Canal-Otolith Interactions After Off-Vertical Axis Rotations
I. Spatial Reorientation of Horizontal Vestibuloocular Reflex

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INTRODUCTION

During off-vertical axis rotation the vestibular system detects head velocity and position from semicircular canal and otolith afferent signals. Whereas the semicircular canal afferents encode endolymph velocity relative to the skull (i.e., relative to a head-fixed reference) the otolith organs provide information about absolute head position relative to gravity (i.e., relative to a space-fixed reference). To determine head motion and orientation in space, there must be considerable central processing of these signals based on an internal representation of the outer physical space.

Earlier studies of the vestibuloocular reflex (VOR) during off-vertical axis rotations have shown that a vertical eye velocity component was generated when a subject was stopped in ear-down position after a constant velocity rotation about the yaw axis (cat: Harris 1987; humans: Harris and Barnes 1987; monkey: Raphan et al. 1992). Thus it appeared that postrotatory eye velocity did not decay along the former rotation axis but rather tended to align with gravity. Although it has become clear that this spatial re-orientation of the VOR is mediated via the velocity storage network in the brain stem, the underlying computational mechanisms are still a matter of debate. In a recent study on the spatial orientation of the optokinetic nystagmus (OKN) in primates, it has been shown that in the horizontal but not vertical system there is a similar alignment of the optokinetic afterresponse with gravity (Dai et al. 1991; Raphan and Sturm 1991). A reorientation of eye velocity toward gravity can also be found during postrotatory VOR when applying quick changes in head (and body) orientation relative to gravity (Angelaki and Hess 1994; Merfeld et al. 1993). In contrast to OKN findings, this reorientation occurred independently of the head rotation axis (before tilting the head) and the particular tilt plane (Angelaki and Hess 1994). Analyzing the spatial characteristics of the yaw or pitch/roll VOR suggested a rotation or projection of postrotatory eye velocity toward the spatial vertical following the head tilt. It is not known whether the same mechanisms underlie the reorientation of postrotatory VOR in static tilt positions. Off-vertical axis rotation (OVAR) is the vestibular analogue of visual surround rotation about a tilted stationary observer. Because during OVAR the observer is rotated relative to gravity, the postrotatory response results from a complex interaction of otolith and semicircular canal signals. In this paper, we determine the relative contribution of the otolith and canal signals after yaw OVAR by extending an empirical analysis of the VOR spatial characteristics with a parametric analysis based on a three-dimensional (3-D) spatial orientation model. In the companion papers, we shall present the results of a corresponding analysis applied on data collected after pitch and roll OVAR. Preliminary results have been published in abstract form (Jaggi-Schwarz et al. 1999).

METHODS

Preparation of animals

Experiments were performed on three juvenile rhesus monkeys (Macaca mulatta; monkeys JU, SU, and RO). The animals were chronically prepared for 3-D eye movement recordings. Using sterile surgical techniques, skull bolts for head restraint and a dual search coil were implanted under intubation anesthesia with O2-N2O supplemented with halothane if required to maintain a constant level of anesthesia (Hess 1990). Animals were trained to fixate small target lights for fluid reward. All procedures were in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals, and the protocol was approved by the Veterinary Office of the Canton of Zürich.

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Measurement of 3-D eye position and calibration

3-D eye positions were measured with the magnetic search coil technique using an Eye Position Meter 3000 (Skalar, Delft, The Netherlands). A horizontal and vertical magnetic field (20 kHz; phase and space quadrature) was generated by coils mounted on a cubic frame of 0.3 m side length.

The output of the dual search coil corresponded to the horizontal and vertical angular orientation of two sensitivity vectors: one pointing roughly in the direction of the visual axis and the other about perpendicular to that. The four voltage output signals of the search coil, as well as the head position and velocity signals, were sampled at a rate of 833 Hz (Cambridge Electronics Device 1401 Plus) and stored on the hard disk of a PC for off-line analysis.

3-D eye position was calibrated as described in detail elsewhere (Hess et al. 1992). Briefly, in an in vitro procedure, the magnitude of the two coil sensitivity vectors as well as the angle between them was computed. In an in vivo procedure performed on each experimental day, the monkeys repeatedly fixated three light-emitting diodes placed at straight ahead, 20° up and 20° down. The measured voltages were used in combination with the coil parameters determined in vitro to compute the orientation of the search coil on the eye and offset voltages. Eye positions were expressed as rotation vectors

$$E = \tan(\alpha/2)n$$

where $n$ is the axis of eye rotation from reference position to the current position, and $\alpha$ is the angle of rotation (Haustein 1989). The direction of $n$ is specified by the right-hand rule. The eye angular velocity vector $\Omega$ was computed as (Hepp 1990)

$$\Omega = 2(dE/dr + E \times dE/dt)/(1 + |E|^2)$$

Eye position and eye velocity vectors were expressed relative to a right-handed, orthogonal, head-fixed coordinate system that was defined by the direction of the two magnetic fields relative to the animal in the standard 15° nose-down position (see Experimental setup and protocol). Hereby, the direction of the horizontal magnetic fields determined the direction of the $y$-axis pointing along the interaural head axis; the direction of the vertical field was inclined backward by 15° relative to the stereotaxic horizontal plane, and the $x$-axis was determined as the direction perpendicular to the $y$- and $z$-axis. Thus $E_x, E_y,$ and $E_z (\Omega_x, \Omega_y,$ and $\Omega_z$) represent the torsional, vertical, and horizontal component of eye position (velocity). Positive directions of the coordinate axes represent clockwise, downward, and leftward components (as seen from the subject’s point of view) of eye position and velocity.

Experimental setup and protocol

The monkeys were seated in a primate chair and secured with shoulder and lap belts. The head was restrained in a 15° nose-down position such that the lateral semicircular canals were approximately earth-horizontal when the monkey was upright. The primate chair was placed inside a vestibular rotator with three motor-driven axes (Acutronic, Bubikon, Switzerland). The accuracy of the position control on each axis was <0.1°. The rotator was surrounded by a light-proof sphere of 0.8 m radius to guarantee complete darkness.

Animals were pitched 24° nose-up (JU and SU; see Fig. 1A) or 90° nose-up (supine; JU, SU, and RO; see Fig. 1B) and rotated around the tilted $z$-axis with a constant velocity of ±60°/s (left- or rightward) for 10 cycles (initial acceleration 180°/s²). In the following we refer to these two paradigms as “24° yaw OVAR” and “90° yaw OVAR.” Then they were stopped with decelerations of 180°/s² to reach any of
12 predefined end positions in space-fixed coordinates, equally spaced at 30° intervals: 30°, 60°, . . . , 360° (positive, i.e., leftward yaw OVAR) or −330°, −300°, . . . , 0° (negative, i.e., rightward yaw OVAR).

For data analysis and for representation of results, we describe the orientation of the gravity vector in a head-fixed coordinate system as follows. The rightward rotation of the head by −240° (Fig. 1C) relative to space is equivalent to a rotation of the gravity vector in the opposite direction by +240° relative to the head, corresponding to a final orientation of the gravity vector of 60° (Fig. 1D).

Data analysis

To compute the velocity vector dE/dt, the three eye position components were digitally differentiated with a quadratic polynomial filter using a 15-point forward and backward window (Press et al. 1992; Savitzky and Golay 1964). This filter has a cutoff frequency with respect to smoothing of 29.3 Hz. Eye angular velocity (\(\Omega\)) was computed using Eq. 2. To compute slow phase eye velocity, fast phases of vestibular nystagmus were removed based on time and amplitude windows, set for the magnitude of the second derivative of eye velocity (jerk).

In a first approach, the spatial orientation of postrotatory slow phase eye velocity was evaluated in several steps. First, the orthogonal response component \(\Omega_{\text{orth}}\) i.e., the vectorial sum of the torsional and vertical eye velocity, was computed. The magnitude of this component reflected the deviation of postrotatory eye velocity from the principal response direction (i.e., from a velocity vector parallel to the vertical eye velocity, was computed. The magnitude of this component reflected the deviation of postrotatory eye velocity from the principal response direction (i.e., from a velocity vector parallel to the z-axis). Second, the sum of two exponentials was fitted (in the least-squares sense) to the time course of each of the three components of eye velocity as well as to the orthogonal component, starting at cessation of chair rotation (see Figs. 3 and 4)

\[
R(t) = c_1 \cdot \exp(-t/T_1) + c_2 \cdot \exp(-t/T_2)
\]

Third, the peak of the exponential function fitted to the orthogonal component was determined (see arrows in Fig. 3). Fourth, a line was fitted to the exponential functions in the yaw (xy-), pitch (xz-), and roll (yz-) planes as well as in a plane spanned by the orthogonal component and the z-axis (resultant plane) starting from the peak to the end where the respective eye velocity component had declined to zero or to a nonzero constant value. The slope of these fitted lines described the tilt of the eye velocity vector in the respective planes as illustrated in the 3-D head-fixed coordinate system of Fig. 2. The orthogonal postrotatory VOR response lies in the yaw plane, which is tilted 24 or 90° relative to earth-horizontal for all final body orientations. The angle \(\varphi\) between the positive x-axis and the fitted line in the yaw plane described the tilt of the orthogonal response component as a function of head orientation relative to gravity (see Figs. 5, 7, and 9). Furthermore, the angle \(\theta\) between the positive (negative) z-axis and the fitted line in the resultant plane described the tilt away from the principal response direction toward alignment with gravity (see Figs. 6, 7, and 9). We defined the sign of the angle \(\theta\) as positive when the orthogonal response was parallel and as negative when it was antiparallel to gravity.

In a second approach, we fitted the postrotatory responses with an analytic function that was derived from an explicit model of the inertial transformation of vestibular signals (Fig. 10). In this 3-D spatial orientation model we assumed that the postrotatory response following off-vertical axis rotation resulted from linear superposition of three signals: 1) a direct input from the lateral semicircular canal (\(\omega_{\text{oto}}\), combined right-left lateral semicircular canal input), 2) an otolith-dependent head velocity signal (\(\omega_{\text{oto}}\)), and 3) a spatially transformed (inertial) head velocity signal (\(\omega_{\text{inertial}}\)). Accordingly we fitted the equation

\[
\omega_{\text{VOR}} = \omega_{\text{oto}} + \omega_{\text{oto}} + k_6 \omega_{\text{inertial}}
\]

to the postrotatory responses. Here, the parameter \(k_6\) described the weighted ratio of the direct and the spatially transformed semicircular canal signal at the motor output site. Each of the three terms on the right-hand side of this equation can be formulated as an analytic function involving a few physiological constants. For example, we used a semicircular canal signal (\(\omega_{\text{oto}}\)) as predicted from the Steinhausen model (Steinhausen 1933) with time constants fixed at 0.003 and 5 s (see Eq. A4 with reciprocal time constants \(v_{\text{oto}} = 1/0.003\) s and \(v_{\text{oto}} = 1/5\) s). The otolith-dependent head velocity signal (\(\omega_{\text{oto}}\)) was modeled as a single exponential function with amplitude \(v_{\text{oto}}\) and time constant \(T_{\text{oto}}\) (see Eq. A7). The amplitude of this signal was the steady-state amplitude of the horizontal response before rotation stop. Finally, an inertial head velocity signal (\(\omega_{\text{inertial}}\)) was computed by spatially transforming and low-pass filtering the lateral semicircular canal signal with a time constant \(T_{\text{inertial}}\) (see \(T_{\text{inertial}} = 1/v_{\text{oto}}\)).

The dependence on head orientation relative to gravity was described by a linear transformation of gravity in head coordinates using the angles \(\varphi\) and \(\theta\) (see Fig. 2). The model was used to estimate the following six physiological parameters by the method of least-square fit of the postrotatory responses: the weighting factor \(k_6\), the centrally estimated angles \(\varphi\) and \(\theta\) of the head orientation relative to gravity, the time constants \(T_{\text{oto}}\) and \(T_{\text{inertial}}\) of the low-pass filtered inertial and otolith-born velocity signals, and the response amplitude of the semicircular canal input at stop of head rotation (\(v_{\text{ino}}\)). In the fit procedure, we also took into account a possible small offset in horizontal eye velocity at the end of the postrotatory response phase (see, for example, the offset in horizontal eye velocity at the end of the record in Fig. 3 and \(v_{\text{ino}}\) in Tables 1 and 2). For a complete derivation of Eq. A4 as a function of these parameters, see Appendix.

RESULTS

Rotating a monkey around its earth-horizontal longitudinal axis (“barbecue-spit rotation”) elicits 3-D vestibuloocular reflexes consisting of a steady-state horizontal nystagmus and a head position−dependent modulation of eye position and velocity (Angelaki and Hess 1996a; Hess and Dieringer 1991). This response pattern perseveres as long as the stimulus lasts. Figure 3 shows an example of perrotatory VOR responses during the last two cycles of yaw rotation at −60°/s and the
following postrotatory responses after the stop of rotation. Superimposed on the horizontal, vertical, and torsional eye velocity vectors (gray curves on top, middle, and bottom panel) are the exponential functions fitted to each velocity component (solid lines; see Eq. 3 in METHODS).

In this example, the monkey was stopped in a final body orientation of $-240^\circ$ in the space-fixed coordinate system (see Fig. 1C). This corresponded to a rotation of the gravity vector through $240^\circ$ from an initial position at $180^\circ$ to a final position at $60^\circ$ in the head-fixed coordinate system, as illustrated by the head caricature (see also Fig. 1D). The time indicated by the vertical dashed line in Fig. 3 represents the midpoint of the deceleration period (with peak deceleration of $180^\circ/s^2$). The postrotatory response consisted of a prominent negative horizontal (rightward) slow phase eye velocity which decayed very slowly, whereas a positive vertical velocity (downward) built up to reach a large peak value from which it declined gradually; similarly a torsional positive eye velocity (clockwise) built up, followed by a slow decay to zero. The observation that horizontal eye velocity sometimes decayed to nonzero offset values was found in all animals and for both OVAR conditions (rotations around 90 or 24° tilted axes). This behavior did not systematically depend on the direction of yaw rotation or the static end position.

If the postrotatory response died off along the original stimulation axis, then one would expect to observe only a horizontal eye velocity component. The relatively large vertical and the smaller torsional velocity components reflect a reorientation of the eye rotation axis toward alignment with gravity: initially, just after the stop of rotation, the eye rotation axis is closely aligned with the (former) rotation axis, i.e., parallel to the earth-horizontal body longitudinal axis. In head coordinates, this corresponds to an ocular rotation around the z-axis and a horizontal (rightward) eye velocity component. Over a time course of a few seconds after rotation stop, the eye’s rotation axis reorients toward alignment with space-vertical. This corresponds to an ocular rotation around an axis in the yaw plane parallel to gravity, i.e., an axis with a large y-, a smaller x-component, and a vanishing z-component.

The effect of the reorientation mechanism on the spatial orientation of the VOR response can be better understood when plotting the projections of the different response components of eye angular velocity onto the respective (pitch, roll, and yaw) planes, Figure 4 shows the projections of the data starting from the midpoint of deceleration (gray curves), the exponential functions fitted to the data (solid lines), and the lines fitted to these exponential functions (dashed lines) beginning at the peak of the orthogonal response (arrows in Fig. 3). Arrowheads plotted along the exponential function give the direction of buildup and subsequent decay of the fitted postrotatory response. Figure 4A displays torsional velocity plotted versus horizontal velocity in the pitch plane. Stop of rotation after horizontal rightward OVAR elicited a postrotatory rightward horizontal eye velocity (i.e., negative horizontal velocity along the abscissa). While this horizontal velocity component decreased, a torsional component built up. After the torsional component reached its peak value, both horizontal or torsional velocities declined approximately along a straight line to small residual values or zero.

A similar pattern can be seen when plotting the vertical component of eye velocity against the horizontal component (in the roll plane, Fig. 4B): while horizontal velocity decreased, an increasing vertical velocity component was generated, reaching a peak and then declining to zero. The ratio between the (larger) vertical and (smaller) torsional eye velocity buildup reflects the orientation of the orthogonal response component in the yaw plane (Fig. 4C). This orientation can be determined by the angle $\varphi$ between the line fitted to the declining part of the postrotatory response in the yaw plane and the positive x-axis (see METHODS).
3 sets of parameters that were either fitted (marked with *) or directly measured (unmarked) from the afterresponse: (1) otolith-dependent parameters: $z_0 \otimes$, amplitude; $T^*_\text{oto}$, low-pass filter time constant ($f_j$ in Fig. 10) characterizing the otolith-born head velocity ($v_0^\otimes$); (2) semicircular canal–dependent parameters: $v_0^\text{SCC}$, amplitude of lateral semicircular canal signal (time constant fixed at 5 s); $w_0$, offset velocity component; $T^*_\text{sc}$, low-pass filter time constant in canal pathway ($f_j$ in Fig. 10); and (3) spatial orientation parameters: $\varphi^*_m$ and $\theta^*_m$ specifying the transformation $R_m$. In addition, a weight factor $k^*_{\theta}$ was fitted that determines the ratio between the direct and the inertially transformed semicircular canal signal in the final common pathway. Data from animal $JU$. OVAR, off-vertical axis rotation; SCC, semicircular canal.

Finally, the orientation of eye velocity in the resultant plane (Fig. 4D) was determined by computing the angle $\theta$ between the $z$-axis and the fitted line in the resultant plane (see methods).

Spatial orientation of the orthogonal response component after rotation about a 90° tilted yaw axis

Postrotatory VOR responses showed precise reorientation toward earth-vertical in two animals ($JU$ and $SU$) and were somewhat more variable in one animal ($RO$). This is illustrated in Fig. 5, which shows the tilt angle $\varphi$ of the orthogonal eye velocity (see methods) plotted versus the orientation of gravity in the yawn plane for all final body orientations. On the right side, individual values for each monkey are displayed for both rotation directions (solid line: $+60°$/s leftward OVAR; dashed line: $-60°$/s rightward OVAR). The left graph shows tilt angles averaged across all three subjects as well as over positive and negative rotations, with vertical bars denoting one standard deviation. Final body orientations of 90°, 0°, $-90°$, and $\pm 180°$ correspond to left ear-down, prone, right ear-down, and supine positions.

If the orthogonal component of the postrotatory VOR response would perfectly align with gravity, then the tilt angle should be equal to the tilt of the gravity vector relative to the head for each body orientation. This is precisely the pattern seen in the data. For example, when the gravity vector tilted 90° left ear-down, then the tilt angle averaged to $-90°$. The close correlation between the tilt angle $\varphi$ and the direction of the gravity vector was quantified by computing the linear regression, for individual subjects (not shown) and averaged data (dotted line, left graph). The $r^2$ value for the averaged data was 0.993.

Spatial orientation of the resultant response after rotation about a 90° tilted yaw axis

Figure 6 shows the tilt angles ($\theta$) of the eye velocity vector in the resultant plane as a function of the orientation of gravity in the yawn plane. The individual $\theta$ angles plotted in Fig. 6A reveal that after positive yaw rotations (filled symbols representing the 3 animals) the horizontal component of the postrotatory eye velocity vector predominantly rotates away from the...
The spatial orientation of postrotatory slow phase eye velocity was also determined by fitting the measured response with an analytic function derived from the 3-D spatial orientation model (see METHODS and APPENDIX for details). Examples of VOR responses fitted with this model (solid lines) are plotted on top of the data (gray curves) in Fig. 8. The diagrams show the same data as in Figs. 3 and 4, in the same views as in Fig. 4, A–C. Clearly, the model fits the data well and deviates only little from the exponential function fitting predictions (cf. Fig. 4); while horizontal velocity decreases, torsional and particularly vertical velocity increases until they direction of the gravity vector, i.e., toward the zenith (negative values, see METHODS). When the animal is rotated in the negative yaw direction, the postrotatory response rotates mainly toward the direction of the gravity vector (positive values). This pattern was consistently observed in one animal and predominantly in the other two animals. If the horizontal component would rotate exactly into the orthogonal plane, we would expect a tilt angle of ±90°.

Figure 6B displays absolute tilt angles as a function of final body orientation, averaged over all animals and both rotational directions (mean ± SD). The data cluster around an overall mean tilt angle θ of 68.6° (dotted line).

### Spatial orientation of orthogonal and resultant eye velocity after rotation about a 24° tilted yaw axis

To examine whether the reorientation pattern seen after the barbecue-spit yaw rotations also holds for less extreme cases, we studied the orientation of postrotatory eye velocity in two monkeys after yaw rotations about an axis that was tilted by only 24° from earth-vertical (0.4 G). The orientation of the orthogonal and resultant responses, quantified by the tilt angles ϕ and θ, are depicted for one animal (JU) in Fig. 7. As can be seen in Fig. 7A, there is a very good correlation between the orientation of declining postrotatory eye velocity in the yaw plane and the orientation of the gravity vector with respect to the head. The regression line (⋯) yielded a mean $R^2 = 0.995$ (positive direction: $R^2 = 0.982$; negative direction: $R^2 = 0.992$). Similar to the findings for barbecue spit rotations, the principal component of eye velocity after negative or positive yaw rotations turns in the direction of or opposite to the direction of gravity (data not shown), yielding an average absolute θ (all final body positions, both directions) of 16.7° (⋯, Fig. 7B), thus undershooting the spatial vertical by ∼29%.

Identical analysis for the second animal (SU, not shown) yielded correlation coefficients $r^2$ of 0.898, 0.728, and 0.850 (positive/negative yaw rotation and averages) and an average absolute θ of 29.6°, thus overshooting the spatial vertical on average by ∼25%.

### Fitting orthogonal and resultant postrotatory yaw VOR responses using the spatial orientation model

The spatial orientation of postrotatory slow phase eye velocity was also determined by fitting the measured response with an analytic function derived from the 3-D spatial orientation model (see METHODS and APPENDIX for details). Examples of VOR responses fitted with this model (solid lines) are plotted on top of the data (gray curves) in Fig. 8. The diagrams show the same data as in Figs. 3 and 4, in the same views as in Fig. 4, A–C. Clearly, the model fits the data well and deviates only little from the exponential function fitting predictions (cf. Fig. 4); while horizontal velocity decreases, torsional and particularly vertical velocity increases until they...
reach some peak value and then decline to zero or some small residual value.

Figure 9 summarizes the performance of the spatial orientation model for this animal and for all final head positions and compares the model predictions with the empirically determined results. The model predicts an accurate reorientation of orthogonal velocity toward earth-vertical (Fig. 9A) along with head orientation invariant reorientation of the resultant response by 73.1° (Fig. 9B). Tables 1 (data from 90° yaw OVAR) and 2 (data from 24° yaw OVAR) compare the tilt angles predicted from fitting the same responses with the analytic model predictions and empirically with the double exponential functions. Clearly, the estimated tilt angles $w$ show a closer correspondence between the two methods of analysis than the tilt angle $q$ (see Fig. 9, A and B; compare $\varphi_m$ with $\varphi_e$ and $\theta_m$ with $\theta_e$ in Tables 1 and 2).

Estimation of the tilt angle $q$ is more difficult because it is a nonlinear function of both the magnitude of the horizontal and orthogonal afterresponse. Because the orthogonal component is the vectorial sum of the torsional and vertical components, it could be biased by a downbeat velocity component that amounted to $\sim 2.5-5^\circ/s$ or less in our animals. In the model fits we accounted for this vertical velocity bias whenever it could be clearly identified.

The 3-D spatial orientation model provides supplementary information on the time constants of the low-pass filters in the semicircular canal and otolith pathways of the inertial system ($f_1$ and $f_2$ in Fig. 10). As a consequence of the model structure,
the time constant of the inertial network \((T_{\text{stor}})\) was not related to the degree of spatial alignment of the inertial response (for further details about the model structure, see DISCUSSION). However, there was a correlation between the length of the otolith and the inertial filter time constants: the shorter the otolith filter time constant \((T_{\text{oto}})\), the shorter the inertial filter time constant \((T_{\text{stor}})\). Moreover, the two time constants tended to be equal in magnitude, although this was not true when the otolith time constant exhibited only little variation (see Table 1, negative rotation). Finally, the time constants of both the otolith and the inertial filters tended to be shorter for rotations about a 90° tilted axis (barbecue-spit) than for rotation about a 24° tilted axis.

**DISCUSSION**

This work studies the interaction of otolith and lateral semicircular canal signals in postrotatory VOR responses when varying final head position. We find a remarkably precise alignment of the head tilt plane and the plane in which postrotatory eye velocity reorients toward the spatial vertical. The ratio between the tilt of the eye velocity vector and head tilt is more variable. Whereas most of the lateral canal signal is used to cancel the otolith-driven bias velocity, only a relatively small fraction of the canal signal that underwent transformation from a head-centered into a gravity-centered reference frame contributes to the total response. In the following paragraphs we discuss these results in the light of a parametric dynamic model of vestibular processing.

**Comparison with previous studies**

A number of recent investigations have shown that the vestibular system codes head velocity in the VOR in space-(gravity-)centered rather than in head-centered coordinates (Angelaki and Hess 1994; Dai et al. 1991; Gizzi et al. 1994; Merfeld et al. 1993; Raphan and Sturm 1991). The difference in coding most clearly emerges when the originally coinciding reference frames dissociate. When rotational motion cues from the semicircular canals fade away during prolonged rotation, the otolith organs continue to signal position and, except for pure earth-vertical axis rotations, velocity of the head-in-space motion (Angelaki and Hess 1996a,b; Darlot and Denise 1988; Denise et al. 1988; Guedry 1965; Harris 1987; Haslwanter and Hess 1993; Hess and Dieringer 1990; Raphan et al. 1981; Young and Henn 1975). Postrotatory VOR after off-vertical axis rotations results from a complex interaction of otolith and semicircular canal signals, each of which functions in different reference frames. It is not a priori clear which reference will prevail in the combined afterresponse. Our findings agree with...
previous studies that have demonstrated that the rotation axis of the afterresponse following a prolonged constant-velocity rotation shifts toward alignment with gravity when the subjects are stopped in ear-down positions (cat: Harris 1987; humans: Harris and Barnes 1987; monkey: Raphan et al. 1992). The present study differs from these investigations, however, by applying a 3-D analysis of postrotatory VOR responses to reveal the underlying computations involved in 3-D spatial reorientation.

Empirical description of spatial reorientation of postrotatory yaw VOR

In our study we applied two methodological approaches to estimate the spatial orientation of postrotatory eye velocity after a constant-velocity rotation. In a first, more descriptive approach, we fitted the sum of two exponentials separately to the horizontal, vertical, and torsional response components as well as to the algebraically determined component orthogonal to the principal (i.e., horizontal) response component. This orthogonal component, i.e., the vectorial sum of the torsional and vertical response component, was by definition located in the yaw plane. Together with the principal response component, it defined the resultant plane, in which postrotatory eye velocity rotated toward the spatial vertical. In all our animals the orientation of this plane was close to parallel to the actual tilt plane, independent of the amount of tilt (Figs. 5 and 7A). This finding proves two important points: 1) rotation of postrotatory eye velocity occurs about a single space-fixed axis, and 2) this axis is always orthogonal to the tilt plane. The internal coding of this plane presumably depends on lateral canal signals that code the axis of head rotation and utricular otolith signals that detect the direction of the projected gravity vector in the utricular plane. The combination of both signals unequivocally determines the orientation of the tilt plane.

The observation of an orthogonal response component that varies with the projection of gravity into the yaw (utricular) plane indicates that the postrotatory velocity vector always rotates toward the spatial vertical. This rotation could be downward, i.e., such that the response vector and gravity end up as parallel vectors (i.e., pointing in the same direction), a pattern usually found after stop of a negative head rotation (solid symbols with negative \( q \) values in Fig. 6A). Alternatively, the response could also rotate upward, i.e., such that the response vector and gravity end up as antiparallel vectors (i.e., pointing in opposite directions), a pattern generally seen after stop of a positive head rotation (see open symbols with positive \( q \) values in Fig. 6A). Whereas the spatial reorientation of the postrotatory responses in one animal always followed this rule, i.e., rotation toward (anti-)parallel alignment with gravity after stop

FIG. 5. Orientation of gravity vector in the yaw plane (\( \dot{\theta} \)) for all final body orientations. A: individual values show that if the rotation is in the positive or negative direction (JU: \( \Box \) or \( \bigcirc \); RO: \( \bigcirc \) or \( \bigtriangleup \); SU: \( \bigtriangleup \) or \( \bigcirc \)) the postrotatory response generally moves opposite to or in the direction of the gravity vector (negative or positive angles). B: absolute values averaged across all subjects for both rotational directions (\( \pm \)SD). Mean across all final head orientations yields \( \dot{\theta} = 68.6^\circ \) (\( \bigcdot \)).

FIG. 6. Tilt angles of postrotatory eye velocity vectors in the resultant plane (\( \psi \)) for all final body orientations. A: individual values show that if the rotation is in the positive or negative direction (JU: \( \bigcirc \) or \( \bigtriangleup \); RO: \( \bigtriangleup \) or \( \bigcirc \); SU: \( \bigcirc \) or \( \bigtriangleup \)) the postrotatory response generally moves opposite to or in the direction of the gravity vector (negative or positive angles). B: absolute values averaged across all subjects for both rotational directions (\( \pm \)SD). Mean across all final head orientations yields \( \psi = 16.7^\circ \) (\( \bigcdot \)). Monkey JU.

FIG. 7. Postrotatory eye velocity after 24° yaw OVAR shows the complete reorientation pattern. A: orientation of the velocity vector in the yaw plane (\( \varphi \)) indicates close alignment with gravity. \( R^2 = 0.995 \) (positive rotation: \( R^2 = 0.982 \), negative rotation: \( R^2 = 0.992 \)). B: absolute values averaged for both rotational directions (\( \pm \)SD). Mean across all final head orientations yields \( \varphi = 16.7^\circ \) (\( \bigcdot \)). Monkey JU.
of a negative (positive) head rotation, responses in the other two animals occasionally broke this rule. In either case, rotations were always toward the spatial vertical, and absolute tilt angles deviated on average by ~20–30% from the head tilt angle (Figs. 6 and 7B). Whereas most of the orientation responses at 90° tilt were undershooting the spatial vertical, overshooting responses could also be observed. At 24° tilt one animal showed consistently undershooting responses (Fig. 7B), whereas the other animal exhibited both under- and overshooting responses. It remains an open question whether there exists a consistent trend for over- and undershooting responses as a function of the tilt following OVAR as has been reported for the spatial reorientation of optokinetic afterresponses (Dai et al. 1991; Raphan and Cohen 1988).

The results obtained from this first descriptive approach were compared with the predictions obtained by fitting the data with a model that implemented a spatial transformation of the lateral semicircular canal input downstream to a low-pass filter. This low-pass filtered VOR pathway has traditionally been called velocity storage integrator to suggest a supplementary function in gaze stabilization at the low-frequency end of head movements (Raphan et al. 1977, 1979). Recent evidence, however, has proven that this network is part of an inertial vestibular system that encodes head motion in space (Angelaki and Hess 1994, 1995; Raphan and Cohen 1988). In the following paragraph we describe this second analytic approach and its significance in disclosing the mechanisms of spatial orientation.

Underlying canal-otolith interactions: 3-D–spatial orientation model for yaw VOR

To reveal the interaction between semicircular canal and otoliths, we describe postrotatory VOR after horizontal head rotations with a 3-D linear dynamic system, in which the spatial transformation is described by an otolith-dependent rotation (Fig. 10). In this spatial orientation model, the postrotatory VOR was analyzed by applying the spatial orientation model to postrotatory responses accurately predicts the empirical data. Black curves show averages of values obtained by separately fitting postrotatory responses to positive ($R^2 = 0.990$) and negative barbecue-spit head rotations ($R^2 = 0.986$). The regression line of $\varphi$ as a function of head tilt yielded $R^2 = 0.993$. The absolute mean $\varphi = 73.1° \pm 11.8°$. Gray curves denote the empirically determined data averaged for both rotational directions.

**FIG. 9.** Estimating the head orientation angles ($A, \varphi, B, \vartheta$) by applying the spatial orientation model to postrotatory responses accurately predicts the empirical data. Black curves show averages of values obtained by separately fitting postrotatory responses to positive ($R^2 = 0.990$) and negative barbecue-spit head rotations ($R^2 = 0.986$). The regression line of $\varphi$ as a function of head tilt yielded $R^2 = 0.993$. The absolute mean $\varphi = 73.1° \pm 11.8°$. Gray curves denote the empirically determined data averaged for both rotational directions. *Animal JU.* Empirical data also shown in Figs. 5 and 6.
tatory response ($\omega_{\text{VOR}}$) results from superposition of three different velocity signals: 1) a direct semicircular signal ($\omega_{\text{canal}}$) due to activation of the lateral semicircular canals, 2) a velocity signal ($\omega_{\text{oto}}$) that has been generated by an otolith-dependent head velocity detection network ($\Omega_g$ and $f_2$), and 3) a head-in-space velocity signal ($\omega_{\text{inertial}}$) from the inertial transformation network ($f_1$ and $R_g$).

The vectorial time signals in the gray panels in Fig. 10 highlight the intermediate steps in lateral semicircular canal signal processing based on the interactions with the static and/or dynamic otolith signals that detect head orientation relative to gravity. In the particular example illustrated (see Fig. 11A) the lateral semicircular canal signals undergo a spatial transformation such that the vectorial output signals of the network are almost perfectly aligned with the spatial vertical. The animal was stopped from rotating about its longitudinal axis in the earth-horizontal plane when it was close to right ear-down ($\delta_{\text{head}} = 90^\circ$, $\varphi_{\text{head}} = 240^\circ$). As shown in the gray panel next to "$\omega_{\text{inertial}}$" in Fig. 10, the spatial transformation network $R_g$ rotates the low-pass filtered head velocity signal in this example such that its $z$-(vertical) component decreases, whereas a relatively large $y$-(vertical) and a smaller $x$-(torsional) component emerges.

How does the inertial transformation network $R_g$ efficiently measure instantaneous head orientation relative to gravity? To see this, it is helpful to notice that any change in head orientation relative to gravity can be understood as a rotation about an earth-horizontal axis. Therefore the transformation $R_g$ can be described by only two parameters: a first parameter, the angular orientation of the tilt axis ($\varphi$), is defined by the line of intersection of the head yaw plane with the earth-horizontal plane (Fig. 2, dashed line). The orientation of this line could be coded by utricular signals because it is always perpendicular to the projection of gravity onto the yaw plane. Because of the fixed geometric relation between the utricles and the head yaw plane, the transformation from utricular sensory to yaw plane coordinates could be hardwired. The second parameter, the head tilt angle $\theta$, is more difficult to estimate by the vestibular system, presumably requiring both utricular and saccular information. On the other hand, least-squares estimation of this parameter in the framework of our proposed model (Fig. 10) depends on the relative strength and dynamics of the lateral semicircular ($\omega_{\text{canal}}$) and the otolith ($\omega_{\text{oto}}$) signals, both of which contribute to the spatial characteristics of VOR velocity ($\omega_{\text{VOR}}$). Whereas the relatively small scatter found in the estimated $\varphi$-angle of final head orientation may be due to the precise spatial tuning of both the canal- and the otolith-born head velocity signals, the larger variability in the dynamics of these signals may underline the larger scatter in the estimated $\theta$-values.

The head velocity detection network $\Omega_g$ estimates absolute head angular velocity relative to space based on the characteristic spatiotemporal pattern of otolith activity due to the rotating gravity vector (Angelaki 1992a,b; Hain 1986; Hess 1992; Schnabolk and Raphan 1992). This otolith-born velocity signal (output from $\Omega_g$) is low-pass filtered to enhance or sustain VOR eye velocity at low-frequency and constant-velocity head rotations where the canal-born velocity signals are deficient in magnitude or fading away (Angelaki and Hess 1996b). At stop of rotation, the postrotatory VOR ($\omega_{\text{VOR}}$) results from convergence of a low-pass filtered output signal from the head velocity detection network $\Omega_g$, a directly transmitted and an inertially transformed lateral semicircular canal signal.

An important feature of the model structure is the functional segregation of the spatial orientation and dynamic elements. Whereas the spatial orientation (angles $\theta$ and $\varphi$) shows no correlation with the filter time constants (compare $\delta_m^\ast$ and $\varphi_m^\ast$ with $T_{\text{store}}^\ast$ in Tables 1 and 2), the dynamics of the postrotatory responses basically reflect the interplay of the low-pass frequency canal and otolith-dependent head velocity signals. If the head velocity signals at stop of rotation should efficiently cancel each other (see $\omega_{\text{canal}}$ and $\omega_{\text{oto}}$ in Fig. 10), the amplitude and time constants need to be appropriately adjusted. Even though the animals were not reinforced to optimize a certain response behavior, yaw eye velocity was often strongly reduced in amplitude at stop of rotation. An example of this cancellation of the horizontal afterresponse that results from a close match of the amplitude and time constants of the
OVAR). Different time scales in mines the late time course of the postrotatory response. Fitted parameters: an overshooting fast initial rise followed by a slower decay of the horizontal 82.2° (90° yaw OVAR).

The underlying mechanisms of the spatial reorientation of posttilt responses (Angelaki and Hess 1994, 1995), it appears that the same model also predicts the spatial characteristics of dynamic head tilts. Whether the same is true for the roll and pitch VORs is still a matter of debate (Angelaki and Hess 1994; Dai et al. 1991; Hess and Angelaki 1995; Raphan and Sturm 1991). From a more practical point of view, our explicit formulation of the spatial transformation network allows to derive an analytic solution of the inertial equations as a function of the input signals, filter time constants, convergence ratios, and spatial orientation parameters. This analytic solution allows the extraction of important information about physiologically relevant parameters.

Conclusions

VOR responses following yaw OVAR show a remarkable precision in alignment with the spatial vertical, in particular with respect to the estimated orientation of gravity in the yaw plane (angle φ). A parametric analysis of the afterresponses based on a 3-D spatial orientation model revealed that inertial vestibular signals represent only a relatively small fraction of the total postrotatory response. We propose that these inertial signals are unimportant for gaze stabilization but, instead, reflect a mechanism that realigns the internal coordinates of the vestibulomotor system with gravity after abrupt changes in body motion. Clearly, such a mechanism may be advantageous for visuomotor coordination and posture control during self-motion.

APPENDIX

Inertial transformation of lateral semicircular canal signals

It has been shown earlier that the horizontal VOR exhibits different spatial characteristics as compared with the torsional and vertical VOR (Angelaki and Hess 1994, 1995). These characteristics are best modeled by a rotation operator downstream to a leaky integrator as shown in Fig. 10. The integration of the right and left lateral semicircular canal signals that operate in push-pull (ωcll) is described by a first-order linear differential equation (ḟ in Fig. 10)

\[
\mathbf{u} + A \mathbf{u} = \omega_{cll} \quad \text{with} \quad A = \begin{pmatrix} a_{11} & 0 & 0 \\ 0 & a_{22} & 0 \\ 0 & 0 & a_{33} \end{pmatrix} \tag{A1}
\]

where \(a_{11}, a_{22},\) and \(a_{33}\) are the reciprocal integration time constants in the roll, pitch, and yaw plane, respectively. The following spatial transformation (\(R_\phi\) in Fig. 10)

\[
\omega = R_\phi(e, \phi)\mathbf{u} \quad \text{with} \quad e = \begin{pmatrix} \cos(\phi) \\ \sin(\phi) \\ 0 \end{pmatrix} \tag{A2}
\]

is a rotation through an angle \(\phi\) about an axis \(e\) that always lies in the yaw plane (see Fig. 2). The subscript \(g\) indicates that this transformation depends on otolith inputs (see Fig. 10). The matrix elements of the unitary transformation \(R_\phi(e, \theta)\) can be found by evaluating the following equation: \(R_\phi(e, \theta) = (e \times e) e - \sin(\theta)(e \wedge e) + \cos(\theta) [e \wedge (e \wedge e)]\) (see METHODS). These basis vectors are the unit vectors defining the orientation of the three orthogonal head coordinate directions. For the yaw VOR, we need only the last column of this matrix (see below) because the input signal is always oriented along the \(z\)-axis. With the solution of the homogeneous part of Eq. A1

\[
\mathbf{u}_0(t) = \exp(-A)\mathbf{u}_0 = \begin{pmatrix} \exp(-a_{11}t) & 0 & 0 \\ 0 & \exp(-a_{22}t) & 0 \\ 0 & 0 & \exp(-a_{33}t) \end{pmatrix} \mathbf{u}_0 \tag{A3u}
\]
the full solution of Eq. A1 can be written as follows (e.g., Kailath 1980)

\[ \mathbf{u}(t) = \exp(-A\tau)[\mathbf{u}_0 + \int_0^t \exp(A\tau)\omega_{\text{int}}d\tau] \]  

(A3b)

To evaluate this last equation for the yaw VOR afterresponse, we represent the semicircular canal input at stop of a yaw rotation by a double exponential function (Steinhausen 1933; Wilson and Melvill-Jones 1979)

\[ \omega_{\text{int}} = v_0[\exp(-v_1t) - \exp(-v_{\text{in}}t)]e_z \]  

with \[ e_z = \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix} \]  

(A4)

Here, the vector \( e_z \) represents the unit vector normal to the yaw plane, \( v_{\text{in}} \) and \( v_1 \) are the short and long reciprocal time constants of the lateral semicircular canals (0.003 and 5 s for the rhesus monkey), and \( v_0 \) represents the response sensitivity. After evaluating the integral on the right-hand side of Eq. A3b, we obtain with the initial condition \( \mathbf{u}_0 = 0 \)

\[ \mathbf{u}(t) = \left[ \frac{\exp(-v_1t) - \exp(-a_{33}t)}{a_{33} - v_1} - \frac{\exp(-v_{\text{in}}t) - \exp(-a_{33}t)}{a_{33} - v_{\text{in}}} \right] e_z \]  

(A5)

Feeding this signal through the spatial transformation \( R_y(\theta, \varphi) \) we have

\[ \omega_{\text{inertial}}(t) = R_y(\theta, \varphi)\mathbf{u}(t) \]

\[ = \left[ \frac{\exp(-v_1t) - \exp(-a_{33}t)}{a_{33} - v_1} - \frac{\exp(-v_{\text{in}}t) - \exp(-a_{33}t)}{a_{33} - v_{\text{in}}} \right] \times \begin{pmatrix} \sin(\theta)\sin(\varphi) \\ -\sin(\theta)\cos(\varphi) \\ \cos(\theta) \end{pmatrix} \]  

(A6)

where the angles \( \theta \) and \( \varphi \) represent the tilt angle and the orientation of the tilt plane of postrotatory eye velocity, respectively (see Eq. A2 and Fig. 2). At stop of yaw rotation, we have to consider a superposition of three signals at the motor output side, namely the lateral semicircular canal signal (\( \omega_{\text{g}} \)), the inertial signal (\( \omega_{\text{inertial}} \)), and the otolith-born velocity signal (\( \omega_{\text{oto}} \)) that drove the VOR during the constant-velocity rotation phase. The latter signal is thought to be generated by a central otolith mechanism (\( \Omega_{\text{g}} \) in Fig. 10), the details of which are of no further concern here. At stop of rotation, this signal decays with a certain time constant

\[ \omega_{\text{oto}} = z_0 \exp(-t/T_{\text{oto}})e_z \]  

(A7)

assuming a low-pass filter with similar dynamics as for the semicircular canal signals ("\( f_2 \)" in Fig. 10). The system matrix of this integrator is diagonal like that in Eq. A1. Only the third diagonal element of this matrix comes into play during yaw rotation. It represents the reciprocal integrator time constant of the otolith velocity signal (\( \omega_{\text{oto}} \)) in the yaw plane. At the motor output side, we have finally

\[ \omega_{\text{VOR}} = \omega_{\text{inertial}} + \omega_{\text{oto}} + k_6\omega_{\text{inertial}} \]  

where \( k_6 \) is an unknown coupling constant.

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