RESEARCH ARTICLE

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Eye-position dependence of three-dimensional ocular rotation-axis orientation during head impulses in humans

Abstract If horizontal saccades or smooth-pursuit eye movements are made with the line-of-sight at different elevations, the three-dimensional (3D) angular rotation axis of the globe tilts by half the vertical eye eccentricity. This phenomenon is named "half-angle rule" and is a consequence of Listing's law. It was recently found that the ocular rotation axis during the horizontal vestibulo-ocular reflex (VOR) on a turntable also tilts in the direction of the line-of-sight by about a quarter of the eye's vertical eccentricity. This is surprising, since, in a "perfect" VOR, the angular rotation axis of the eye should be independent from the position of the eye to fully compensate for the 3D angular head rotation. We asked whether this quarter-angle strategy is a general property of the VOR or whether the 3D kinematics of ocular movements evoked by vestibular stimulation would be less eye-position dependent at higher stimulus frequencies. Nine healthy subjects were exposed to horizontal head impulses (peak velocity ~250°/s). The line-of-sight was systematically changed along the vertical meridian of a tangent screen. Three-dimensional eye and head movements were monitored with dual search coils. The 3D orientation of the angular eye-in-head rotation axis was determined by calculating the average angular velocity vectors of the initial 10° displacements. Then, the difference between the tilt angles of the ocular rotation axis during upward and downward viewing was determined and divided by the difference of vertical eccentricity ("tilt angle coefficient"). Control experiments included horizontal saccades, smooth-pursuit eye movements, and eye movements evoked by slow, passive head rotations at the same vertical eye eccentricities. On average, the ocular rotation axis during horizontal head-impulse testing at different elevations of the line-of-sight was closely aligned with the rotation axis of the head (tilt angle coefficient of pooled abducting and adducting eye movements: 0.11±0.17 SD). Values for slow head impulses, however, exceeded somewhat the quarter angle (0.33±0.12), while smooth-pursuit movements (0.50±0.09) and saccades (0.44±0.11) were closest to the half angle. These results demonstrate that the 3D orientation of the ocular rotation axis during rapid head thrusts is relatively independent of the direction of the line-of-sight and that ocular rotations elicited by head impulses are kinematically different from saccades, despite similar movement dynamics.

Keywords Eye movements · Listing's law · Vestibulo-ocular reflex · Dual search coils · Rotation vectors

Introduction

If the direction of the line-of-sight is moved from one fixation to another, there are, in theory, unlimited ways how the axis about which the eye rotates can be oriented in three-dimensional space. In reality, however, the three-dimensional orientation of the ocular *rotation axis*[1] follows a specific strategy, depending on the class of the eye movement that the ocular motor system performs to redirect the line-of-sight: for instance, during a horizontal saccade, the axis about which the eye rotates is not in a head-fixed frontal plane, but tilts as a function of vertical eye eccentricity. The tilt of the axis amounts to about half of this vertical angle (Tweed and Vilis 1990). In contrast, during horizontal slow phases of vestibular nystagmus at different vertical elevations, the rotation axis remains closer aligned to the rotation axis of the head (Crawford and Vilis 1991; Misslisch et al. 1994).

How much the ocular rotation axis tilts in the direction of the line-of-sight directly relates to the question of whether an eye movement passes through eye positions that conform to Listing's law (Tweed and Vilis 1987;

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[1] The term "rotation axis" denotes the instantaneous axis about which a body rotates with a given velocity. This axis is parallel to the angular velocity vector.

Straumann et al. 1996). By definition, Listing's eye positions can be reached from a reference position by rotations about axes, which all lie in a plane (Helmholtz 1867). This can best be visualized by describing eye positions as rotation vectors (Haustein 1989) or quaternion vectors (Westheimer 1957; Tweed and Vilis 1987), since such vectors also lie in a plane, if eye-position trajectories obey Listing's law. Due to the non-commutativity of rotations, the rotation axis used to move the eye from one Listing's position to another tilts out of Listing's plane, unless the trajectory follows a radial line that passes through the reference position (Tweed and Vilis 1987). If a trajectory is orthogonal to this radial line, the ocular rotation axis tilts out of Listing's plane by exactly half the angle of the eye's eccentricity. This geometrical fact is known as the "half-angle rule".

Data from many laboratories have shown that, in normal human subjects and rhesus monkeys, saccades and smooth-pursuit eye movements start and end in eye positions that approximately obey Listing's law (Ferman et al. 1987; Tweed and Vilis 1990; Haslwanter et al. 1991; Straumann et al. 1991; Tweed et al. 1992). Thus, the average ocular rotation axis of orthogonal movements tilts by half the angle of the eye's eccentricity. Note, however, that there are small, but consistent deviations from Listing's law during and shortly after movements (Straumann et al. 1995, 1996; Bruno and Van den Berg 1997).

Recently, Misslisch et al. (1994) reported that, in humans, a 30° vertical change in eye position during yaw head rotation caused a 7.5° tilt of the eye rotation axis in the vertical direction of the line-of-sight; the same was observed when the line-of-sight changed horizontally during pitch vestibular stimulation. Hence, the vestibulo-ocular reflex (VOR) seems to have an eye-position dependence of the ocular rotation axis, similar to saccadic and pursuit eye movements. The tilt angle, however, is only a quarter of the eye's eccentricity (so-called "quarter-angle rule"). This is surprising, since a kinematically perfect VOR must have an ocular rotation axis which is always parallel to the axis of vestibular stimulation, irrespective of eye position, to prevent retinal slip of the visual world (Crawford and Vilis 1991).

We asked whether the eye-position dependence of the ocular rotation axis during vestibular stimulation decreases as the frequency of the head movement increases. In our hypothesis, we assumed that, during high-frequency vestibular stimulation, there would not be sufficient time for a feedback of eye position to modify the three-dimensional orientation of the ocular rotation axis and, hence, this axis would, independent of the eye's eccentricity, closely align with the rotation axis of the head. During low-frequency vestibular stimulation, however, the VOR would have enough time for feedback of eye position, e.g., via the cerebellum, to implement an eye-position-dependent behavior of the ocular rotation axis, according to the quarter- or even half-angle rule.

To test this hypothesis, we applied the Halmagyi-Curthoys head impulse maneuver to normal human subjects (Halmagyi and Curthoys 1988). This test allows rapid rotations of the head with peak accelerations of up to $20\,000°/s^2$, during which head and eye movements can be monitored with dual search coils (Aw et al. 1996). We specifically examined by how much the ocular rotation axis tilts as a function of the vertical elevation of the line-of-sight during horizontal head impulses. The kinematics of this high-frequency vestibulo-ocular reflex were compared to those of other classes of eye movements with similar (saccades) or slower dynamics (smooth-pursuit eye movements, slow vestibulo-ocular reflex).

Preliminary data of this study were presented in abstract form at the Key West meeting of the Society for the Neural Control of Movement in April 1998.

Materials and methods

Subjects

Nine healthy human subjects (seven female, two male, age 23–32 years) participated in the study. After being informed about the experimental procedure, all subjects gave their written consent. The protocol was approved by a local ethical committee and was in accordance with the ethical standards laid down in 1964 Declaration of Helsinki.

Recording setup

Head and eye rotations were simultaneously measured in three dimensions with the dual search coil technique (Robinson 1963; Collewijn et al. 1985). One annulus was mounted on the right eye (after anesthetizing the conjunctiva with 0.4% Oxybuprocaine), the other was tightly fixed on the forehead with adhesive tape. We used commercial annuli manufactured by Skalar, Delft, The Netherlands. During experiments, subjects sat inside an aluminum, cubic coil frame (side length: 1.4 m), by which three orthogonal magnetic fields with frequencies of 42.6, 55.5, 83.3 kHz were produced; synchronous detection of amplitude-modulated signals yielded instantaneous voltages induced by the three magnetic fields (modification of the Remmel system by A. Lasker). With a bandwidth filter of 0–90 Hz, peak-to-peak noise was 0.2° in the torsional and 0.1° in the horizontal and vertical directions. Signals were digitized at a frequency of 1000 Hz with 16-bit resolution and stored on a computer hard-disk for off-line processing.

Calibration

Details of the calibration procedure are given elsewhere (Straumann et al. 1995). In short, dual search coils were calibrated in vitro before each experiment: voltage offsets were nulled after placing the annuli in a metal tube, which shields the coils from the magnetic fields (method introduced by D. Roberts). On a gimbal system, the relative gains of the three magnetic fields were determined. No further calibration was necessary during experiments, except for a short fixation of the reference position "straight-ahead" at the beginning of each paradigm.

From raw signals and calibration values, we computed rotation vectors, which describe three-dimensional eye positions as single rotations from the reference position. A rotation vector r is oriented parallel to the axis about which the eye has to rotate from the reference (zero) position to the current position. The length of r is given by $\tan(\rho/2)$, where ρ is the amount of rotation about the axis. The orthogonal coordinate system is defined by the right-hand rule with the x-axis pointing forward, the y-axis leftward, and the z-axis upward. Thus, clockwise, downward, and leftward movements, as seen by the subject, are positive.

Experimental protocol

After placing dual search-coil annuli on the right eye and the forehead, the subject was seated with the head in the center of the magnetic coil frame. An experimenter standing behind the subject firmly held the subject's head with his hands. To exclude skin artifacts onto the head coil, special care was taken that the experimenter's hands did not touch the subject's forehead. In a pilot study, we specifically checked that there were no signal differences between fixing the head coil on the forehead or a bitebar.

At the beginning of each paradigm, the subject was asked to fix a light in the center of a tangent screen (screen distance: 1.2 m) to collect the raw signals with the eye in the reference position. An experimental session consisted of four paradigms, which were all performed with the lights switched on.

VOR fast

Horizontal fast vestibulo-ocular reflex in the light = head impulse. With the subject fixing the light in the center of the screen, the experimenter quickly rotated the subject's head from the reference position (natural upright position) to the right or left (amplitude: 15–25°; duration: 150–200 ms; peak velocity: ~250°/s; peak acceleration ~10 000°/s^2). In a pseudo-random order, five head rotations were applied to each side. The procedure was repeated with the subject fixing a light on the vertical meridian at elevations of 15° and –15°. Special care was taken that no head pitch occurred when the subject looked at the upper or lower target; off-line, this could be checked by plotting the vertical head signal. The "VOR fast"-paradigm was repeated twice in each subject.

VOR slow

Horizontal slow vestibulo-ocular reflex in the light = slow passive head movement. This paradigm was analogous to the "VOR fast"-paradigm, except that the experimenter moved the head much slower, with an average velocity of about 10–20°/s.

Purs

Horizontal smooth-pursuit eye movement. With the head held still in the reference position by the experimenter, the subject was asked to follow the light, which moved with 20°/s in a horizontal centrifugal direction. Eye movements to both sides were elicited three times. The procedure was repeated with the light moving horizontally at elevations of 15° and –15°. Again, there was no pitch movement of the head when the subject changed the vertical eccentricity of the eyes.

Sacc

Horizontal saccade. This paradigm was analogous to the "Purs"-paradigm, expect that the target jumped from the center position to 15° in the horizontal direction at the different elevations of the eye.

Data analysis

Rotation vectors of eye-in-frame (*g*) and head-in-frame (*h*) were further processed on a PC using interactive programs written in MATLAB, version 5.2. First, eye-in-head rotation vectors (*e*) were computed using the formula[2]:

$$e=(-h+g-h\times g)/(1+h\times g)$$

Eye-in-head rotation vectors were then smoothed with a Gaussian filter (17 data points from center to 2% of full height). Trials with

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[2] '×' denotes the cross product.

movements to the same side and at identical eye-in-head elevations were aligned according to the onsets of centrifugal displacements.

From eye-in-head rotation vectors (*e*) and their derivative (d*e*), we computed angular eye-in-head velocity vectors (ω) applying:

$$\omega=2(de+e\times de)/(1+|e^2|)$$

Angular eye-velocity vectors are oriented parallel to the instantaneous ocular rotation axis; their lengths denote the velocity of rotation in rad/s. For convenience of the reader, values were converted to °/s. Note that, due to the non-commutativity of rotations, an angular velocity vector is not simply the derivative of a rotation vector. The final steps of analysis will be described in the Results section.

Results

Figure 1 depicts examples of horizontal eye movements to the right at 15° upward and 15° downward ocular eccentricities in one subject (subject z161). Angular velocity vectors (ω) are shown in the side projection, as seen from the right, i.e., the ω_x-component is plotted against the ω_z-component. This type of plot illustrates the orientation of the ocular rotation axis in the sagittal plane during each movement. Trajectories are shown from the beginning of the movement to the moment of maximal eye velocity. (Recall that, according to the right-hand rule, leftward, downward, and clockwise movements are positive.)

The left panel (Fig. 1A) shows trajectories during two saccades to the right. At 15° upward eye eccentricity, the trajectory is tilted backward, while at 15° downward eye eccentricity, the trajectory is almost vertical. Hence, the orientation of the ocular rotation axis in the sagittal plane depends on the vertical direction of the line-of-sight in the sense that the ocular rotation axis is pitched in the direction of the vertical eye position. In contrast, two horizontal eye-in-head movements to the right elicited by horizontal head impulses to the left with the eyes looking 15° upward or downward do not show a clear difference in pitch orientation (Fig. 1B). Note that the two head-in-space trajectories (dashed lines), which are both directed
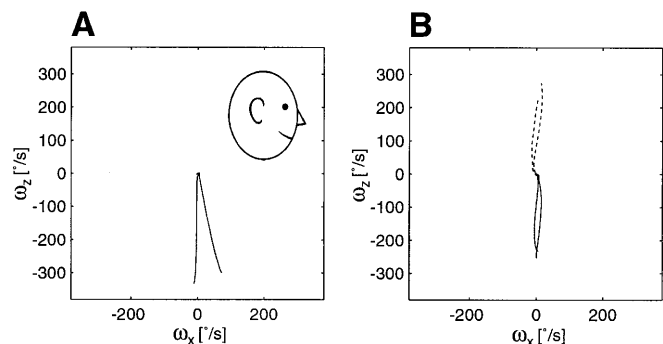

Fig. 1A, B Example (subject z161) of fast, horizontal eye movements to the right at 15°-upward and 15°-downward vertical ocular eccentricities. Side projection of angular velocity vectors (ω). Trajectories are clipped at the moment of peak eye velocity. Signs of directions according to the right-hand rule. **A** Saccades. **B** Eye-in-head (*solid lines*) and head-in-space (*dashed lines*) movements during head impulses
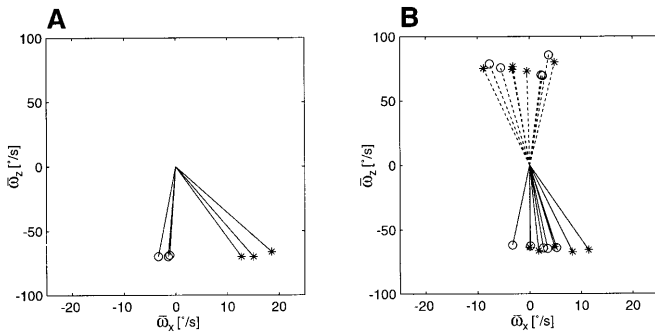
Fig. 2A, B Example (subject z161) of *repetitive*, fast, horizontal eye movements at different vertical eye eccentricities. Side projection of *average angular-velocity vectors* of the first 10° of the movements (ω̄). Vector endpoints indicate the 15°-upward (*asterisks*) or 15°-downward (*circles*) vertical eccentricity during the movement. **A** Saccades. **B** Eye-in-head (*solid lines*) and head-in-space (*dashed lines*) movements during head impulses

Fig. 3 Same data as in Fig. 2B. The torsional component of average angular-velocity vectors of eye-in-head (Eye ω̄) and head-in-space (Head ω̄$_x$) movements during horizontal head impulses are plotted against each other. Vertical eye eccentricity was 15° upward (*asterisks*) or 15° downward (*circles*). First-order linear regression: "Eye ω̄$_x$"=2.5–0.63·"Head ω̄$_x$"; *r*=0.71; *P*=0.019

to the left, closely overlay. Clearly, the trajectories of eye movements evoked by horizontal head impulses are less straight than of saccades. This is a result of the trajectories of the head impulses, which show curvature into the torsional direction, especially at the beginning of the impulse. Probably neck mechanics do not allow a purely horizontal rotation of the head.

Figure 2 summarizes the kinematics of repetitive saccades and head-impulse-evoked eye movements to the right in one subject (subject z161). Each line denotes the average angular-velocity vector ω̄ during the first 10° of every horizontal displacement. Symbols indicate whether the horizontal eye movement took place at 15°-upward (asterisks) or 15°-downward (circles) eccentricity of the line of sight. As in the previous figure, the data are shown in the side projection, but here, for better visualization, the range of the scale of the ω̄$_x$ component is four times smaller than the scale of the ω̄$_z$ component.

During horizontal saccades (Fig. 2A), the three average angular velocity vectors with the subject looking 15° downward are clearly segregated from the three average angular-velocity vectors with the subject looking 15° upward. During horizontal head impulses (Fig. 2B), however, the average angular velocity vectors of horizontal eye-in-head movements (solid lines) with the line-of-sight directed 15° upward (*n*=5) or 15° downward (*n*=5) overlapped. There is a small tendency that the vectors are pitched more backward during 15° upward than during 15° downward ocular eccentricity. The average angular velocity vectors of the head-in-space (dashed lines) showed a similar directional variations as the eye, but they overlapped even more.

To quantitatively check whether the directional variation of eye-in-head trajectories is due to the variation of head-in-space trajectories, we plotted the torsional components of eye and head vectors against each other. As an example, Fig. 3 shows the scatterplot with the data taken from Fig. 2B. Clearly, there is a linear correlation between the torsional average angular velocity vector components of the head and the eye (*r*=0.71), which was
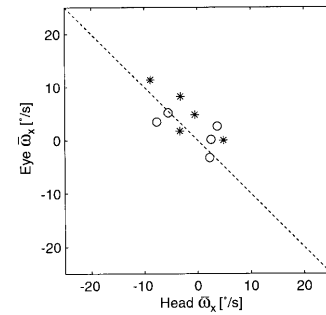
significant (*P*=0.019). This was the case in all tested subjects (*P*<0.05). Hence, the variation of the torsional eye-in-head movement component was largely due to the variation of the torsional head-in-space movement component via the VOR.

Besides saccadic ("Sacc") and head-impulse ("VOR fast") stimuli, experiments also included manually induced, slow vestibular stimuli ("VOR slow") in the light and slow-smooth pursuit movements ("Purs"). The latter two paradigms served, together with the saccadic paradigm, as controls to the head-impulse paradigm. While the saccadic paradigm elicited eye movements with similar dynamics as the head-impulses paradigm, the other two paradigms were only similar to the head impulses in terms of starting position and amplitude of movement. Peak eye velocities of all 15° saccades ("Sacc") of the nine subjects ranged from 164 to 306°/s. In comparison, the pooled peak eye-in-head velocities during head impulses ("VOR fast") ranged from 75 to 336°/s. Horizontal smooth pursuit movements ("Purs") showed peak velocities between 8 and 25°/s, while eye-in-head peak velocities during slow passive head movements were between 5 and 30°/s. All four paradigms were repeated several times at identical vertical ocular eccentricities (see Methods).

Figure 4 summarizes all trials of each of the four paradigms in one subject's right eye (again, subject z161). Here, we computed the axis tilt angle, α, of each average angular-velocity vector (ω̄) in the sagittal plane:

$$\alpha = \text{atan}(\bar{\omega}_x / \bar{\omega}_z)$$

Dashed lines connect median values of data points in downward and upward eccentricity of the eye. The smallest change as a result of vertical eye position can be seen for the head impulses ("VOR fast"), the largest changes for the smooth pursuit ("Purs") and saccadic ("Sacc") eye movements. Slow passive head rotations ("VOR slow") lead to changes of the axis tilt angle in-between. As expected, smooth-pursuit movements and saccades closely obey the half-angle rule and, therefore, Listing's law, i.e., the difference of the axis tilt angle is
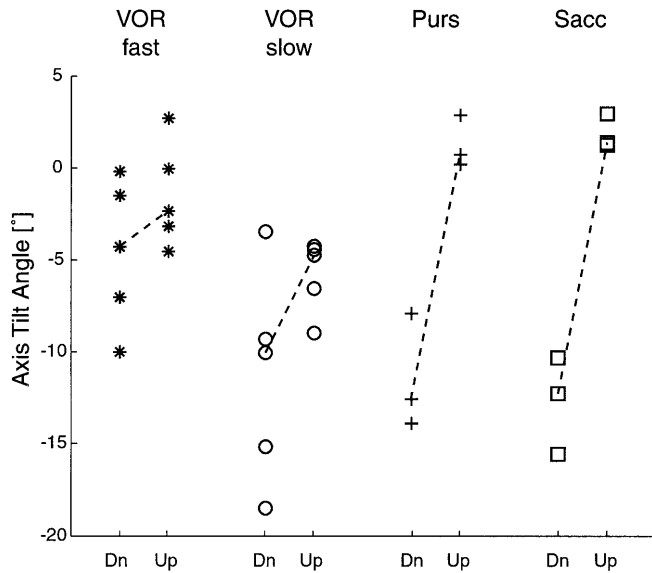
Fig. 4 Data from the same subject as in Figs. 1, 2, 3 (subject z161). Axis tilt angles (definition in the text) of leftward eye-in-head movements during head impulses (*VOR fast*), slow head movements (*VOR slow*), smooth pursuit movements (*Purs*), and saccades (*Sacc*)

close to 15° for a vertical eye eccentricity difference of 30° (15° down, 15° up).

In order to quantify the exact amount of eye-position dependence on vertical eye eccentricity for horizontal eye movements, the difference between the tilt angles of the ocular axis in upward and downward eye eccentricity was divided by the difference of the elevation of the line-of-sight, which yields the *tilt-angle coefficient*. Since each paradigm was repeated several times, we took the median tilt-angle coefficient for each block of trials. Table 1 contains the median tilt angle coefficients of all subjects (always right eye) for horizontal movements to both sides in the four paradigms. Since the block of five head impulses was repeated twice, the column "VOR fast" includes two values for each subject. In the table, we intentionally did not pool adduction and abduction movements, since horizontal symmetry of eye-position dependence cannot be expected a priori. Each data column is statistically summarized by its median, mean, and standard deviation.

Horizontal smooth-pursuit and saccadic eye movements to both sides showed tilt-angle coefficients close to the half angle (range of means: 0.41–0.53) with standard deviations around one tenth of the full angle. Tilt-angle coefficients of horizontal eye-in-head movements evoked by head impulses, however, were much smaller (means to the left: 0.08, to the right: 0.14) with standard deviations being about 50% larger than for saccades and pursuit movements. Horizontal eye movements evoked by slow passive head rotations in the light had tilt-angle coefficients and standard deviations that were in-between those of head-impulse-induced movements and pursuit or saccades, respectively.

Since the standard deviations were relatively large, we performed *t* tests to examine whether the differences of means were significant ($P<0.05$): for eye movements to the left, "VOR fast" was different from "VOR slow" ($P<0.05$), "Purs" ($P<0.01$) and "Sacc" ($P<0.01$). Also, "VOR slow" was different from "Purs" ($P<0.05$) and "Sacc" ($P<0.05$). As expected, "Purs" was not signifi-

Table 1 Summary table of all nine subjects. Tilt-angle coefficients (definition in the text) of leftward and rightward eye-in-head movements during head impulses (*VOR fast*), slow head movements (*VOR slow*), smooth pursuit movements (*Purs*), and saccades (*Sacc*)

Eye movement to the left					Eye movement to the right				
Subject	VOR fast	VOR slow	Purs	Sacc	Subject	VOR fast	VOR slow	Purs	Sacc
z118	0.09	0.25	0.50	0.41	z118	−0.10	0.16	0.57	0.41
	0.04					0.21			
z150	0.19	0.41	0.54	0.55	z150	0.27	0.35	0.54	0.35
	0.24					−0.04			
z151	0.13	0.59	0.55	0.59	z151	0.12	0.30	0.54	0.46
	−0.17					0.09			
z153	0.13	0.33	0.46	0.37	z153	0.22	0.31	0.36	0.22
	0.07					−0.16			
z154	−0.25	0.43	0.60	0.58	z154	0.32	0.34	0.43	0.57
	−0.12					0.28			
z156	0.42	0.24	0.59	0.38	z156	0.27	0.00	0.57	0.50
	0.32					0.13			
z159	−0.01	0.48	0.51	0.48	z159	0.15	0.32	0.45	0.39
	0.12					−0.10			
z161	0.07	0.41	0.64	0.49	z161	0.11	0.18	0.44	0.46
	0.20					0.11			
z165	−0.13	0.37	0.42	0.32	z165	0.09	0.40	0.29	0.30
	0.05					0.46			
Median	0.08	0.41	0.54	0.48	Median	0.13	0.31	0.45	0.41
Mean	0.08	0.39	0.53	0.46	Mean	0.14	0.26	0.47	0.41
SD	0.17	0.11	0.07	0.10	SD	0.16	0.13	0.10	0.11

cantly different from "Sacc'" For eye movements to the right, the same pattern and levels of significance were found, except that "VOR slow" was not significantly different from "Sacc" (*P*>0.05).

Discussion

In nine healthy human subjects, we recorded three-dimensional eye movements during the horizontal head-impulse test (Halmagyi and Curthoys 1988), but the direction of the line-of-sight was systematically changed in the vertical direction. We found that, on average, the orientation of the eye's rotation axis tilted in the vertical direction of the line-of-sight by only about one tenth of the change of the eye's elevation. In contrast, horizontal saccades with similar dynamics and similar eye-in-head trajectories showed a tilt in the vertical direction of the line-of-sight by near to half the elevation angle, as expected from Listing's law. The orientation of the ocular rotation axis during horizontal pursuit movements was similar as during horizontal saccades. During slow, horizontal passive head movements in the light, however, the vertical tilt of the ocular rotation axis was about one third of the eye's elevation change.

There are some experimental limitations of our study, which have to be taken into account for the interpretation of the data:

1. The "horizontal" head impulses, which we applied, were not perfectly horizontal; especially during the initial phase of the head-in-space movement, there was a considerable torsional component present (Fig. 1). This initial torsional deviation is probably a result of biomechanics (neck of the subject, hand/arm movements of the experimenter) and cannot be averted. Preferably, the head should be moved by a mechanical device that allows restriction of the movements to the horizontal plane. For safety reasons, however, this cannot be done with such high accelerations.
2. Our setup did not allow measurement of eye movements in total darkness. This is most likely not important for the eye movements evoked by head impulses, but it might have influenced the kinematics of eye movements evoked by slow head movements, such that they were enhanced by the smooth pursuit system, and, hence, the ocular rotation axis tilted more as a function of vertical eye position.
3. Eye movements evoked by head impulses scattered considerably in terms of acceleration and amplitude because it was not possible to produce series of identical vestibular stimuli by hand. This was the reason why we chose to investigate the orientation of the ocular rotation axis for the initial 10° displacement, during which the evoked eye movements were consistent enough to be statistically analyzed. Typically, this period was close to the moment of maximal head velocity. Since the deceleration phase of the head impulse

was much more variable, corresponding eye movements were not consistent enough to determine their kinematical properties.

The rather small eye-position dependence of the ocular rotation axis during head impulses, which we found in this study, is in contrast to the findings of Misslisch et al. (1994). These authors reported that, during horizontal oscillations on a turntable with 0.3 Hz and 20° amplitude, the eyes of normal human subjects tilted in the direction of the line-of-sight by about a quarter of the eye's vertical eccentricity. Clearly, accelerations applied to the labyrinths during head-impulse testing, as used in our study, are much higher (peak accelerations: ~10'000°/s²) than during the turntable oscillations (peak velocities: ~70°/s²), which were used in the study by Misslisch et al. Hence, it appears that the kinematics of the vestibulo-ocular reflex depends on the dynamics of the stimulus.

A "perfect" vestibulo-ocular reflex should not modify the orientation of the ocular rotation axis as a function of eye position, since only an ocular rotation axis that aligns with the rotation axis of the head minimizes the slippage of the visual world on the retina (Crawford and Vilis 1991). It seems that, indeed, the three-dimensional kinematics of the vestibulo-reflex is close to "perfect" during high accelerations. The question whether a further increase of vestibular stimulus frequency would lead to an additional decrease of eye-position dependence cannot yet be answered. It is conceivable, however, that this small, remaining eye-position effect of about one tenth of the gaze angle simply reflects mechanical properties of the eye plant.

Despite similar dynamics, eye movements elicited by head impulses and eye movements during saccades show kinematical properties that differ fundamentally: while the 3D orientation of the ocular rotation axis during rapid head thrusts is relatively independent of the direction of the line-of-sight, the ocular rotation axis during saccades tilts in the direction of gaze, according to the "half-angle rule" (Tweed and Vilis 1990]. This striking kinematical difference cannot be explained by the mechanical properties of the eye plant and, hence, must be a result of central ocular motor control.

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