Static Roll and Pitch in the Monkey: Shift and Rotation of Listing's Plane

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In three rhesus monkeys three-dimensional eye positions were measured with the dual search coil technique. Recordings of spontaneous eye movements were made in the light and in the dark, with the monkeys in different static roll or pitch positions. Eye positions were expressed as rotation vectors. In all static positions eye rotation vectors were confined to a plane, i.e. Listing's plane was conserved. Tilt about the roll axis shifted the plane along this axis, i.e. a constant torsional component was added to all eye positions. Tilt about the pitch axis changed the pitch angle of Listing's plane.

INTRODUCTION

The extraocular muscles are arranged in such a way that the eyes can turn about arbitrary axes. This can be shown easily by rotating a monkey about different head-fixed axes, which elicits compensatory eye movements with horizontal, vertical, and torsional components (vestibulo–ocular reflex). When the head is not moving, the torsional eye position component is determined by the direction of the line of sight, i.e. by the horizontal and vertical components (Donders, 1848). The quantitative relation between horizontal, vertical, and torsional eye position components for the head in the upright position has been given by Listing (Helmholtz, 1866), and is now commonly called *Listing's law*.

Ocular torsion was originally determined by measuring the orientation of afterimages. Later, photographic images of the iris or fundus were used. These historic developments have been reviewed by Simonsz (1985). The magnetic search coil technique introduced by Robinson (1963) allows the precise measurement of 3-dimensional eye movements in humans with high temporal and spatial resolution, and Listing's law was found to be approximately correct (Ferman, Collewijn & Van den Berg, 1987). This technique has also been successfully applied to monkeys (Tweed, Cadera & Vilis, 1990; Hess, 1990).

Confusion has been created by the fact that the numeric value of eye torsion in tertiary positions depends on the data representation chosen. In the Helmholtz- or Fick-representation, eye positions are described by three consecutive rotations. Since rotations are not commutative, tertiary eye positions have in these representations torsional components, which are specific for the system chosen and usually called *false torsion*. This problem is

eliminated by using the quaternion representation (Tweed & Vilis, 1987) or the almost equivalent rotation vector representation (Haustein, 1989; Hepp, 1990), which describe eye positions by a *single* fixed-axis rotation from a reference position to the current position. For our data analysis we use the rotation vector representation.

If the position of the body with respect to gravity is changed, the otolith–ocular reflex induces a change in eye position: e.g. static tilt about the naso–occipital axis (roll) leads to partly compensatory eye torsion. This effect has usually been studied in subjects instructed to look straight ahead, i.e. along the axis of body rotation, and has been called *ocular counterrolling* (Diamond, Markham, Simpson & Curthoys, 1979; Collewijn, Van der Steen, Ferman & Jansen, 1985). For small head tilts, the effects of different roll and pitch positions on Listing's plane have been investigated in humans by Straumann, van Opstal, Hess, Henn and Hepp (1989) with a similar approach as adopted here. In monkeys, Crawford and Vilis (1991) have reported a torsional shift of Listing's plane for the 90° right-ear-down and left-ear-down position, and a forward tilt of the plane for the monkey in a supine position.

In our experiments, we have examined the properties of Listing's plane for the monkey in the upright position, and then systematically analyzed the effects of different pitch and roll positions. Part of this work has been presented in abstract form (Haslwanter, Straumann, Henn & Hess, 1990).

METHODS

Experiments were performed on three juvenile rhesus monkeys (*Macaca mulatta*). In order to calibrate the eye position measurements, they were trained to fixate a light spot according to the paradigm of Wurtz (1969):

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whenever the monkey pressed a trigger-bar, a light spot with an angular extension of 0.3° appeared on a tangent screen. After 3–5 sec, the light spot was dimmed for 0.5 sec, and then turned off completely. If the monkey released the trigger-bar during the dimming period, it received a reward.

Surgery

Surgery was done under inhalative anesthesia with an O_2/N_2O mixture, initiated by i.p. administration of pentobarbital (35 mg/kg), and supplemented by halothane as necessary. Head bolts were implanted to restrain the head during experiments. A specially designed, calibrated dual search coil for 3-dimensional eye position measurements was then implanted around the cornea, under the conjunctiva, and anterior to all eye muscle insertions (Hess, 1990).

Experimental setup and paradigm

During the experiment the monkey sat in a primate-chair. Its head was restrained, with the horizontal stereotaxic plane tilted 15° nose down from the earth horizontal. The body was secured with shoulder- and lap-belts, and the extremities were loosely tied to the chair. The primate chair was put onto a turntable, with the head of the monkey at the center of rotations.

Two different 3-dimensional turntables were used: the first one was a wooden construction in which the monkey could be positioned manually. All but 2 experiments with monkey I were done with this setup (in the light only). All other experiments were done on a second turntable: its two inner frames were manufactured from carbonfiber enhanced epoxy resin, and all three axes were motor driven and position controlled, with a resolution better than 0.1° (constructed by Acutronic, Jona, Switzerland). This setup was surrounded by a sphere with a diameter of 1.7 m, which provided a structured visual surround consisting of black spots of different size on a white background.

During the experiment the monkey was put in 10–20° steps in different roll or pitch positions. In each position, spontaneous eye movements were recorded for 30–45 sec. The recordings were done in the light as well as in the dark. Unless explicitly stated otherwise, we refer in the following to experiments done in the light. In order to provide a visual input without reference to the earth vertical, the sphere was closed during most experiments.

If the experiments lasted longer than 1 hr the monkey received a small dose of amphetamine (2 mg, orally) to keep it alert.

Eye position measurement

Eye positions were measured with the 3-dimensional magnetic search coil technique. We recorded from either eye with an "Eye Position Meter 3000" (Skalar, Delft, The Netherlands), and digitized the data at a rate of 833 Hz. The data were written directly onto the computer hard disk and processed off-line.

Prior to implantation the sensitivity of the search coils and the angle between them were determined. The dual search coil, composed of two coils with approximately orthogonal orientation vectors, was mounted on a gimbal system in the center of the magnetic field. This field consisted of two components in phase and space quadrature. With a phase sensitive detector, the voltages induced in the search coils were recorded for different symmetric displacements of the assembly relative to the reference position. For the calculation of the relative orientation of the two search coils and their sensitivities we took offset voltages into consideration which are independent of the orientation of the coils in the external magnetic field.

At the start of each experimental session an in vivo calibration was made to determine voltage offsets, as well as the orientation of the dual search coil on the eye. The monkey had to fixate in sequence light points along a midsagittal line at different vertical positions at a distance of 0.85 m. From the voltages measured during these fixations, the orientation of the coil on the eye as well as voltage offsets were determined by a linear best fit procedure. The in vivo calibration relied on the following assumptions:

(i) the relative angular orientation of the search coils is not changed by the implantation;
(ii) the sensitivity of the measuring system does not change; and
(iii) the eye torsion is constant for fixation of the different vertical targets arranged along a vertical meridian straight ahead.

The pertinent equations as well as further details will be reported elsewhere (Hess et al., 1992).

The maximum absolute error of the eye position measurement was about 2° in secondary eye positions; the maximum relative error (i.e. the difference between two measurements with the eye in the same position) was about 0.2°.

Data representation and analysis

For our measurements the reference position was chosen as looking straight ahead. This corresponds to the line of sight being parallel to the intersection-line of the mid-sagittal plane and the horizontal plane, after the monkeys head has been tilted 15° nose down relative to the horizontal stereotaxic plane. It is the direction of the x-axis in Fig. 1.

Every eye position can then be described by a 3-dimensional vector: the direction of the vector is given by the direction of the axis of the rotation from the reference position [Fig. 1(A)] to the current eye position [Fig. 1(B)], and the length by $\tan(\alpha/2)$, with α the angle of the rotation. Using the coordinate system displayed in Fig. 1, x, y, and z components of such an eye rotation vector correspond to torsional, vertical, and horizontal eye positions, respectively. The positive directions for eye movements are, according to the right hand rule, extorsion of the right eye, down, and left.

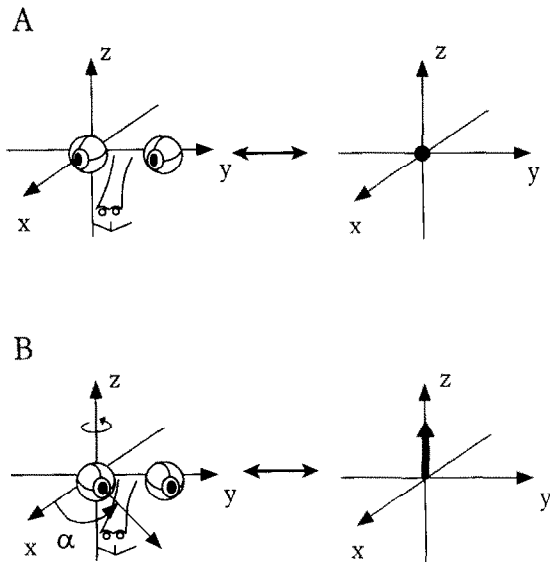## Eye Positions   Rotation Vectors

A

B

FIGURE 1. Every eye position is characterized by one rotation vector: (A) the reference position corresponds to the origin of the rotation–vector space (zero rotation vector). (B) Every other position corresponds to one rotation from the reference position to the current eye position. The direction of the respective rotation vector is given by the axis of this rotation, and its length by tan $(\alpha/2)$, with α the angle of the rotation.

The rotation matrices that characterize these rotations from the reference position to the current eye position can be derived as follows.

Let $\{f_i\}$ be the basis vectors of an eye-fixed orthonormal coordinate system, with the eye in the reference position. Such vectors can be calculated from the coil orientation vectors determined in the *in vivo* calibration. With $\{g_i\}$ being the corresponding vectors with the eye in the current position, the rotation matrix R that characterizes the rotation from the reference position to the current eye position is given by

$$R = G \cdot F^T$$

with $G_{ij} = (g_j)_i$, $F_{ij} = (f_j)_i$, and "·" the matrix product.

From the rotation matrix, the rotation vector can easily be calculated.

Listing's law (Helmholtz, 1866) states that when the head is upright and not moving, all eye positions can be described by rotation vectors that lie approximately in one plane (Haustein, 1989; Hepp, 1990).

Figure 2 shows the eye positions of a monkey in the upright position, while it made spontaneous eye movements in the light. The recording lasted 90 sec, and eye positions are expressed as rotation vectors.

The rotation vectors are approximately confined to a plane, which is indicated by a thin dashed line. This best-fit plane to the data points was determined for each trial. For data analysis we used the following parameters (Fig. 2):

Average eye torsion, this value is given by the intersection of the best-fit plane with the x-axis, which represents eye torsion.

Thickness, defined as the standard deviation of the data points from the plane. This parameter characterizes how well eye positions are confined to the plane, i.e. how well they obey Listing's law.

Orientation, the direction perpendicular to the plane of rotation vectors, indicated in Fig. 2(A) by a solid arrow.
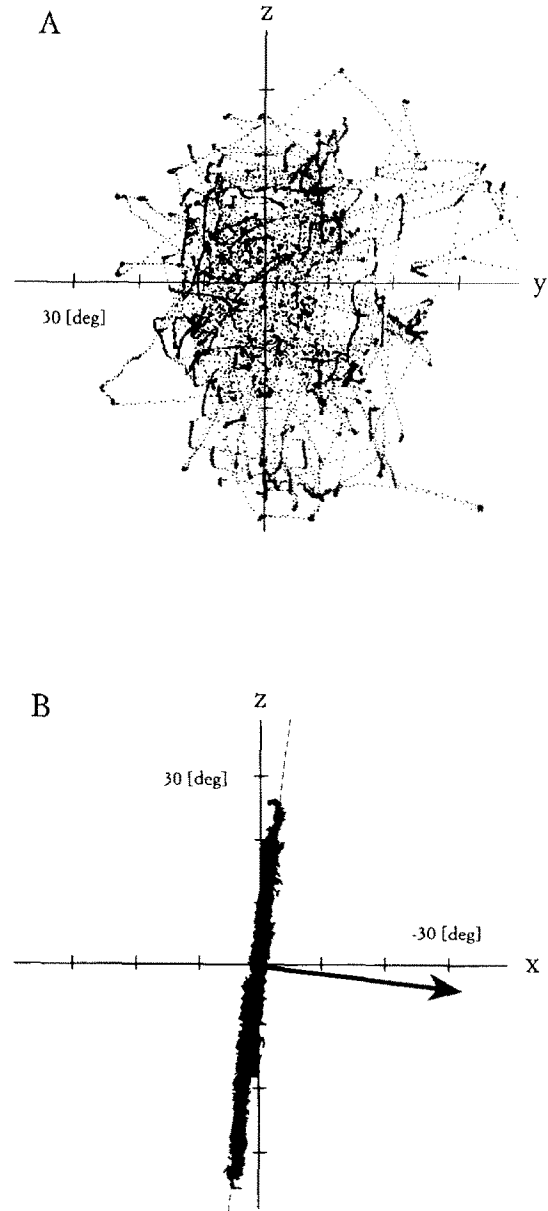
A

B

FIGURE 2. Rotation vectors of a recording of 90 sec of spontaneous eye movements in the light, while the monkey was in the upright position. (A) Frontal view of the eye rotation vectors, with the z-components plotted against the y-components. Points on the z-axis correspond to eye positions reached by a rotation from the reference position about the z-axis, i.e. horizontal eye positions, points on the y-axis correspond to vertical eye positions. (B) Side view of the same data, with the z-components vs the x-components (torsional eye positions). All rotation vectors are approximately confined to a plane, which is indicated by the thin, dashed line. The arrow shows the *orientation* of the plane. The SD of the data points from this plane is 0.6°.

Monkey	Forward tilt	Thickness	Directional deviation	# Trials
I	1.3 ± 0.8	0.6 ± 0.3	0.9 ± 0.4	7
II	6.8 ± 1.1	0.8 ± 0.1	1.3 ± 0.7	55
III	−9.0 ± 1.8	1.1 ± 0.2	2.7 ± 1.4	16

Forward tilt is the angle between the plane of rotation vectors and the *y–z*-plane of the coordinate system. *Thickness* gives the SD of rotation vectors from the linear best-fit plane. *Directional deviation* gives the average deviation from the mean orientation. # *Trials* gives the number of recordings used to determine the given values. Each recording was made on a different day; thus, the standard deviations for *Forward tilt* and *Thickness* reflect the day-to-day variations. All angular values are given in deg.

The properties of rotation vectors entail that a change of the reference position by 2α corresponds to a change of the orientation of the plane in the same direction, but of only α (Tweed *et al.*, 1990).

One *in vivo* calibration was made for each experimental day. All data presented in the following use the same reference position. Whenever the rotation vectors are aligned along a plane, a reference position can be found, which leads to a plane of rotation vectors aligned with the *y–z*-plane of our reference system. This reference position is called *primary position* (Tweed *et al.*, 1990; Haustein, 1989); the plane of rotation vectors is then commonly called *Listing's plane*.

RESULTS

Measurements in the Light

Listing's plane in the upright position

The *orientation* of the plane of rotation vectors with the monkey in the upright position was different for each monkey. Table 1 gives the values characterizing the orientation of this plane, as well as its day-to-day fluctuations, for each monkey. In monkey I the plane was approximately aligned with the *y–z*-plane of our coordinate system; in monkey II it was tilted about 7° forward [Fig. 2(B)], and in monkey III 9° backward. The orientation of the plane was approximately constant from day to day for each monkey.

The *average eye torsion* occasionally showed an unsystematic drift, reaching values of up to 1.7° over a period of a few hours. The *thickness* of the plane of monkey III (1.1°) was bigger than for monkey I or II. This was due to some transient eye torsion during saccades and blinks. Nevertheless, it was still smaller than the values reported for humans (Tweed & Vilis, 1990, 1.5°; Straumann, Haslwanter, Hepp & Hepp-Reymond, 1991, 1.3°).

Shift of Listing's plane in different roll positions

When a monkey was tilted about the *x*-axis (i.e. roll), ocular torsion increased or decreased for all eye positions, during saccades as well as during fixations. For looking straight ahead, this corresponded to the well known *ocular counterrolling*. Thus Listing's law held for

all static roll positions in the sense that eye rotation vectors were always closely aligned to a plane. However, different roll positions shifted this plane along the *x*-axis [Fig. 3(A)]. This shift was about proportional to the sine of the roll-angle [Fig. 3(B)].

The maximum negative and maximum positive ocular torsion of all three monkeys during a stepwise rotation about the roll-axis are summarized in Table 2. For the maxima, the largest measured values and the respective body roll angles were taken. Note that measurements were made in 10–20° steps.
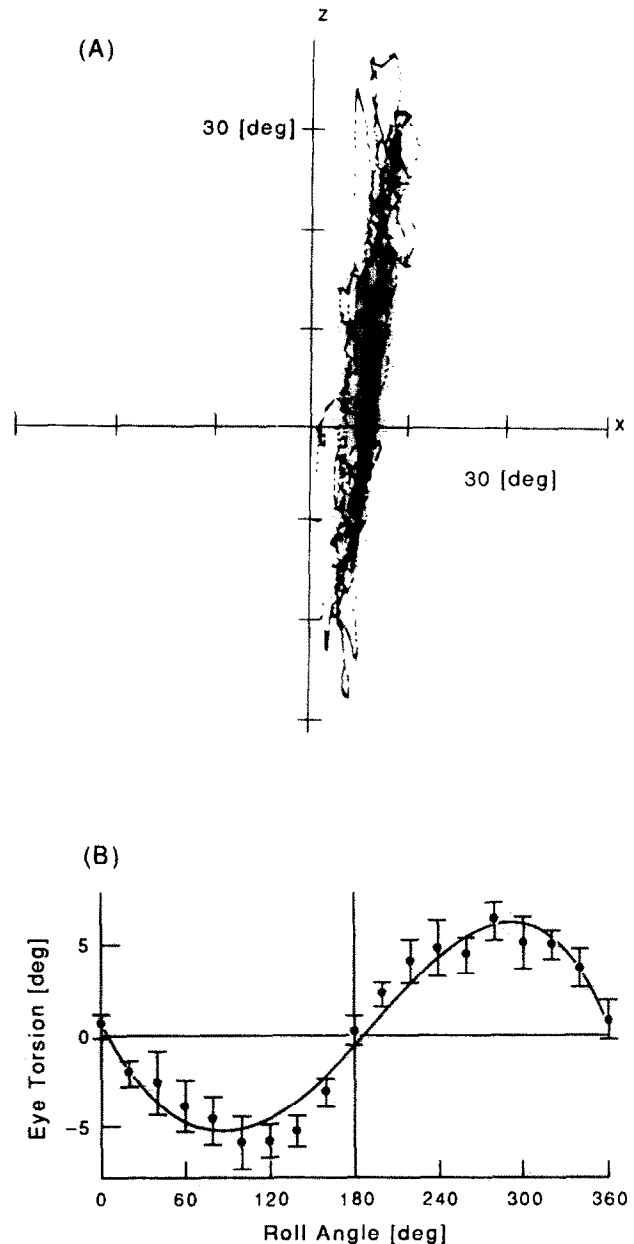

FIGURE 3. The shift of the plane of rotation vectors along the torsional axis is proportional to the sine of the roll angle. (A) Horizontal vs torsional eye positions during 90 sec of spontaneous eye movements in the light, with the monkey in a 60° left-ear-down position [corresponding to an angle of 300° in (B)]. The torsional shift of the plane of rotation vectors relative to Fig. 2(B), which shows the plane for the monkey upright, is 5.7°. (B) *Average eye torsion* as a function of the roll angle. The solid line represents the best fit sine curve to the data points. Error bars indicate ±1 SD of eye positions from an ideal plane.

TABLE 2. Maximum negative and positive eye torsion of the monkeys and the respective roll-angles

Monkey	Maximum negative eye torsion		Maximum positive eye torsion		# Trials
	Torsion (deg)	Roll angle (deg)	Torsion (deg)	Roll angle (deg)	
In the light					
I	-5.5 ± 1.2	79 ± 9	5.7 ± 1.3	297 ± 9	5
II	-7.7 ± 1.1	97 ± 9	6.3 ± 1.4	277 ± 5	7
III	-6.2 ± 1.2	86 ± 12	6.0 ± 1.2	273 ± 14	2
In the dark					
II	-9.3 ± 2.2	113 ± 12	9.1 ± 1.3	287 ± 23	3

The SDs show the size of the day-to-day fluctuations within 1 monkey.

Pooling the data for all three monkeys, we got an average maximum eye torsion of $6.4 \pm 1.2°$ (14 trials). The maxima and minima of ocular torsion varied for different monkeys. The standard deviations from the mean values reflect the daily variations for each monkey (Table 2). In all but 3 experiments maximum and minimum eye torsion had about the same absolute value, i.e. the curves were symmetrical for right- and left-ear-down positions. Occasionally monkey II showed a violation of this symmetry: the eye torsion in the 90° right-ear-down position exceeded the eye torsion in the 90° left-ear-down position by 2.5–3.0°. This is the cause for the asymmetry of the averaged values for monkey II in Table 2.

For the 90° right-ear-down or left-ear-down position the thickness of the plane increased to $1.5 \pm 0.2°$ (from 0.6–1.1° in the upright position). Possible curva-

tures of the plane as a function of pitch or roll were not systematically investigated. The error bars in Fig. 3(B) indicate ± 1 standard deviation of the eye positions from an ideal plane. When the monkey was not alert, the standard deviation was usually larger.

Besides the shift along the torsional axis, no other systematic changes of the plane of rotation vectors were induced by changes of the roll position in the light.

Change of orientation of Listing's plane in different pitch positions

Also during pitch eye rotation vectors were aligned along a plane. The pitch angle of this plane, indicated in Fig. 4(A), changed as a function of the body pitch angle: when the monkey was pitched backwards, the plane tilted forwards and vice versa.
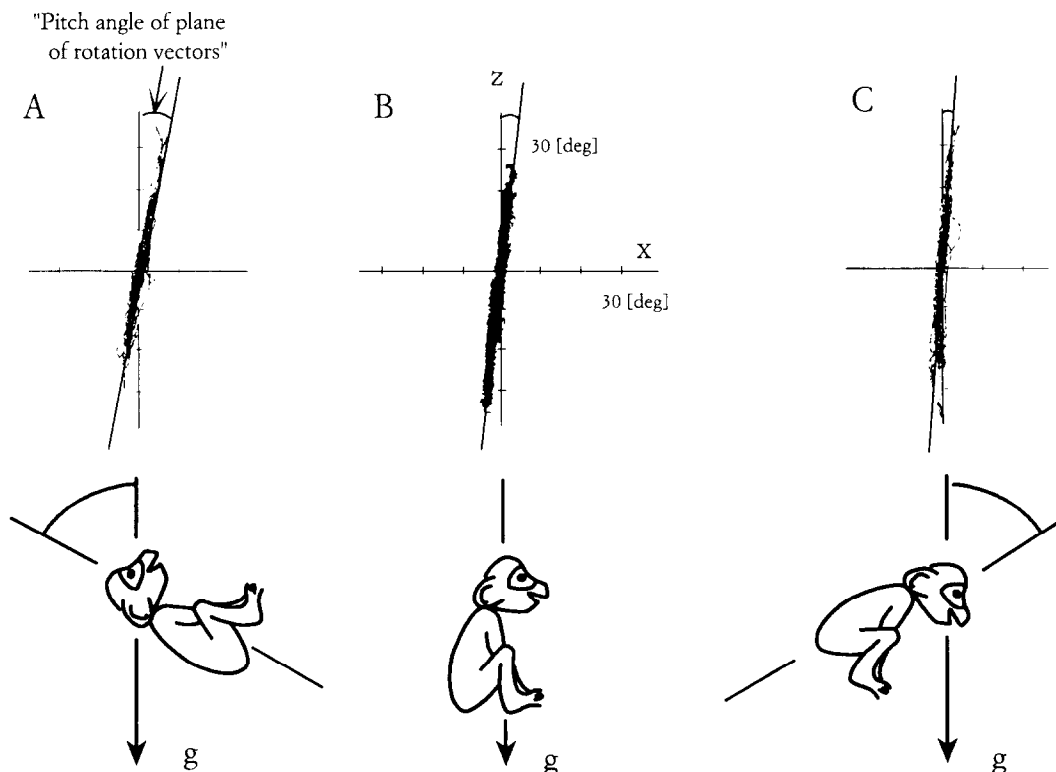

FIGURE 4. Horizontal vs torsional eye positions during spontaneous eye movements in the light, with the monkey (monkey II) (A) pitched 60° backward, (B) upright and (C) pitched 60° forward. The solid line through the data clouds in the upper row indicate the respective planes of rotation vectors. In the lower row, *g* (gravity) indicates the direction of the earth-vertical.
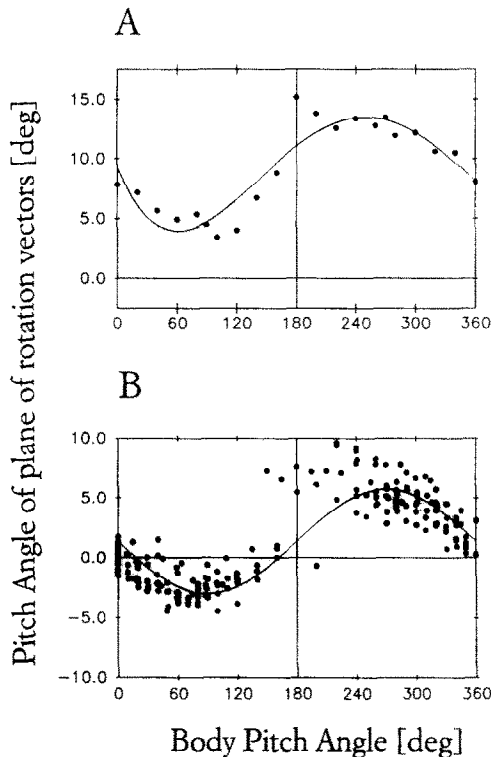
A

B

Body Pitch Angle [deg]

FIGURE 5. (A) The pitch angle of the plane of rotation vectors as a function of the body pitch angle in a typical experimental session, where the monkey was sequentially put in different pitch positions through a total of 360°. The pitch angle of the plane changes in a direction opposite to the body pitch angle. Positive body pitch corresponds to a tilt nose down. The solid line is the best fit sine wave through the data. (B) Pooled data from all pitch experiments in the light. In order to make the data comparable, the average pitch angle of the plane of rotation vectors with the monkey in the upright position was subtracted from the data of each run. Again, the solid line is the best fit sine wave through the data.

Figure 5(A) shows the modulation of the pitch angle of the plane of rotation vectors as a function of the body pitch angle.

To compare data from monkeys with a different orientation of the plane of rotation vectors, the average pitch angle of this plane with the monkey in the upright position was subtracted from the data of each run. Pooled data from all pitch experiments in the light are plotted in Fig. 5(B). The region around 180° body pitch angle contains fewer data points, since the first experimental setup allowed pitch experiments only up to

$\pm 120°$. In a Fourier analysis of these data, which took into consideration the first 3 terms (base frequency, 2nd and 3rd harmonic), the base frequency contributed about 94% to the total fit. Thus the modulation of the pitch angle of the plane of rotation vectors is in a first approximation sinusoidal.

Table 3 summarizes the body pitch angles at which the pitch angle of the plane of rotation vectors was smallest and largest, and the difference between these maxima and minima. Again, the largest measured values and the corresponding positions were used for the table.

For each monkey, the values were averaged over all trials, and the standard deviations reflect the size of the daily variations. The largest forward tilt of the primary position during pitch in the light occurred at $-85 \pm 23°$ [275° in Fig. 5(B); about supine] (9 trials in 3 monkeys), the largest backward tilt at $69 \pm 21°$ (about prone). The average change of the pitch angle of the plane of rotation vectors during a typical pitch-experiment (i.e. stepwise forward or backward rotation by 360°) was $11.0 \pm 2.5°$. It should be noted that a shift of the orientation of the plane corresponds to a shift of the primary position in the same direction, but by twice the angle.

Measurements in the Dark

Measurements in the dark were only made with monkeys II (roll and pitch) and III (pitch only). When roll or pitch angles exceeded $\pm 90°$, these monkeys showed spontaneous nystagmus in the torsional and sometimes also in the vertical direction, which led to planes of rotation vectors with a thickness of up to 2.7°. Spontaneous nystagmus was not observed in the upright position in the dark.

The maximum *average eye torsion* induced by roll in the dark (9.2°, 2 trials; Table 2) was clearly larger than in the light. In addition, the roll experiments in the dark indicated a sinusoidal modulation of the orientation of the plane: in the right-ear-down position, the orientation of the plane turned about 4.5° to the left, in the left-ear-down position 4.5° to the right (experiments with monkey II only).

During pitch in the dark, the monkeys showed qualitatively the same behavior as in the light; the change of the pitch angle of the plane was greater than in the light (about 17°, 2 experiments; Table 3).

TABLE 3. Body pitch angles at which the *pitch angle of the plane of rotation vectors* was smallest and largest, and the difference between the maximum and minimum pitch angles of this plane

| Monkey | Body pitch angle (deg) | | Difference between smallest and largest pitch angle of plane of rotation vectors (deg) | # Trials |
	At smallest pitch angle of plane of rotation vectors	At largest pitch angle of plane of rotation vectors		
In the light				
I	55 ± 6	272 ± 28	9.8 ± 1.6	4
II	75 ± 19	278 ± 26	12.3 ± 3.1	4
III	105	270	9.7	1
In the dark				
I	90	250	13.7	1
II	90	255	19.6	1

DISCUSSION

Our results show that Listing's law holds in a generalized sense not only for the upright position, but for all static body positions: the rotation vectors are always closely confined to a plane. Thus the degrees of freedom for eye movements are effectively reduced from 3 to 2. While the orientation of this plane of rotation vectors is fairly constant, its position with respect to the axis representing eye torsion could drift by 1–2° over a period of a few hours. This is in agreement with Collewijn, Ferman and Van den Berg (1988), who pointed out that the oculomotor system seems to minimize torsional movements on short time scales. More significant changes of position and orientation of this plane can be induced by changing the body position with respect to gravity.

Different roll positions change the average eye torsion in a systematic way. The same amount of ocular torsion is added to all eye positions, during saccades as well as during fixations. In terms of rotation vectors, this torsional offset is reflected in a shift of the plane of rotation vectors along the axis representing eye torsion. The shift is proportional to the sine of the roll angle, and may directly reflect a head-position dependent modulation of tonic otolith inputs (Fernandez & Goldberg, 1976). Our values of ocular torsion are in good agreement with those reported by other groups for gaze straight ahead (humans, about 6°, Diamond & Markham, 1983; humans and monkeys, 5–7°, Cohen, 1974).

The orientation of the plane of rotation vectors is a function of the head pitch angle, and shows further variation with each individual monkey. For the upright position, the plane of rotation vectors does in general not coincide with the y–z-plane of a stereotaxically defined coordinate system. The forward or backward tilt of the plane can reach up to 10° in the upright position. Thus the primary position can deviate substantially between different monkeys. These variations could be correlated to similar variations of the orientation of the horizontal semicircular canals (Blanks, Curthoys, Bennet & Markham, 1985).

While different roll positions leave the orientation unchanged, different pitch positions clearly modulate it. The change is opposite to the rotation of the body position: when the monkey is pitched nose down, the plane of rotation vectors tilts up and vice versa. Since a change of the orientation is equivalent to a change of the primary position in the same direction but by twice the angle, the effect of pitch can also be described as a change of the primary position in the direction opposite to the change of the body position. The modulation of the orientation is to a first approximation sinusoidal. This could be related to the sinusoidal modulation of the shear forces on the otolith maculae. The apparent discontinuity at the head down (180°) position in Fig. 5(A, B) could reflect an instability of the vestibulo–oculomotor system in this position. Such an instability could also be the cause for the appearance of spontaneous torsional and vertical nystagmus in the head-down position in the dark. For all static positions the pitch angle stays within a range of about ±6° around the value for the upright body position. This is in agreement with findings in humans (Straumann et al., 1989).

The pitch angle of the plane of rotation vectors has the following implications: if the plane is aligned with the y–z-plane of the coordinate system, as is approximately the case in Fig. 4(C), horizontal movements to and from the reference position have no torsional component; if the plane is tilted forward as in Fig. 4(A), looking from the reference position to the left is associated with a positive torsion, looking to the right with a negative one. This means that differently pitched planes lead to different eye torsion for horizontal eye positions.

Any rotation or shift of a plane of rotation vectors can be compensated for by a rotation of the reference system. The term "Listing's plane" is commonly restricted to the one reference system where the plane of rotation vectors coincides with the y–z-plane. In this case primary and reference position are identical. Given the differences of the orientation of this plane between individual monkeys, and the validity of Listing's law for all static body positions, we propose that the term "Listing's plane" should be generalized to denote every plane of rotation vectors.

As we have shown, tonic effects of otolith input onto spontaneous eye movements are rather small, and the plane of rotation vectors keeps its orientation roughly stable for different head orientations in space. This could facilitate synergies during combined eye-head movements (Straumann et al., 1991). The modulation of primary position as a function of body pitch angle, as well as the torsional shift of the plane of rotation vectors in different roll positions, can be used to quantify static otolith ocular reflexes for all head positions relative to gravity.

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