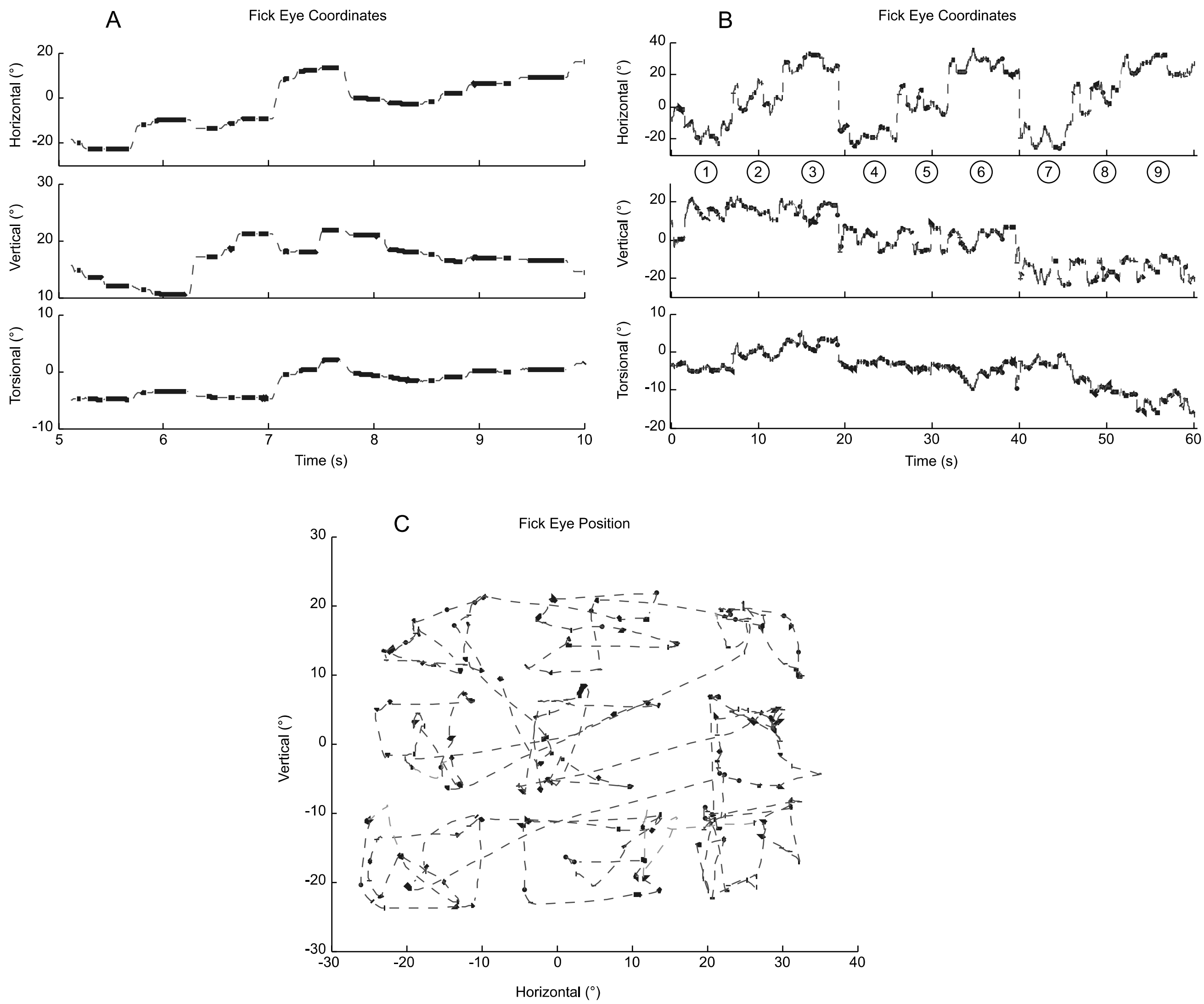

Fig. 2. Eye movements during a 30° nose-up tilt of a 69-year-old female subject. (A) An expanded segment of horizontal, vertical, and torsional (Fick) components of gaze illustrates the identification of fixation periods (thick solid lines), separated by more rapid movements (thin dashed lines). (B) Eye movements during the entire trial viewing the nine-panel visual scene. The top horizontal gaze component shows three left-to-right progressions to view panels 1–3 (panel number indicated just below the horizontal trace), then panels 4–6, and panels 7–9, while the vertical component shows the progression from the top row of panels (1–3) to the bottom row (7–9). (C) In this gaze plot (horizontal versus vertical components), the periods of fixation show up as dots (short thick lines), interspersed with more rapid eye movements (thin dashed lines). Note the fairly random distribution of gaze within each of the nine panels.

"fixation", we considered only the horizontal and vertical eye position, as this represents the direction of gaze.

The stability of the eye positions during each epoch of visual fixation was evaluated by computing the average standard deviation of eye position, as described in Section 2. For all of our subjects, this value was less than 0.1, demonstrating that our selection/editing criteria for identifying periods of fixation were adequate. Across our subjects, the median duration of the fixation epochs ranged from 0.18 to 0.34 s.

The entire trial is shown in Fig. 2B. An examination of the eye movements shows the progression across the nine sections of the visual scene, from left to right (top row, horizontal eye movements) and from top to bottom (middle row, vertical eye movements). The spatial trajectory of the eye movements is shown in Fig. 2C, which illustrates the eye position while the subject randomly scanned the nine sections of the visual scene.

Fig. 3 shows the rotation vectors, computed with respect to Primary Position, corresponding to the 166 fixation epochs illustrated in Fig. 2. Fig. 3A shows the vectors and Listing's plane in perspective. For this subject, Listing's plane is slightly yawed (21.6°) and pitched (−5.7°) with respect to the frontal (*YZ*) plane. Fig. 3B shows the same data, but with the axes rotated so as to view the plane of points "edge-on", which

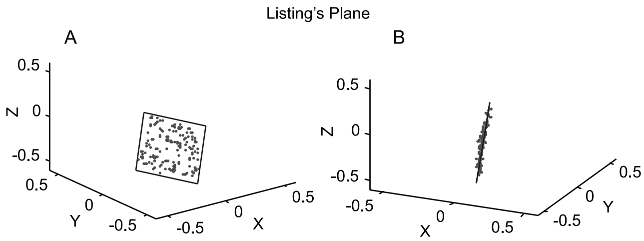

Fig. 3. Listing's plane for data from Fig. 2. The gaze positions were expressed as rotation vectors and a displacement plane was fit to the data. Listing's plane was then determined, and Primary Position identified. These vectors, and a representation of Listing's plane, are illustrated here, in two views. (A) Listing's plane, in general, is not parallel to the (head) coordinate axes. In this example, the azimuth (corresponding to the yaw of the plane) of the plane is 21.6° and its elevation (the pitch of the plane) is −5.7°. The view in this figure is looking from slightly behind the subject's right ear (subject's nose facing toward the right). Note that the $+X$ axis is in the direction of the subject's nose, while the $+Y$ axis points out the left ear. The units of the plot are in "half-radians"; 0.5 half-radians is approximately 50°. (B) By rotating the figure about the Z axis, we can view the data points looking along Listing's plane, and thereby visually evaluate the goodness of fit of the rotation vector points to the plane. In this example, the standard deviation (thickness) of the points from the plane corresponded to 1.2°.

provides a visual impression of its thickness (the standard deviation of the points about the plane corresponded to 1.2° in this example).

The parameters for Listing's plane while subjects were upright are plotted in Fig. 4 and are summarized in Table 1. The orientation of Listing's plane of all our subjects had a positive azimuth, implying the plane (of the left eye) was yawed to the left. The elevation, or pitch of the plane, and offset of the plane from the coordinate origin, were not significantly different from zero (two-sided binomial test, $p > 0.1$). If one considers the young and older sub-populations, there was no significant difference for azimuth, elevation, or offset (two-sided Mann–Whitney U test, $p > 0.1$).

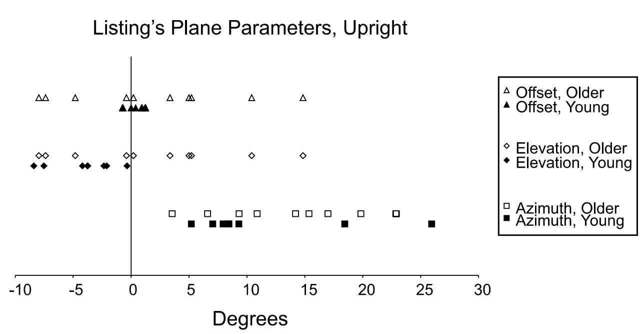

Fig. 4. Distribution of offset, elevation, and azimuth of Listing's plane during upright posture for a population of young (closed symbols) and older (open symbols) human subjects. There does not seem to be an effect of age.

The experimental paradigm involved determining Listing's plane under identical visual conditions, but with the subject (both body and head) in five different orientations with respect to gravity. In particular, during roll tilt, the eyes are known to undergo a counterroll (with respect to the head). If this is considered as an additive torsional eye component for any particular direction of gaze, this might be expected to shift Listing's plane along the X axis. One measure of such a shift is the distance of Listing's plane from the origin. As the plane is generally close to the frontal plane, such an offset from the origin will be predominantly in the direction of the X axis.

Fig. 5A illustrates, for a 27-year-old male subject, the offset of Listing's plane for three different body orientations: upright, rolled 30° left ear down (LED), and rolled 30° right ear down (RED). As in Fig. 3, the planes are illustrated from a perspective of "looking down the plane". The origin of the coordinate system is indicated by a black dot on the figure. When the subject is tilted to the left, the plane develops a positive offset; if we consider the offset as being predominantly in the direction of the X axis, this corresponds to a right-handed rotation of the eye about the X axis, or counterrolling, as expected. Tilt to the right produces a negative offset, corresponding to a left-handed rotation of the eye about the X axis, also counterrolling.

The variation of the offset parameter as a function of roll tilt for all of our subjects is shown in Fig. 6C. The effect illustrated in Fig. 5A, i.e. that the offset of Listing's Plane varies with roll tilt in a manner consistent with the phenomenon of ocular counterrolling, is evident by the negative slopes of these data. In this figure (and in Fig. 7), the subjects are listed in the key in order of advancing age.

We found that in response to pitch tilt, Listing's plane appeared to show a change in elevation, which can be considered to be a "counterpitching" of the plane. An example is shown in Fig. 5B. For clarity of illustration, the three sets of data points have been offset slightly

Table 1
Median parameters (and range in parentheses) of the orientation, offset, and thickness of Listing's plane in normal human subjects while upright

	Azimuth	Elevation	Offset	Thickness
All subjects ($N = 18$)	10.1° (3.6°, 26.0°)	−2.2° (−8.4°, 14.8°)	0.0° (−3.1°, 1.9°)	1.0° (0.5°, 2.0°)
Young subjects ($N = 8$)	8.4° (5.2°, 26.0°)	−3.8° (−8.4°, −0.3°)	0.6° (−0.8°, 1.3°)	0.8° (0.5°, 1.2°)
Older subjects ($N = 10$)	14.8° (3.6°, 22.9°)	1.8° (−8.0°, 14.8°)	−0.6° (−3.1°, 1.9°)	1.3° (0.7°, 2.0°)

Note that data are reported as though the recording coil was in the subject's left eye. These parameters have been averaged across the multiple "upright" determinations made for each subject.

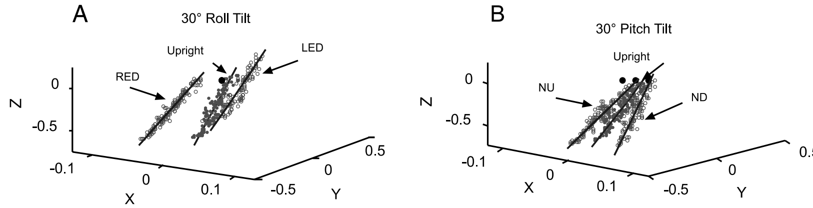

Fig. 5. Variation of Listing's plane with roll and pitch of a 27-year-old male subject. For clarity of illustration, the X axis has been expanded fourfold (0.1 half-radians corresponds to approximately 10°). Eye positions corresponding to upright orientations are shown as solid dots, while eye positions when the subject was tilted are shown as open circles. (A) The offset of Listing's plane shifts in response to 30° roll tilt (RED, right ear down; LED, left ear down); this change is consistent with the phenomenon of ocular counterrolling. The large dot on the figure shows the location of the coordinate origin. (B) The elevation of Listing's plane changes in response to 30° pitch tilt. For clarity of illustration, the nose-up (NU) points have been shifted slightly to the left and nose-down (ND) points have been shifted slightly to the right to minimize overlap of data points. The amount of the shift is indicated by the three coordinate origins in the figure. Note that Listing's plane "counterpitches", e.g. nose-up tilt of the subject results in a nose-down tilt of Listing's plane.

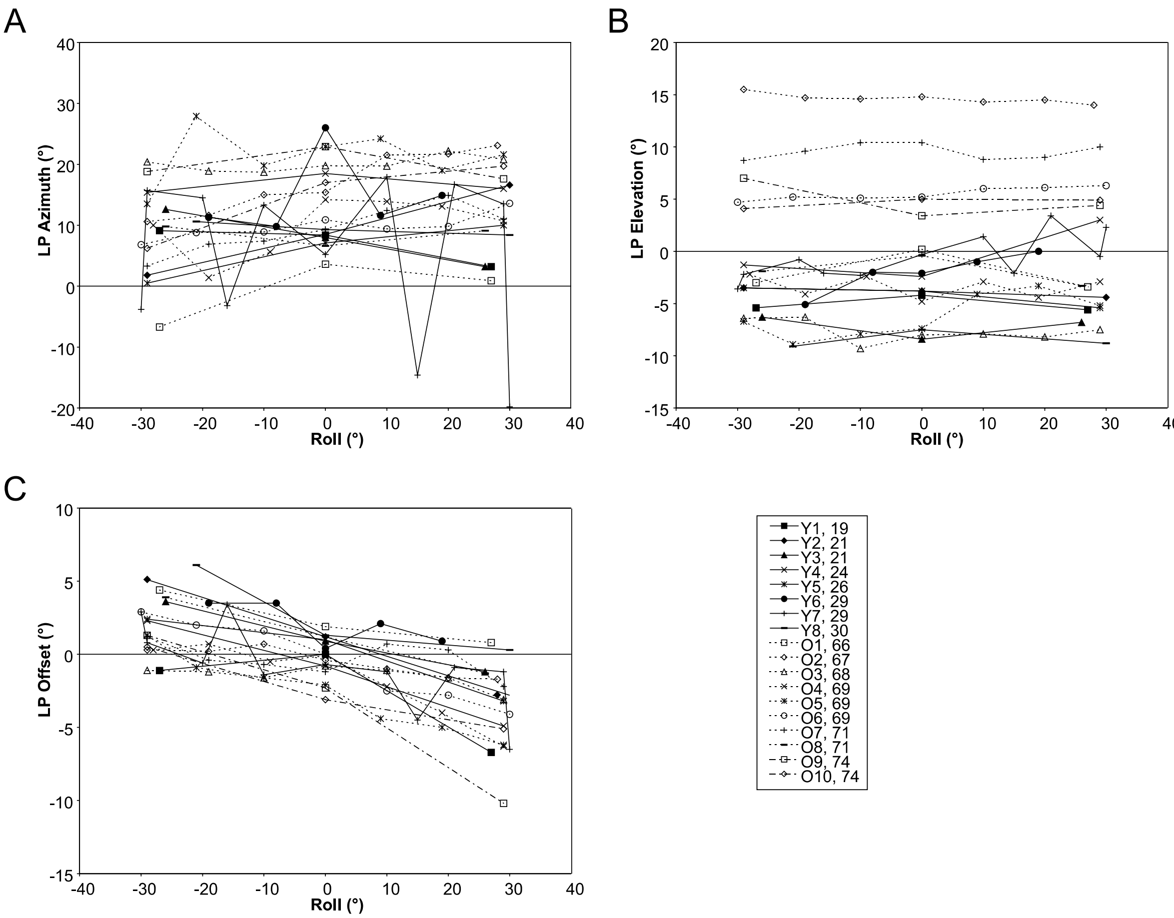

Fig. 6. Orientation and offset of Listing's plane as a function of roll tilt for all subjects. (A) The azimuth (or yaw of Listing's plane) does not appear to vary as a function of tilt. In this figure, and in Fig. 7, the subjects are listed in the key in order of increasing age. Younger subjects are illustrated with closed symbols and solid lines, older with open symbols and dashed or dotted lines. (B) Elevation does not appear to vary significantly with roll. (C) Increasing roll tends to produce a decreasing offset in all subjects, corresponding to the phenomenon of ocular counterrolling.

from one another (note the three coordinate origins); the actual data points have offsets differing by less than one degree. To interpret these elevations, note that the $+X$ axis is to the right, while the $-Y$ axis is in the front. This view thus illustrates the subjects with their head facing to the right, presenting the right ear toward the viewer. During 30° nose-up pitch, Listing's plane has a more negative elevation, i.e. it counterpitches slightly downward with respect to the head. During nose-down pitch, Listing's plane counterpitches slightly upward. Fig. 7B shows the relationship of the elevation of Listing's plane as a function of pitch tilt for all of our subjects; most

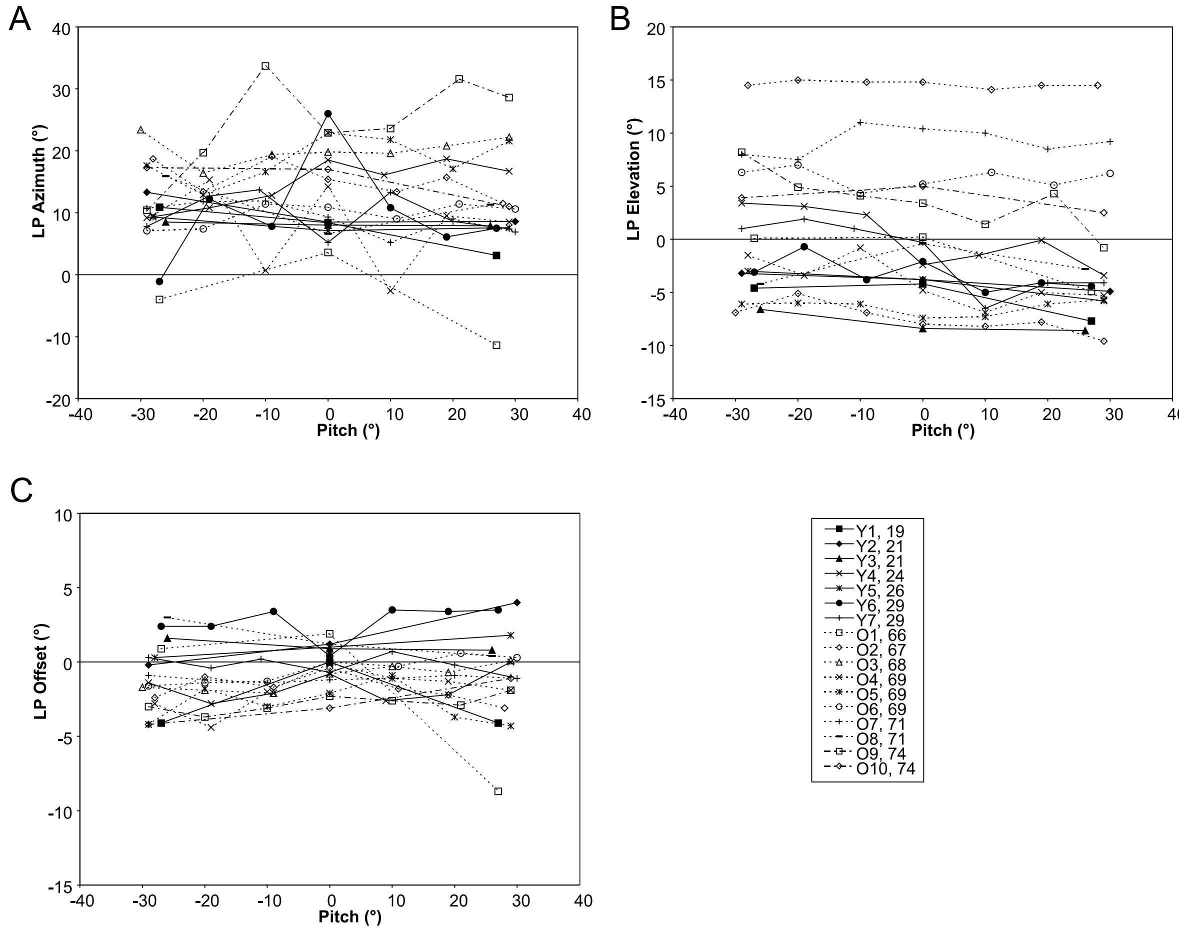

Fig. 7. Orientation and offset of Listing's plane as a function of pitch tilt for all subjects. (A) Azimuth does not appear to vary significantly with pitch. (B) There is a small negative correlation between elevation and pitch. (C) There appears to be no significant variation of offset with pitch.

subjects clearly show a downward slope for this relationship.

We have characterized the orientation of Listing's plane by the three parameters of azimuth, elevation, and offset, and have shown that offset varies when the subject is tilted in roll, and elevation varies when the subject is tilted in pitch. To illustrate that these are the only significant variations with these tilts, we have plotted all three Listing's plane parameters as functions of subject roll (Fig. 6) and pitch (Fig. 7). For each subject, we computed the slope of the line that best describes the relationship between the Listing's plane parameter and the angle of tilt. Fig. 8A illustrates the this slope for roll tilt, i.e. the change in Listing's plane as a function of roll. For all subjects, the slope of offset as a function of roll had a negative slope, while the relationships for both elevation and azimuth as functions of roll were scattered on either side of zero, indicating no significant effect (two-sided binomial test, $p > 0.1$). The data for the younger (lower symbols) and older (upper symbols) subjects are plotted separately on this figure. Note that there does not seem to be any significant difference in the slope relationship between the young and older populations (two-sided Mann–Whitney U test, $p > 0.1$). Fig. 8B shows how the three Listing's parameters vary with the pitch tilt of the subjects. All but two subjects show a negative slope for elevation as a function of pitch tilt (highly significant by binomial test), while the slope relationships for offset and azimuth are scattered on both sides of zero (not significant). Again, subject age does not appear to be a significant factor (Mann–Whitney U test).

The thickness of Listing's plane, that is, the RMS distance of the cloud of points representing the rotation vectors from the best-fit plane, appears to show an age-dependence. This is illustrated in Fig. 9, and shows that the older subjects tend to have "thicker" Listing's planes, i.e. older subjects do not appear to constrain their three-dimensional eye positions quite as precisely to a planar surface as do younger subjects. This difference is statistically significant (two-sided Mann–Whitney U test, $p < 0.05$).

We also examined whether or not thickness of Listing's plane appeared to be a function of either the stimulus parameters (i.e. roll or pitch tilt of the subject), the orientation (azimuth or elevation) of Listing's plane,

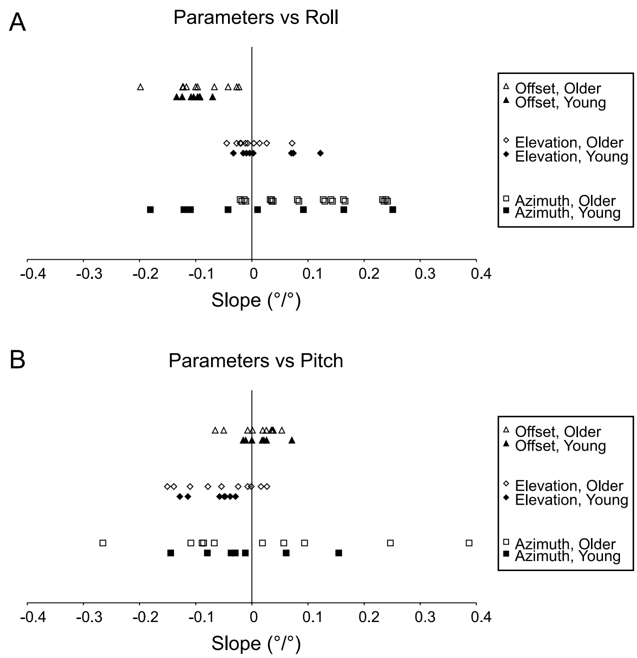

Fig. 8. Slopes of the relationship between tilt and the parameters of Listing's plane parameters in young (closed symbols) and older (open symbols) human subjects. (A) Changes in Listing's plane parameters as a function of roll tilt. Each point represents the slope of the best-fit line through the corresponding points in Fig. 6. There does not appear to be a consistent effect of roll tilt on azimuth or elevation. In contrast, all subjects show a negative slope for offset as a function of roll. There does not appear to be a difference in the distribution of slopes for older and younger subjects. (B) Changes in Listing's plane parameters as a function of pitch tilt (slopes from Fig. 7). There does not appear to be a consistent effect of pitch tilt on azimuth or offset. However, all but two subjects (both older) show a negative slope for elevation as a function of pitch tilt. Again, there does not seem to be an age effect.

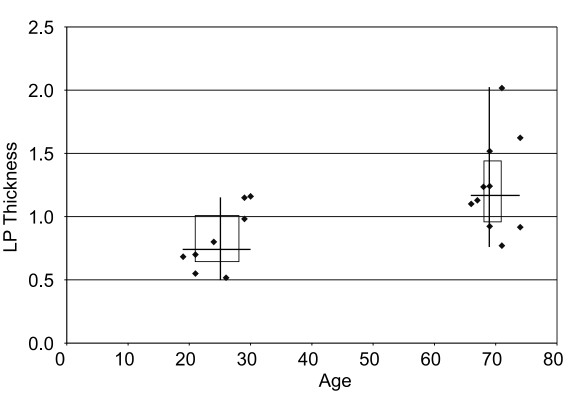

Fig. 9. Thickness of Listing's plane as a function of age. For each subject, we averaged the thickness of Listing's plane (the standard deviation of the rotation vector endpoints from the plane) over all trials. The horizontal and vertical lines indicate the median and range of age and thickness within each group of subjects; the box represents the quartile values. The young subjects tend to have "thinner" Listing's planes than the older subjects.

or the offset of Listing's plane. Across our sample of 18 subjects, thickness did not appear to be related to any of these parameters. For those data obtained when the subjects were not tilted, the Spearman rank correlation coefficients between median thickness and median azimuth, elevation, and offset were not statistically significant ($p > 0.05$).

4. Discussion

We computed Listing's planes for eight young and ten older normal human subjects. The computation was based on periods of fixation as subjects gazed freely at a complex visual scene. The computed Listing's planes were consistent with those described by others: the rotation vectors appear to lie in a plane, the plane is slightly yawed laterally from a frontal position (Bruno & van den Berg, 1997; Haslwanter et al., 1994) and the thickness of the plane is about 1° (Desouza, Nicolle, & Vilis, 1997). Increased age was assorted with increased thickness of Listing's plane.

Our population, and our experimental paradigm, differs in some respects from those of other studies reporting the orientation of Listing's plane in human subjects (Bockisch & Haslwanter, 2001; Haslwanter et al., 1994). First, our population is fairly large (18 subjects), and consists of subjects who have little or no experience with recordings of eye movements. Second, subjects did not look at a small number of specific target positions, but were asked to look around at a series of nine visually "busy" scenes without further instructions. Third, our study includes both young (age < 30) and older (age > 60) subjects, allowing a determination of how age affects the constraints on eye movements described by Listing' law. Fourth, we restricted tilt to 10°–30° from the vertical, allowing us to probe the influence of gravity on Listing's plane in and around upright posture.

Our results confirm that orientation of the head with respect to gravity influences the orientation and offset of Listing's plane with respect to the head (Bockisch & Haslwanter, 2001). This effect of subject orientation on Listing's plane appears to be quantitatively similar for both young and older subjects.

When subjects are rolled about the naso-occipital axis, the offset of their Listing's plane changed, i.e. the plane translated toward or away from the origin. This corresponds to an additional rotation (torsion) of the eye, and can be interpreted as an ocular "counterrolling". We believe, however, that the translation of Listing's plane is a slightly different phenomenon than the phenomenon of ocular counterrolling, which is typically recorded by tilting the subject about the roll axis and examining the (counter) roll of the eye when gazing along the axis of tilt. If Listing's plane happens to be frontal, then it can be shown that the amount of additional "false torsion" produced by a translation of Listing's plane is the same for all gaze positions, that is, the eye "counterrolls" (or torts) the same amount. However, if Listing's plane is anything other than frontal, the amount of additional false torsion will depend on the direction of gaze. Thus the translation of Listing's plane allows the phenomenon of ocular torsion in response to roll tilt of the head to be generalized and described unambiguously for all directions of gaze.

While the response to roll of the subject could be predicted in terms of the known ocular counterrolling phenomenon, the response to pitch tilt, a "counterpitching" of Listing's plane, is less obvious. When subjects are pitched, say, nose up, the orientation of their Listing's plane *with respect to their (pitched) head* counterpitches slightly nose down, thereby reducing the change in orientation of Listing's plane with respect to gravity. Vertical movements of the eyes are largely unaffected by a pitch of Listing's plane. Instead, a downward pitch of Listing's plane means that, for example, leftward eye positions are associated with a larger clockwise torsion. A counterpitch of Listing's plane does correspond to a reorientation of Primary Position with respect to the head such that Primary Position remains more nearly earth-horizontal than the subject's head-fixed straight ahead. This reorientation of Primary Position toward earth-horizontal may represent an effort by the central nervous system to reorient the ocular motor system to gravity.

Signals from the otolith organs are known to influence eye movements primarily via the VOR. Such influences include the linear VOR and semicircular canal–otolith interaction. The data from this study suggest that static otolith signals also alter the spatial orientation of the ocular motor system. Specifically, when the head is pitched up or down, Primary Position, i.e. the direction that is perpendicular to Listing's plane, remains more nearly earth-horizontal than an individual's straight ahead does. Aging is known to influence both the angular (Baloh, Jacobson, & Socotch, 1993; Paige, 1992; Peterka et al., 1990) and linear (Furman & Redfern, 2001) VOR, and semicircular canal–otolith interaction (Furman & Redfern, 2001). The linear VOR and semicircular canal–otolith interaction are less effective physiologically with advanced age. This finding holds for both static and dynamic otolith influences on the angular VOR and probably results from age-related changes in the central rather than the peripheral vestibular system (Furman & Redfern, 2001), despite degeneration of utricular and saccular otoconia (Ross, Peacor, Johnsson, & Allard, 1976) and a reduction in hair cells and afferent fibers (Bergstrom, 1973; Engstrom, Ades, Engstrom, Gilchrist, & Bourne, 1977; Johnson & Hawkins, 1972; Richter, 1980; Rosenhall & Rubin, 1975). The data from the present study indicate that older individuals exhibit changes in the expression of Listing's law, i.e. a thicker Listing's plane. This effect of age was small but fairly consistent and suggests that Listing's law is not obeyed as rigidly in older subjects. What might be the causes of an increased thickness of Listing's plane in older individuals? The type of ocular motor task can alter the thickness of Listing's plane (Desouza et al., 1997) but our young and older subjects performed the same task. A possible biomechanical mechanism is increased flaccidity in the ocular motor plant of older subjects such that the same neural control signal leads to slightly different eye positions. Possible neural mechanisms include nonsystematic inaccuracies and decreased repeatability of torsional eye position as a result of age-related degradation in ocular motor pathways. The structures that have been shown to be important for the implementation of Listing's law include the nucleus reticularis tegmenti pontis (Van Opstal, Hepp, Suzuki, & Henn, 1996) and the cerebellum (Straumann, Zee, & Solomon, 2000). Some evidence exists for age-related loss of cerebellar Purkinje cells, which supports the idea that age-related changes in the cerebellum may cause an increase in the thickness of Listing's plane. Another structure that may be implicated is the rostral interstitial nucleus of the medial longitudinal fasciculus (Suzuki et al., 1995). This structure influences the location of Listing's plane, i.e. mean torsion. Thus, altered function in this structure could lead to variability in torsional eye position from one saccade to another and thereby increase the apparent thickness of Listing's plane. Yet another mechanism to consider is that of alertness, which has been shown to influence the thickness of Listing's plane wherein drowsiness is related to increased thickness (Suzuki, Kase, Kato, & Fukushima, 1997; Suzuki, Straumann, & Henn, 2000). Possibly, despite attempts to maintain alertness, our older subjects were less alert then our younger subjects. Another neural mechanism that may explain in part the increased thickness of Listing's plane in older subjects is a higher variability in vergence eye movements. Vergence angle is known to be associated with a yaw rotation of Listing's plane (Bruno & van den Berg, 1997; Kapoula, Bernotas, & Haslwanter, 1999; Mikhael, Nicolle, & Vilis, 1995; Minken & Van Gisbergen, 1994; Mok, Ro, Cadera, Crawford, & Vilis, 1992; Van Rijn & van den Berg, 1993). Thus, increased variability in vergence angle during the individual trials in older subjects might have resulted in an apparent increase in the thickness of Listing's plane. We simulated the effect of a large random vergence error by assuming that the point of fixation had a standard deviation of 10 cm (about a target distance of 44 cm). We found that this large vergence variability added only 0.2° to the thickness of the simulated Listing's plane. Thus increased variability in vergence is unlikely to account for the larger thickness of Listing's plane in the older population. Some portion of the thickness of Listing's plane in our data is possibly related to the slight variation in vergence required to fixate targets in our experimental setup, which used a flat screen. Simulation shows that under the most conservative assumptions (that Listing's plane will yaw 1° for every degree change of vergence when viewing targets mounted on a flat screen at a fixed target distance), this effect, which would be identical for both age groups, is small, less than half a degree.

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