THREE DIMENSIONAL EYE MOVEMENTS OF SQUIRREL MONKEYS FOLLOWING POSTROTATORY TILT

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Abstract — Three-dimensional squirrel monkey eye movements were recorded during and immediately following rotation around an earth-vertical yaw axis (160°/s steady state, 100°/s² acceleration and deceleration). To study interactions between the horizontal angular vestibulo-ocular reflex (VOR) and head orientation, postrotatory VOR alignment was changed relative to gravity by tilting the head out of the horizontal plane (pitch or roll tilt between 15° and 90°) immediately after cessation of motion. Results showed that in addition to postrotatory horizontal nystagmus, vertical nystagmus followed tilts to the left or right (roll), and torsional nystagmus followed forward or backward (pitch) tilts. When the time course and spatial orientation of eye velocity were considered in three dimensions, the axis of eye rotation always shifted toward alignment with gravitoinertial force, and the postrotatory horizontal VOR decay was accelerated by the tilts. These phenomena may reflect a neural process that resolves the sensory conflict induced by this postrotatory tilt paradigm.

Keywords — vestibulo-ocular reflex; eye movements; otolith organs; semicircular canals; monkey.

Introduction

When an upright subject is rotated at a constant velocity about an earth vertical axis and then rapidly decelerated, a postrotatory horizontal nystagmus occurs which then gradually decays. Studies have shown that the time course of the horizontal postrotatory response is dramatically affected by the orientation of the subject relative to gravity (1–3).

Recent studies in monkeys (4), humans (5), and cats (6) have also demonstrated the presence of a decaying vertical nystagmus as part of the postrotatory response following off-vertical axis rotation (OVAR). In each of these studies, the vertical component of the eye movement shifted the plane of the response toward the earth-horizontal. Earlier studies (7,8), using low-velocity centrifuges, also reported the presence of a vertical nystagmus when the upright humans were facing the motion or had their backs to the motion. When these paradigms were repeated with monkeys, the axis of eye rotation clearly shifted toward alignment with gravitoinertial force (9,10).

Since a common neural element (11) has been hypothesized to explain the time course of optokinetic afternystagmus (OKAN) and to yield horizontal postrotatory nystagmus which outlasts the end-organ response, a similar influence of gravity might be expected following optokinetic stimulation. Research has confirmed this prediction in monkeys by showing that the axis of eye rotation during OKAN shifted toward alignment with gravity when the subject and optokinetic stimulus were tilted with respect to gravity (12), while human experiments have not confirmed this large axis shift (13).
While many of these studies have indicated the presence of a shift in the axis of eye rotation toward alignment with gravity, none have measured three dimensional (3-D) eye orientation, corrected for cross-talk between the eye position signals, quantified the extent of the axis shift, and quantified the time course of the angular VOR decay following constant velocity rotation. In this study, we quantified the effects of tilt on the angular VOR in an attempt to investigate the interaction of sensory information from the semicircular canals and the otoliths. 3-D eye movements were recorded during and after reorientation of the monkey immediately following rapid deceleration from constant angular velocity around an earth-vertical axis. Postrotatory tilts were performed in both roll (left ear down/right ear down) and pitch (nose up/nose down), and the shift in the axis of eye rotation and the decay time constants were determined.

Methods

Experiment Design

Monkey preparation. Five adult male squirrel monkeys (Saimiri sciureus) weighing between 0.9 and 1.0 kg were the subjects. [These monkeys were also used in other studies (9,10,14).] A stainless steel bolt was used to stabilize the head of the monkey while allowing repeatable head positioning. The bolt was anchored to the skull using dental acrylic and miniature stainless steel screws which were inverted and secured in keyhole slots drilled in the skull. Right eye position was measured using a search coil technique (15). Prefabricated coils made of insulated stainless steel wire were implanted on the right eye. An 11-mm diameter 3-turn coil was sutured to the sclera concentric to the limbus in the eye's frontal plane, and an 8-mm diameter 4-turn coil was sutured to the globe laterally and posteriorly to the frontal coil in the eye's sagittal plane. The leads left the orbit such that they did not interfere with normal movements of the eye. See Paige and Tomko (14) for a complete description of all surgical procedures.

Experimental paradigm. The upright monkeys were accelerated (100°/s²) about an axis aligned with gravity and the monkey's spinal axis to a constant velocity (160°/s) using a servo-controlled rotatory device at the NASA Vestibular Research Facility. The monkey's head was positioned such that the plane of the horizontal canals was perpendicular to the axis of rotation and such that the axis of rotation was directly between the left and right vestibules. When the horizontal angular VOR was nearly extinguished (>60 seconds), the monkey was quickly decelerated (100°/s²) to a stop. While the postrotatory ocular response was still strong (1 to 3 seconds after stopping), the monkey was manually tilted (1 to 2 seconds) 15, 32, 45 or 90 degrees in one of the four primary directions: nose up, nose down, left down, and right ear down. The lights were turned on between trials and extinguished just prior to the start of a trial. Three of the monkeys were tested on more than one occasion, with one monkey (B) tested five times. The order of the trials was randomized. To maintain monkey alertness, d-amphetamine (0.3 mg/kg) was administered intramuscularly 15 minutes before the beginning of each test session.

Eye movement recording. The eye measurement system was calibrated using two orthogonal search coils similar to those implanted in the monkeys. The reference coils were mounted on a model eye secured to a non-metallic three-axis calibration jig, which was used to set the measurement sensitivities. The accuracy of this calibration procedure has previously been verified (14,16).

Data Analysis

Eye kinematics. Using two search coils we can accurately estimate the 3-D orientation of the eye. For eye movements that do not deviate far from the primary eye position, the detector circuits accurately indicate yaw, pitch, and roll of the eye. However, as the eye position deviates from the primary gaze position a number of nonlinear errors become important (15). These errors are enhanced by any mis-
alignment of the search coils on the globe (17). An electronic correction scheme had been developed (14,16) to minimize these errors. As long as coil placement errors and eye displacements were limited to less than 10 degrees for each axis of eye rotation, the worst-case eye position measurement error was less than 10%, and the mean error was less than 3%.

The electronic correction method proved inadequate for this study since eye displacements sometimes exceeded 20 degrees, leading to worst case errors of greater than 20%. To minimize these errors, we developed and applied here an exact solution algorithm that corrected for coil placement errors (9,18). With eye displacements of up to 20 degrees, this algorithm yields worst case measurement errors of less than 10% (18).

Coordinate system. Dynamic knowledge of the three-dimensional eye orientation allowed us to calculate a three dimensional representation of eye velocity (18). Eye velocity is a vector quantity and may be represented in a number of different coordinate frames. We chose to represent eye velocity in a head-fixed Cartesian coordinate system to allow us to compare the eye responses directly to the motion stimuli. We defined the head-fixed, right-handed coordinate system such that the x-axis aligns with the naso-occipital axis, the y-axis aligns with the interaural axis, and the z-axis is perpendicular to the x- and y-axes. The positive direction is forward for the x-axis, leftward for the y-axis, and upward for the z-axis. In this Cartesian representation, eye velocity is represented by a vector with components in each of the three directions (x, y, and z). With the eye in the primary position, horizontal eye velocity is represented by a vector aligned with the head fixed z-axis ($\omega_z$). Similarly, vertical ($\omega_y$) and torsional ($\omega_x$) eye velocities are presented by vectors aligned with the monkey's y-axis and x-axis, respectively (Figure 1). This representation is different from the commonly used Fick representation, where eye velocity is represented by three quantities, called Euler rates, which represent rates of ocular yaw, pitch, and roll. Euler rates are a reasonable approximation to eye velocity when eye movements are small (<5 degrees) or when responses are limited to a single plane (yaw or pitch or roll), but are a poor choice during 3-D eye rotation because the Fick coordinate system moves with the eye, because the Euler rates are nonorthogonal (except in the primary position), and because the representation of eye velocity depends upon eye orientation.

Using the Cartesian representation, the primary postrotatory response following yaw rotation (around the z-axis) is a horizontal eye movement ($\omega_z$; also around the z-axis). To evaluate the extent to which postrotatory tilts caused the axis of eye rotation to shift away from the z-axis, we calculated the shift in the axis of eye rotation in both the roll (coronal) and pitch (sagittal) planes (Figure 1). The roll shift in the axis of eye rotation ($\theta_r$) represents the angle by which the response shifts from the z-axis ($\theta_r = 0$) toward the left or right ear (y-axis). This occurs when the response includes a head vertical component as well as the predominant head horizontal component. The pitch shift in the axis of eye rotation ($\theta_p$) represents the angle by which the response shifts from the z-axis ($\theta_p = 0$) toward or away from the nose (x-axis). This occurs when the response includes a torsional component as well as the predominant head horizontal component. To keep the axis of eye rotation aligned with gravity following postrotatory roll tilts of the head, the axis of eye rotation, measured relative to the head, must shift in roll ($\theta_r$), with no change in pitch ($\theta_p$). Similarly, to keep the axis of eye rotation aligned with gravity following postrotatory pitch tilts of the head, the axis of eye rotation must shift in pitch ($\theta_p$), with no change in roll ($\theta_r$).

Fast phase removal. Since we were interested in the slow phase eye velocity as representative of the VOR, we used a computer algorithm to identify and remove the fast phases of the nystagmus. The algorithm used low-order digital filters to calculate three-dimensional eye velocity and eye acceleration. The movement was marked as a fast phase and removed if the acceleration of the eye exceeded a threshold set by the user. All edited data
Figure 1. Post-rotatory tilt trials for subject B. Left column shows data obtained for a 32-degree postrotatory tilt to the right. Right column shows data obtained for a 32-degree postrotatory tilt backward. Diagrams in the center column define the quantities plotted. The angular yaw stimulus as well as the horizontal ocular response are shown in the first row. The vertical and torsional ocular responses are shown in the second and third rows, respectively. The roll shift ($\theta_r$) and the pitch shift ($\theta_p$) in the axis of eye rotation are shown in the fourth and fifth rows, respectively. Dashed vertical lines mark the postrotatory tilt. Discontinuities in the fourth and fifth rows result from uncertainty in the calculation of the axis of eye rotation when the horizontal response nears zero.
were manually reviewed and compared to the original data to verify the integrity of the algorithm and to remove any fast phases which were missed. This simple algorithm removed more than 95% of the fast phases; a limited number of fast phases were manually removed. All gaps were filled with a zero-order hold of the eye velocity preceding the saccade. [Data processing details including eye kinematics, coordinate systems, and fast phase removal are presented elsewhere (9,13).] Curve fits. Least squares regression (19) was used to perform linear fits to the data. To determine the dominant decay characteristics of the VOR responses, we estimated the decay time constant ($\tau$) of the responses by fitting the curve,

$$y = K + Ae^{-t/\tau},$$

[1]

to the data ($K$, $A$, and $\tau$ are the parameters determined by the curve fit). This fit was obtained by minimizing the mean square error between the data and the curve [Levenberg-Marquardt algorithm (20)]. $K$ and $A$ were necessary to obtain an acceptable curve fit, but were not analyzed further.

To minimize the effect of the axis shift on the estimated time constant we began the curve fit after the primary off-axis response (vertical for roll tilts; torsional for pitch tilts) had reached its maximum magnitude. This curve fit ignores the complex dynamics that occur during the build-up of the off-axis response and concentrates upon the decay of the response.

Large secondary responses (for example, horizontal and vertical VOR in the left column of Figure 1) were relatively rare, but to be sure that these responses were not systematically affecting our determination of the dominant time constant we also fit the curve,

$$y = A_1e^{-t/\tau_1} + A_2e^{-t/\tau_2},$$

[2]

to some of the data showing significant secondary responses. No large or systematic differences between the dominant time constant determined by the single exponential curve fit (equation 1) and the double exponential curve fit (equation 2) were observed, so we chose to fit all the data with the single exponential.

Results

VOR Response

Roll trials. A representative trial showing a 32-degree postrotatory roll tilt to the right is shown in the plots in the left column of Figure 1. The $-15^\circ/s$ spike in the torsional VOR at approximately 70 seconds is a compensatory response to the roll rotation. The horizontal response decays immediately following the tilt, but then recovers slightly before decaying more gradually with a time constant of 7.3 seconds. Approximately 2.2 seconds after the tilt, a strong vertical ocular response appears and decays with a time constant of 6.4 seconds. In this trial, the vertical slow phase velocity reached a peak magnitude of approximately 50°/s. Note that the horizontal and vertical responses reverse at nearly the same time (approximately 90 seconds), indicating that the responses may be loosely coupled.

The last two rows in Figure 1 show the time course of the shift in the axis of eye rotation. Since the primary horizontal and vertical responses are both negative, the roll shift of the axis of eye rotation is positive with a peak magnitude of approximately 45 degrees while the peak magnitude of the pitch shift is less than 10 degrees. The secondary horizontal and vertical responses following reversal are both positive, which again yield a positive shift in the axis of eye rotation. In this case the roll shift during the secondary response almost exactly equals the roll tilt of 32 degrees, while the secondary pitch shift is near zero. This response is characteristic of the roll tilt trials with the roll shift of the axis of eye rotation tending to align with gravity following the postrotatory tilt.

Pitch trials. A representative trial showing 32-degree nose up tilt following rotation is shown in the plots in the right column of Figure 1. The $40^\circ/s$ spike in the vertical response at ap-
approximately 70 seconds occurs as a compensatory response to the pitch rotation. Shortly after the tilt, a strong torsional ocular response appears and decays with a time constant of 2.4 seconds, while the horizontal ocular response decays with a time constant of 4.4 seconds. In this trial, the torsional slow phase velocity reached a peak of approximately 15°/s.

The last two graphs in the column show the shift in the axis of eye rotation. Since both the horizontal and torsional responses are negative, the pitch shift of the axis of eye rotation is positive with a magnitude of approximately 20 degrees, while the roll shift is near zero. This pitch shift tends to align the axis of eye rotation with gravity following the nose up postrotatory pitch tilt. Comparable results were obtained during nose down tilts, with the sign of the torsional response always opposite that obtained during nose up trials. The reversed sign of the torsional response led to a reversal in the calculated pitch of the axis of eye rotation, once again aligning the axis of eye rotation with gravity.

**VOR Spatial Characteristics**

The shift in the axis of eye rotation was determined for all trials for each monkey by calculating the average shift in the axis of eye rotation for one second after the peak vertical or torsional response was obtained.

We chose to average over a full second to minimize the affect of noise on the estimated angle. We chose the first second after the off-axis peak because the measurement becomes very sensitive to noise as the responses, particularly the horizontal, decay toward zero. The tilt angle measurement was relatively insensitive to alternate parameterizations, since both the horizontal and off-axis responses were simultaneously decaying. For example, we compared the chosen measure with one-second averages, starting one second and two seconds after the peak. No consistent or significant differences (always <10%) existed in these three measures. As an example, once the torsional velocity in the right column of Figure 1 reaches a peak value and begins to decay, the pitch of the eye rotation axis remains relatively constant at approximately 20 degrees until the horizontal velocity decays to near zero. At this point, significant uncertainty in the calculated angle is evident in the increasing oscillations in the pitch of the eye rotation axis.

**Roll trials.** Figure 2 Panel A shows a plot of the roll shift (θr) of the axis of eye rotation for a single monkey (B). The slope of the least squares fit, shown as the thin line, is 0.96. The pitch shift (θp) of the axis of eye rotation is also plotted for these roll tilt trials. The slope of the least squares fit, shown as the thick line, is -0.03. Prior to head tilt, gravity and the axis of eye rotation are aligned. Following head roll tilt, the axis of eye rotation, relative to the head, shifts in a direction opposite the head roll. This axis shift with respect to the tilted head tends to maintain the orientation of the angular VOR response relative to gravity.

Perfect alignment of the axis of eye rotation with gravity would require that the response roll shift equal the head roll tilt (slope of plus one), while the pitch shift remains zero (slope of zero). More generally, a shift toward alignment with gravity requires that the roll shift (θr) demonstrate a positive correlation with roll tilt. These data show that the axis of eye rotation shifts toward alignment with gravity following roll tilts. The roll shift in the response shows a significant (P < 0.001) positive correlation (r = 0.984) with the head roll tilt, while the pitch data are not significantly correlated (r = -0.026). Furthermore, since the slope of the linear fit to the roll shift (0.96) is not significantly different from one, we can state that the axis of eye rotation closely aligned with gravity.

**Pitch trials.** Figure 2 Panel B shows a plot of the pitch shift (θp) of the axis of eye rotation as a function of head pitch for a single monkey (B). The slope of the least squares fit, shown as the thick line, is 0.46. The response roll shift (θr) is also plotted, and the slope of the least squares fit, shown as the thin line, is -0.030.
Figure 2. Shift in the axis of eye rotation. Panel A shows the calculated shift in the axis of eye rotation for monkey B during postrotatory tilts to the left and right. The roll of the axis of eye rotation (θ, from Figure 1) for each trial (+) is plotted versus the magnitude of the tilt. Thin line represents the least squares fit. The pitch of the axis of eye rotation (θp, from Figure 1) for each trial (x) is also plotted. The thick line represents the least squares fit. Panel B shows the calculated shift in the axis of eye rotation for monkey B during tilts forward and backward. As before, the roll of the axis of eye rotation (θ, for each trial (+) is plotted versus the magnitude of the tilt. The pitch of the axis of eye rotation (θp) for each trial (x) is also plotted. [Panel A after Merfeld and Young (18).]
Analogous to the above head roll tilt experiments, alignment of the axis of eye rotation following head pitch requires that the response pitch shift (?p) equal head pitch (slope of one), while the response roll shift (?r) show no correlation (slope of zero). More generally, a shift toward alignment with gravity requires that the pitch shift (?p) demonstrate a positive correlation with head pitch. Again, the data show that the axis of eye rotation shifted toward alignment with gravity. Statistically, the pitch response shows a significant (P < 0.001) positive correlation (r = 0.985), while the roll response is not significantly (P > 0.4) correlated (r = -0.124) with the pitch tilt. Unlike the roll experiment, the realignment of the ocular response axis with gravity following head pitch was incomplete and was roughly half (0.46) that required for alignment with gravity.

Comparison of pitch and roll responses. Table 1 shows a summary of the axis shift analysis for each monkey during roll tilts and pitch tilts. During roll tilt, data for each monkey clearly indicate that the axis of eye rotation shifted toward alignment with gravity, since the roll shift of the axis of eye rotation for each of the five monkeys has a high positive correlation (r > 0.96) with the roll tilt. Similarly, the pitch shift data from each monkey during pitch tilt show a high positive correlation (r > .98), again indicating that the axis of eye rotation shifted toward alignment with gravity.

Data from three of the five monkeys (B, E, F) tested with postrotatory roll tilts indicated that the axis of eye rotation closely aligned with gravity since the slopes of the linear fit to the roll shift were greater than 0.95. In contrast, none of the four monkeys (A, B, E, F) tested with postrotatory head pitch displayed a shift in the axis of eye rotation that fully aligned with gravity. The slope of the linear fit never exceeded 0.9. In fact, data from three of the four monkeys (B, E, F) during pitch tilts showed that the slope of the linear fit was less than 0.5. On the whole, the pitch shifts of the axis of eye rotation following pitch tilts were less than the roll shifts of the axis of eye rotation following comparable roll tilts. Only one monkey (A) had comparable response axis shifts for roll and pitch tilts of the head.

### Table 1. Axis Shift Regression Analysis

<table>
<thead>
<tr>
<th>Monkey</th>
<th>Roll Tilts (as in Figure 2A)</th>
<th>Pitch Tilts (as in Figure 2B)*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>?p versus angle of tilt</td>
<td>?r versus angle of tilt</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>s</td>
</tr>
<tr>
<td>A</td>
<td>9</td>
<td>-0.007</td>
</tr>
<tr>
<td>B</td>
<td>15</td>
<td>-0.026</td>
</tr>
<tr>
<td>D</td>
<td>12</td>
<td>-0.025</td>
</tr>
<tr>
<td>E</td>
<td>3</td>
<td>-0.105</td>
</tr>
<tr>
<td>F</td>
<td>3</td>
<td>0.025</td>
</tr>
<tr>
<td>A</td>
<td>11</td>
<td>0.870</td>
</tr>
<tr>
<td>B</td>
<td>15</td>
<td>0.462</td>
</tr>
<tr>
<td>E</td>
<td>3</td>
<td>0.399</td>
</tr>
<tr>
<td>F</td>
<td>3</td>
<td>0.422</td>
</tr>
</tbody>
</table>

*Monkey D not included because torsion coil failed before forward/backward tilt trials were completed.

Notation:
- n is the number of trials.
- s is the slope of the linear regression.
- r is the sample regression coefficient.
- t is the calculated t-value representing the significance of the correlation.
- P represents the statistical significance of the correlation.
- ?p and ?r represent the axis shift of the eye as shown in Figure 1.
**Time Course of the VOR Decay**

**Roll trials.** The time course of the VOR decay was also affected by the postrotatory tilt. Figure 3 shows the effect that the postrotatory tilt has on the decay of the VOR. In Figure 3 Panel A, the horizontal time constants are plotted for varying head roll tilts. Despite a great deal of variability, the data indicate that the time constant decreases as the angle of head tilt increases. The dashed line shows the least squares linear fit. This trend was highly significant ($P < 0.001$). Since the misalignment of gravity and the postrotatory head axis (z-axis) will vary with the sine of the magnitude of the tilt angle ($|x|$), we also used linear regression to fit the equation:

$$y = y(0) + A \sin(|x|). \quad [3]$$

The solid curve shows this fit. This simple nonlinear curve provides a better fit to the data as measured by a decreased mean square error and an increased regression coefficient (Table 2).

Figure 3 Panel C shows the vertical decay time constants versus the horizontal decay time constants during roll tilt. The time constants are positively correlated ($r = 0.82$) with high significance ($P < 0.001$). The slope of the regression ($s = 0.77$) is somewhat less than one, indicating that, in general, the vertical response decayed a little more rapidly than the horizontal response.

**Pitch trials.** Figures 3 Panel B shows the horizontal VOR time constants for pitch tilts. Once again the data indicated that the horizontal time constant decreased as the angle of tilt increased to 90 degrees. Similar to the data for roll tilts, these data indicated that the nonlinear fit is better than the simple linear fit (Table 2) and that the downward trend was highly significant ($P < 0.001$).

Figure 3 Panel D shows the torsional decay time constants versus the horizontal decay time constants during pitch tilts. Again the time constants were positively correlated ($r = 0.78$) with high significance ($P < 0.001$), and the slope of the regression ($s = 0.76$) was, again, somewhat less than one, indicating that, in general, the torsional response decayed a little more rapidly than the horizontal response.

**Comparison of pitch and roll responses.** The similarity of the linear regression for roll tilts (Figure 3 Panel C) and pitch tilts (Figure 3 Panel D) and the similarity of the effects of tilt on the time course of the horizontal angular VOR (Figure 3) suggest that the plane of the head tilt does not dramatically affect the time course of the response. This is in contrast to the spatial characteristics, which show that the magnitude of the shift in the axis of eye rotation is less for pitch than for roll tilts.

**Summary**

These experiments quantified eye movement responses by determining the spatial and temporal characteristics of 3-D ocular responses following roll and pitch postrotatory tilt and showed that whole body tilts affect the postrotational angular VOR responses of monkeys. Most dramatically, the axis of eye rotation was shown to shift toward alignment with gravity following tilt. Quantitative analysis indicated that the axis shift was greater for roll than it was for pitch tilts (Figure 2 and Table 1). These results are similar to the previous quantitative findings showing that postrotatory eye movements following OVAR shifted toward an earth-horizontal plane (4–6).

The time course of the decay of the horizontal angular VOR was also affected by the postrotational tilt in both pitch and roll (Figure 3 and Table 2). Specifically, the decay time constant was shown to decrease as the angle of tilt increased, independent of the plane (pitch or roll) of the postrotatory tilt. This is consistent with previous research (2,3) that did not take the axis shift into account when determining the decay time constants. Furthermore, the decay time constant of the off-axis VOR response (vertical for roll tilt; torsional for pitch tilt) was correlated with the decay time constant of the horizontal VOR response with the slope of the correlation less than one. This indicates that the decay of the off-axis
Figure 3. Effect of postrotatory tilt on VOR time constants. Panel A shows a plot of the decay time constant for the horizontal ocular response versus the postrotatory tilt angle for roll tilts, while Panel B shows a plot of the decay time constant for the horizontal ocular response versus the postrotatory tilt angle for pitch tilts. Dashed lines show the least squares linear fits. Solid curves show the least fit to the equation, \( y = y(0) + A \sin(|x|) \), where \( |x| \) is the magnitude of the tilt angle. Panel C shows the decay time constant for the vertical ocular response plotted against the decay time constant for the horizontal ocular response for postrotatory roll tilts. Panel D shows the decay time constant for the torsional ocular response plotted against the decay time constant for the horizontal ocular response for postrotatory pitch tilts. Lines represent the least square linear fits to the data.
### Table 2. Correlation of Horizontal VOR Time Constant with Tilt

<table>
<thead>
<tr>
<th>Line fit ( y = y(0) + s \cdot x )</th>
<th>Sine fit ( y = y(0) + A \cdot \sin(x) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( s )</td>
<td>( y(0) )</td>
</tr>
<tr>
<td>Roll tilts</td>
<td>-0.17</td>
</tr>
<tr>
<td>Pitch tilts</td>
<td>-0.19</td>
</tr>
</tbody>
</table>

**Notation:**
- \( s \) is the slope of the linear regression.
- \( y(0) \) is the \( y \)-intercept.
- \( A \) is the amplitude of the sine correlation.
- MSE is the mean square error.
- \( r \) is the sample regression coefficient.
- \( t \) is the calculated \( t \)-value representing the significance of the correlation.
- \( P \) represents the statistical significance of the correlation.

Response may be somewhat faster than the decay of the horizontal VOR.

### Discussion

**VOR Spatial Characteristics**

While the time course of the horizontal VOR was not strongly dependent on the plane (pitch or roll) of the postrotatory tilt, the plane of rotation did significantly affect the direction of the eye movement responses, since large vertical responses followed roll tilt and large torsional responses followed pitch tilt. In all trials the off-axis responses shifted the axis of eye rotation toward alignment with gravity. Previous studies are consistent with this finding. For example, vertical responses were observed during eccentric yaw rotations of humans about an earth-vertical axis (7,8). When this paradigm was repeated with monkeys, the vertical component of the response was shown to always shift the axis of eye rotation toward alignment with gravitoinertial force (9,10). Studies have also shown that postrotatory eye movements shift toward an earth-horizontal plane immediately following OVAR stimulation (4–6). This is consistent with the 3-D measurements, showing that the axis of eye rotation aligns with gravity.

We propose that the shift in the axis of eye rotation indicates that the CNS resolves this sensory conflict by shifting a central estimate of rotation toward alignment with gravity (Figure 4) (9,10,18). In order to discuss this hypothesis we must clearly and unambiguously define what we mean by “central estimate of rotation” and “sensory conflict”.

We define the “central estimate of rotation” as a neural representation of angular velocity that is derived from the sensory afference. It has long been known that the time course of angular VOR responses differs significantly from the dynamics of the semicircular canals, and that visual stimuli can modify the VOR responses (11,23,24). For these reasons, Robinson explicitly hypothesized that the angular VOR reflects a central estimate of self-rotation (24), which is induced by a process of sensory integration that includes visual as well as semicircular canal signals. Since the neural processing required to transform retinal images to an estimate of self-motion exceeds the neural processing required to transform otolith afference, it is not difficult to believe that otolith cues could play a similar role in determining a central estimate of self-rotation. OVAR studies, which show that the rotation of gravity can induce a bias response component that partially compensates for the actual rotation (4–6,25,26), and postrotatory tilt studies reveal that otolith signals may influence the central estimate of rotation.

We, like Guedry (21,22), define "sensory conflict" to be an incongruity between at least two sensory systems. In this case, the sensory conflict occurs because the semi circular canals and the otoliths provide conflicting information regarding self motion. Immediately
following deceleration the otolith signal indicating gravity is aligned with the canal signal indicating rotation, but during the postrotatory tilt the semicircular canals tilt with the body and continue to indicate rotation about the body's z-axis, while the otoliths indicate the constant orientation of gravity which is now tilted with respect to the body. If, in fact, the tilted body were rotating about the body's z-axis (yaw) as indicated by the semicircular canals, then the otoliths would be expected to measure the rotation of gravity about the yaw axis. Conversely, if gravity were truly fixed with respect to the body, then rotation could only occur about an axis aligned with gravity. Therefore, the sensory signals indicating the state of motion are incongruent and produce "sensory conflict."

We also define two ways to resolve the sensory conflict. Temporally, the conflict can be resolved by reducing the central estimate of rotation (Figure 4 Panel B). This resolution

![Conflict Resolution](image)

**Figure 4.** Sensory conflict resolution. Panel A demonstrates the sensory conflict created when the central estimate of rotation ($\vec{\omega}$) doesn't align with the head-fixed orientation of gravity ($\vec{g}$) following postrotatory tilt. Sensory conflict results since the central estimate of rotation should lead to a change in orientation of gravity with respect to the head, while the otoliths just as clearly indicate that the orientation of gravity with respect to the head is constant. One way to resolve the conflict is to eliminate the central estimate of rotation (Figure 4 panel B). Another way to resolve this conflict is to align the central estimate of rotation with gravity (Figure 4 panel C), since the rotation no longer leads to a change in the orientation of gravity. The two resolution processes are not mutually exclusive.
process may manifest itself as a weaker VOR response or as a more rapid decay of the response. Spatially, the conflict can be resolved by modifying the central estimate of rotation such that the axis of the central estimate aligns with gravity (Figure 4 Panel C). This resolution process may manifest itself by realigning the axis of the VOR with gravity.

We might expect that the size of the eye response axis shift would depend upon whether the off-axis response is vertical or torsional, since the gain of the vertical and torsional VORs are known to differ (27). By quantitatively analyzing the 3-D axis of eye rotation, we found that the shift in the axis of eye rotation was less for pitch than for roll tilts (Figure 2; Table 1). For roll tilts (left ear down/right ear down), where the off-axis response was primarily vertical, the axis of eye rotation aligned closely with gravity in the majority of the monkeys. For pitch tilts (forward/backward), where the off-axis response was primarily torsional, the axis of eye rotation never aligned with gravity. We hypothesize that this difference in the axis of eye rotation, with roll shift responses greater than pitch shift responses, might at least in part be due to the fact that the vertical angular VOR is 30% to 100% larger than the torsional angular VOR (27). Since the horizontal and vertical angular VOR gains are comparable (27), the measured axis of eye rotation might provide an accurate estimate of the axis of self rotation for roll tilts. On the other hand, since the torsional VOR gain is less than the horizontal VOR gain, the measured axis shift for pitch tilts may not quantitatively represent the shift in the central estimate of rotation.

While the magnitude of the axis shift may not always represent the magnitude of the shift in the central estimate of rotation, the time course of the axis shift might still represent the time course of the shift in the central estimate of rotation. In the absence of perceptual or other physiological measures of the apparent vertical, the time course of this axis shift may provide the best estimate for the time course of the shift in the central estimate of rotation and, in turn, of the time course of the shift in the central estimate of gravity (18). Axis shifts similar to those measured following postrotatory tilt have also been measured following OVAR (2,4–6). The qualitative similarity of the responses following off vertical axis rotation (OVAR) and following postrotatory tilt (3,9,18) indicates that the exact paradigm used to reach a tilted postrotatory orientation might be less important than that such an orientation be obtained. In other words the rapid decay and axis shift depend only upon the presence and magnitude of the competing otolith signal.

Axis shifts have also been noted following optokinetic stimulation when monkeys and the optokinetic stimulus were tilted with respect to gravity (12). Raphan and colleagues (23) hypothesized that optokinetic stimulation “charges” a velocity storage mechanism which is responsible for optokinetic nystagmus, optokinetic afternystagmus, and vestibular nystagmus. It has also been suggested that canal and visual cues might be merged to yield a single central estimate of head angular velocity (24). If we assume that the velocity storage mechanism is charged by both canal and visual cues and that a central estimate of head angular velocity results, then the response induced during tilted OKAN should be similar to that induced during postrotatory tilts and, therefore, should yield the observed shift in the axis of eye rotation.

Human studies have not confirmed the presence of a strong shift in the axis of eye rotation following optokinetic stimulation (13) or following postrotatory tilt (28). Other studies, using eccentric rotation stimuli, have shown that the axis shift is more gradual and weaker for humans (7,8) than it is for monkeys (9,10). Similarly, the axis shift following constant velocity OVAR stimulation has been shown to be weaker in humans (5) than in monkeys (4). This, along with that fact that OKAN is weaker in humans than in monkeys, may partially explain these species differences. Furthermore, some of the paradigms involve another difference. The monkey postrotatory tilts were passive, while the human postrotatory tilts were active. Perhaps the active process of tilt interferes with the axis shift due to information from either the neck receptors in-
indicating tilt of the head with respect to the torso or a copy of the efferent signals sent to the neck muscles.

**Time Course of the VOR Decay**

**Horizontal VOR.** Earlier studies, while not noting the shift in the axis of eye rotation, documented the effect of gravity on the horizontal postrotatory response by showing that the postrotatory nystagmus elicited by earth-vertical and earth-horizontal rotation differed. Specifically, horizontal postrotatory nystagmus following a velocity trapezoid was shown to be weaker and to decay more rapidly when subjects were rotated around an earth-horizontal axis (1,2,25). Guedry (21,22) suggested that the difference was due to the sensory conflict induced following constant-velocity earth-horizontal rotation, since the otoliths correctly indicate the absence of orientation changes with respect to gravity while the postrotatory response of the semicircular canals indicates rotation after all motion has stopped (Figure 4 Panel A). Guedry proposed that the weaker response and more rapid decay were direct effects of the conflict, since the sensory conflict would be reduced or more rapidly eliminated by diminishing or eliminating the central estimate of rotation.

Benson (3) provided evidence supporting Guedry's hypothesis when he tilted his subjects immediately following constant velocity rotation about a vertical axis. He found that the horizontal postrotatory response decayed more rapidly following tilt, and that the rate of horizontal VOR decay was dependent on the amount of tilt. However, the shift in the axis of eye rotation was not yet documented, so Benson could not take this shift into account while determining the decay time constant of the horizontal VOR. Our analysis (Figure 3) takes the axis shift into account by beginning the curve fit after the initial rapid decay (see Figure 1) and indicates that, in general, the time constant does decrease as tilt increases. It is important to note that the time constant did not always decrease with increased tilt, but the general trend is compelling (Figure 3 Panels A and B). The data were similar for both roll tilts and pitch tilts, with the fastest decay occurring after tilts of 90°. These data are consistent with a process of sensory conflict resolution, since larger tilts, at least up to 90°, increase the sensory conflict induced by the graviceptor afference (29).

The data shown in Figure 1 provide examples which qualitatively support this interpretation of the results. Note that immediately following tilt the horizontal response begins to rapidly decay. This is consistent with Guedry's hypothesized process for resolving the sensory conflict. However, the horizontal response recovers and decays much more gradually once the off-axis response (vertical-left column; torsional-right column) is initiated. This might indicate that the sensory conflict that initiated the rapid decay of the response was reduced once the axis shift was underway. If we assume that the axis shift represents a manifestation of sensory conflict resolution and that the rapid decay is another manifestation of the resolution process, then the data shown in Figure 1 are consistent with both conflict resolution hypotheses (Figure 4 Panels B and C).

Guedry's hypothesis provides one explanation for the effect of gravity on the decay time constant of the VOR, but other mechanisms have been proposed to explain this effect. For example, the velocity storage models (30,31) provide good phenomenological explanations for the observed gravitational effects by assuming that model parameters directly depend upon the orientation of gravity. In contrast to these models, another modeling approach (32) assumes that the signals from the various sense organs are dynamically merged to minimize sensory conflict. This dynamic interaction of sensory signals appears more typical of our current knowledge of neural processing than is the idea of sensory signals dynamically and instantaneously changing the characteristics of the VOR neural network.

**Off-axis VOR responses.** The time constant of the off-axis response (vertical for roll tilts; torsional for pitch tilts) was highly correlated with the time constant of the horizontal re-
sponse (Figure 3), and the slope of the correlation (approximately 0.75) was similar for pitch and roll. A previous study, with tilted subjects rotated about an earth-vertical axis at constant velocity, showed a similar effect (33). Analysis showed that the vertical component of the response had a shorter time constant than the horizontal response. This was interpreted as indicating that the time constant for vertical velocity storage is less than the time constant for horizontal velocity storage even when both responses are stimulated simultaneously. The same mechanism might explain the decay characteristics of the off-axis VOR responses following postrotatory roll tilt.

**Summary**

We measured three-dimensional eye movements and quantitatively showed that the axis of eye rotation always shifted toward alignment with gravity following postrotatory tilt. We also showed that the time constant of the horizontal postrotatory response was reduced depending on the magnitude of the postrotatory tilt. These observations led us to hypothesize that the sensory conflict induced by postrotatory tilt might explain the VOR axis shift which has been observed in monkeys (4,9,10,12,18), humans (5), and cats (6). This process of conflict resolution may work in conjunction with the process described by Guedry (21,22) to reduce sensory conflict and may provide a physical explanation for the effect of gravity on velocity storage.

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**REFERENCES**


15. Robinson DA. A method of measuring eye movement
3-D Eye Movements Following Postrotatory Tilt


