Semicircular Canal–Otolith Organ Interaction During Off-Vertical Axis Rotation in Humans

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Received: 10 December 1999; Accepted: 02 October 2000; Online publication: 23 March 2001

ABSTRACT

The aim of this study was to examine the interaction of signals from the semicircular canals and the otolith organs during off-vertical axis rotation (OVAR). We recorded horizontal eye position using electro-oculography in 22 young normal human subjects and stimulated the vestibulo-ocular reflex with both constant velocity trapezoids and sinusoidal yaw rotations, using both earth-vertical axis rotation (EVAR) and OVAR. We found that per-rotatory long vestibulo-ocular reflex (VOR) time constants during velocity trapezoids were shorter for OVAR than for EVAR, suggesting a reduction in the efficacy of the velocity storage system during OVAR. However, when we tested with very-low-frequency sinusoids (0.01 Hz and below), the phase lead of the VOR *re* head velocity was smaller during OVAR than EVAR, suggesting a longer time constant and enhanced efficacy of velocity storage during OVAR. These rotational responses can be explained by two competing influences of signals from the otolith organs, one that diminishes the effectiveness of velocity storage and another that contributes to an estimate of head velocity.

Keywords: VOR, human, otolith, vestibulo-ocular reflex, velocity storage

INTRODUCTION

The vestibulo-ocular reflex (VOR) produces compensatory eye movements that counter normal head movements and is driven by vestibular signals arising from both the semicircular canals and the otolith organs. For rotations about an earth-vertical axis, which primarily stimulate the horizontal semicircular canals, the performance of the VOR is better at low frequencies of head movements than would be predicted by examining the vestibular signals arising directly from the semicircular canals. This improvement in the performance of the VOR at low frequency is due, in part, to a phenomenon called “velocity storage” (Robinson 1977; Raphan et al. 1977), which appears to act as a memory, or storage, of current head velocity. Such storage is also manifested by a lengthening of the VOR time constant beyond that predicted from semicircular canal afferents.

The aim of the present study was to assess semicircular canal–otolith organ interaction during yaw rotation about an axis tilted slightly from earth-vertical, so-called off-vertical axis rotation (OVAR). OVAR produces both a time-varying otolith stimulation and a simultaneous horizontal semicircular canal stimulus. Two aspects of the otolith organ influence on the dynamics of the horizontal component of the VOR are well known. One is the appearance of a unidirectional “bias” component during rotation at constant velocity about an off-vertical axis (Guedry 1965; Stockwell et al. 1971; Raphan et al. 1981; Darlot et al. 1988; Furman et al. 1992). Another is the shortening of the VOR time constant produced either by tilting the head immediately following cessation of rotation about an earth-vertical axis (Benson and Bodin 1966a; Schrader et al. 1985; Waespe et al. 1985; Hain et al. 1988) or by stopping OVAR and leaving the axis tilted (Benson

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and Bodin 1966b; Raphan et al. 1981; Koizuka et al. 1996).

We have been evaluating OVAR as a convenient, clinically feasible, otolithic stimulus. Both constant-velocity and sinusoidal earth-vertical axis rotation (EVAR) are used routinely in the clinical testing of vestibular function (Baloh and Honrubia 1990). We assessed similar rotational paradigms using OVAR (Furman et al. 1992, 1993) and reported in a preliminary study (Furman and Schor 1997) the following paradoxical response to sinusoidal OVAR: Using an acceleration pulse to quickly reach constant velocity rotation, we found that the time constant of the decay of the per-rotatory horizontal slow-component velocity (SCV) was shorter with OVAR stimuli than with EVAR, a result consistent with responses during earth-horizontal axis rotation (Wall and Furman 1989). One can interpret this as saying that during OVAR, the VOR is "less good" at maintaining eye velocity near the ongoing head velocity than during EVAR. However, during sinusoidal OVAR stimuli, responses were more in phase with the rotation, i.e., "better," or closer to head velocity, than those observed with EVAR. Although the observation that eye velocity during sinusoidal earth-horizontal axis rotation tracks head velocity better than during sinusoidal EVAR has been reported by Benson (1974), and Angelaki and Hess (1996a) showed similar responses from rhesus monkeys, the apparent discrepancy in eye velocity response between constant velocity and sinusoidal OVAR responses has not been explored previously.

The shortening of the OVAR time constant with constant-velocity rotation suggests a reduction in the efficacy of velocity storage. However, the reduced phase lead when stimulating with OVAR sinusoids can be interpreted as an enhancement of velocity storage, just the opposite phenomenon. The present study was designed to clarify and explain these *observations*. In a large group of normal subjects, we systematically compared responses to OVAR at constant velocity with OVAR responses during sinusoidal rotation using several different tilt angles, rotational velocity amplitudes, and frequencies.

METHODS

Young, healthy volunteers (10 females and 12 males, 18–30 years old) were used in this study. None of the subjects had any history of otologic or neurologic abnormality, or abnormalities on a standard laboratory battery of ocular motor tests and caloric irrigations. All experimental subjects signed an informed consent form approved by the Institutional Review Board of the University of Pittsburgh prior to testing. Twenty subjects (10 females and 10 males) underwent the

complete set of rotational tests described below. Two additional males underwent a limited set of ultra-low-frequency sinusoidal rotations.

Subjects were seated on a rotation chair affixed to a computer-controlled 80 ft-lb (110 Nm) turntable attached to a tilt stand. A cylindrical enclosure with a radius of 1 m surrounded the test chair and was mounted to a tilt platform. A head restraint device limited relative motion between the head and the chair. Subjects wore insert earphones that allowed communication and masked localizing auditory cues.

This study focuses on the dynamics of the per-rotatory VOR induced by yaw EVAR and OVAR stimuli. For EVAR, the resulting eye movement has only a horizontal component. During OVAR, there are some vertical and torsional components to the eye movements, perhaps because of an effect of otolith organ signals on the orientation of Listing's Plane (Darlot et al. 1988; Angelaki and Hess 1996b; Furman and Schor 1998), but the major component of the eye movement, certainly the one elicited by the horizontal semicircular canal response to the (yaw) rotation, is horizontal. We accordingly analyze and report only the horizontal component of the eye movements, which were measured with DC-coupled electro-oculography using an optically isolated preamplifier (Templin Engineering, Claytonville, CA) and an amplifier with a low-pass filter whose cutoff frequency was 40 Hz. Eye movements were recorded on a chart recorder and sampled by a PDP 11/73 computer using a 12-bit analog-to-digital converter with a sampling rate of 100 Hz. The horizontal electro-oculography signal was calibrated by asking each subject to gaze at targets placed 10° to the left and right of center. Vertical eye movements were recorded only as an aid in detecting blink artifacts in the horizontal traces. To maintain subject alertness, prerecorded trivia questions were presented through the earphones and subjects were instructed to answer them throughout each trial.

Rotational testing consisted of both EVAR (tilt of 0°) and OVAR (tilts of 10°, 20°, or 30°) stimuli with eyes opened behind darkened goggles. Two types of rotation profiles were used. One was a velocity trapezoid consisting of a brief acceleration (100°/s²) to a final velocity (30°/s–180°/s, see Tables 1–3), a period of constant velocity lasting about 50–70 s until the per-rotatory nystagmus appeared to reach a baseline, then a deceleration to a stop. For EVAR, the chair remained at 0° tilt; for OVAR, the chair was tilted 10°–30° (see Tables 1–3). The second profile consisted of 3–5 cycles of low-frequency (0.01, 0.02, or 0.05 Hz) sinusoids of varying peak velocity (see Tables 4 and 5). Sinusoidal trials were performed using both EVAR and 30° OVAR. The stimuli were randomized (including the direction of the velocity trapezoid); several visits were required

TABLE 1

Gain of per-rotatory slow-component eye velocity during velocity trapezoid rotation. Four stimulus velocities were tested using either EVAR (0° column) or OVAR (10°, 20°, or 30° columns). For OVAR trials, the upper value is obtained from a single-exponential model [Eq. (1)], the lower from a model that incorporates the buildup of the OVAR "bias component" [Eq. (2)]. Values represent the mean and standard deviation of the values obtained from 20 subjects

Chair velocity	Tilt angle			
	0° (EVAR)	10°	20°	30°
30°/s	0.54 ± 0.19			0.48 ± 0.17 0.49 ± 0.24
60°/s	0.56 ± 0.13			0.48 ± 0.18 0.49 ± 0.15
120°/s	0.56 ± 0.12		0.55 ± 0.14 0.58 ± 0.12	
180°/s	0.54 ± 0.13	0.59 ± 0.15 0.58 ± 0.12		

TABLE 2

Time constant (s) of slow-component eye velocity during constants-velocity rotation

Chair velocity	Tilt angle			
	0° (EVAR)	10°	20°	30°
30°/s	16.2 ± 6.2			11.0 ± 5.6 10.3 ± 5.8
60°/s	18.0 ± 7.7			13.3 ± 5.8 13.8 ± 9.0
120°/s	15.0 ± 4.8		10.6 ± 5.8 11.0 ± 4.8	
180°/s	12.9 ± 3.2	9.0 ± 3.0 9.7 ± 3.4		

TABLE 3

Offset for EVAR trials and bias for OVAR trials of slow-component eye velocity during velocity trapezoid rotation

Chair velocity	Tilt angle			
	0° (EVAR)	10°	20°	30°
30°/s	-0.7 ± 1.3			2.5 ± 1.6 3.2 ± 2.0
60°/s	-2.1 ± 2.2			3.9 ± 3.1 3.3 ± 4.1
120°/s	-3.3 ± 2.6		3.1 ± 5.2 1.2 ± 3.9	
180°/s	-4.0 ± 3.2	0.6 ± 2.6 -1.1 ± 3.8		

for each subject to complete all of the experimental trials.

Horizontal eye position data were digitally differentiated and the fast components of nystagmus identified and removed by computer (Wall and Black 1981) with operator intervention. The resulting SCV records were

used to generate parametric measures of the responses. To analyze the per-rotatory, postacceleratory EVAR and OVAR responses to velocity trapezoids, we fit (using standard nonlinear least-squares methods) a decaying exponential to the SCV to estimate the long (dominant) VOR time constant. To account for the

TABLE 4

Gain of slow-component eye velocity during sinusoidal rotation. All OVAR trials used 30° tilt

Chair velocity	EVAR frequency			OVAR frequency		
	0.01 Hz	0.02 Hz	0.05 Hz	0.01 Hz	0.02 Hz	0.05 Hz
25°/s	0.29 ± 0.09	0.38 ± 0.09		0.25 ± 0.05	0.32 ± 0.07	
50°/s	0.31 ± 0.10			0.24 ± 0.06		
100°/s			0.49 ± 0.11			0.47 ± 0.11
150°/s		0.42 ± 0.12	0.50 ± 0.12		0.38 ± 0.09	0.47 ± 0.12

TABLE 5

Phase lead of slow component eye velocity during sinusoidal rotation

Chair velocity	EVAR frequency			OVAR frequency		
	0.01 Hz	0.02 Hz	0.05 Hz	0.01 Hz	0.02 Hz	0.05 Hz
25°/s	57° ± 11°	26° ± 7°		38° ± 8°	25° ± 6°	
50°/s	49° ± 7°			39° ± 9°		
100°/s			12° ± 3°			13° ± 4°
150°/s		33° ± 6°	16° ± 5°		32° ± 7°	17° ± 5°

“bias” component observed during OVAR, we added a constant term to our equation. We expected that, for EVAR trials, this constant term would be near zero or perhaps slightly negative because of the small undershoot of the response to a velocity trapezoid (Sills et al. 1978). The equation for velocity trapezoids, fit using a nonlinear least-squares regression algorithm, is

$$\text{SCV}(t) = \text{Mag} \cdot e^{-t/\tau} + C \quad (1)$$

where Mag is the initial magnitude of the exponential response, τ is the dominant VOR time constant, and C is the baseline observed once the SCV decays to a constant value and corresponds to the bias component of OVAR. To better account for a presumed gradual buildup of the bias component during constant-velocity OVAR, we also fit the OVAR responses with a slightly modified equation:

$$\text{SCV}(t) = \text{Mag} \cdot e^{-t/\tau} + \text{Bias} \cdot (1 - e^{-t/5}) \quad (2)$$

which assumes that the bias component attains its steady-state value with a time constant of 5 s. We chose a time constant of 5 s based on OVAR data from Raphan et al. (1981), who rapidly tilted the axis of rotation from vertical to off-vertical. We relied on these data from monkey because comparable data are not available from humans. Moreover, a time constant of 5 s is reasonable given other human time-dependent VOR phenomena, such as the reorientation of postrotatory nystagmus and optokinetic after-nystagmus. Also, our data from constant-velocity rotate-then-tilt OVAR paradigms, which require about 20 s to reach

a 30° off-vertical tilt, indicate that the bias component has reached a steady state by the time the off-vertical tilt has been achieved (Furman et al. 1992). We computed a gain for velocity trapezoid trials by dividing the Mag coefficient by the stimulus velocity.

In using Eqs. (1) and (2) to estimate the gain, bias, and dominant time constant of the per-rotatory OVAR responses, we are, perforce, ignoring the small sinusoidal modulation, often called the “modulation component,” that OVAR induces. These sinusoidal responses were not of interest to us in this study, and, for the stimuli used, these sinusoidal responses are small, with an amplitude of a few degrees per second (Furman et al. 1992). To ensure that our estimates of fit parameters were not unduly affected by ignoring the modulation component, we fit Eqs. (1) and (2) to simulated responses with modulation components of 6°/s (larger than we typically observed) and varying phase and found that the errors in parameter estimates were less than 5%. Thus, ignoring the modulation component did not introduce a significant error in our estimates of OVAR response parameters. We chose this simpler analysis to avoid fitting an excessive number of parameters to data that were often noisy.

For sinusoidal trials the first cycle of data was discarded to avoid any influence of a transient response. Each of the remaining cycles were fit on a cycle-by-cycle basis by the following equation:

$$\text{SCV}(t) = \text{Mag} \cdot \sin(2\pi ft + \varphi) + \text{Offset} \quad (3)$$

where f is the stimulus frequency (in Hz), φ is the

response phase *re* head velocity, and Offset is the (typically near-zero) DC offset. These quantities were then averaged across the cycles of the trial. We adopted a phase convention where a phase of 0 corresponds to a perfect compensatory response, i.e., eye movement exactly opposite to the rotational stimulus.

To guard against a few outlier points distorting the estimates of the fit parameters, we adopted an iterative wild-point editing scheme. For each data set for which a fit was obtained, we calculated the standard deviation of the observed data points from the predicted values. Data points lying more than three standard deviations from the predicted fit were eliminated, and another set of fit parameters were obtained until no more outlier points were eliminated. In general, 1% of the data points were eliminated by this procedure.

A statistical analysis was performed using several ANOVAs with a repeated measures design and *post hoc* contrasts. For responses to velocity trapezoids, two ANOVAs were performed, one for gain and one for time constant. EVAR vs. OVAR and velocity were factors. For sinusoidal data, two ANOVAs also were performed, one for gain and one for phase. EVAR vs. OVAR, stimulus frequency, and peak velocity were factors. Before performing the ANOVAs, we removed from the data set those fits that contained a parameter estimate that, when compared across our subject population, lay more than 3 standard deviations from the mean. Using this criterion, eight of 240 fits of responses to velocity trapezoids were removed. No fits were removed from the sinusoidal data, but one sinusoidal trial for one subject was not performed for technical reasons.

RESULTS

Response to velocity trapezoids (constant velocity)

The response of one subject to a 60°/s velocity trapezoid is illustrated in Figure 1. Note that during the EVAR trial, the eye velocity takes longer to decay to a baseline than during the OVAR trial. The gain of the response (peak eye velocity/chair velocity) was relatively constant across trials and across subjects, with no obvious dependence on either the speed of chair rotation or the presence (or lack thereof) of axis tilt (see Table 1). In contrast, the time constants estimated from Eqs. (1) and (2) were shorter following OVAR stimuli (Table 2). This effect of tilt on the time constant was statistically significant ($p < 0.01$) and suggests that the stimulation of the otolith organs during OVAR velocity trapezoids resulted in reducing velocity storage.

The offset [C, Eq. (1)] and bias [Bias, Eq. (2)]

FIG. 1. The per-rotatory responses of one subject to constant-velocity rotation at 60°/s, both earth-vertical (EVAR) and while the axis of rotation was tilted 30° (OVAR). Superimposed on the slow-component eye velocity responses are the exponential fits used to estimate the magnitude, dominant time constant, and offset (or bias) of the response. Note that the OVAR response has a shorter time constant (9 s) than does the EVAR response (16 s).

estimates are given in Table 3. Note that the value of the offset during EVAR is near zero but slightly negative. This suggests that there is a small adaptation component in the response that, in our single-exponential model, appears as a small negative offset. For OVAR trials, the bias values for the most part were positive, especially for the larger tilt angles. When compared with the small negative offset seen in the EVAR trials, this positive bias in the OVAR response reflects the contribution of the otolith organs to the estimate of rotational head velocity.

Responses to low frequency sinusoidal stimulation

Tables 4 and 5 show, respectively, the gain and phase of the sinusoidal responses during both EVAR and OVAR rotations. There was a small but statistically significant ($p < 0.01$) reduction of the gain of the response during OVAR stimuli (notice the mean gain is smaller for every stimulus frequency and peak velocity combination tested). The effect of the axis tilt on the response phase was statistically significant ($p <$

FIG. 2. Responses of one subject to ultra-low-frequency sinusoidal oscillation, both EVAR and OVAR (30° tilt). The stimulus was a $60^\circ/\text{s}$ 0.0025-Hz sinusoid (rotational velocity plotted on lower graph). Superimposed on the slow-component eye velocity are the sinusoidal fits to the data. Note that the OVAR response has a smaller phase lead (25° *re* perfect compensation) than does the EVAR response (94°).

0.01), but more complex, as there was a significant interaction between the “axis effect” and the stimulus frequency. *Post hoc* comparisons revealed that the significant effect of tilt on phase lead was restricted to the 0.01-Hz trials. Thus, at the lowest frequency, the OVAR response is temporally better aligned with the stimulus velocity, which in a linear system corresponds to a *lengthening* of the VOR time constant in the time domain.

This apparent discrepancy between the response to constant-velocity OVAR, which appears to exhibit a reduction of velocity storage (and therefore a “worse” velocity response compared with EVAR), and the response to sinusoidal OVAR stimulation, which at the low frequency of 0.01 Hz appears to show a better velocity response compared with EVAR, led us to test two additional subjects (males, ages 23 and 26) using sinusoidal frequencies of 0.0025 and 0.005 Hz at a peak velocity of $60^\circ/\text{s}$. One such response is illustrated in Figure 2. Note that the response during the OVAR trial (30° tilt) is aligned more closely with the stimulus than during the EVAR trial. The gain and phase data are illustrated in Table 6. They confirm the observation that, at very low frequencies, the phase lead of the VOR during sinusoidal OVAR is smaller than during EVAR, implying that eye velocity during OVAR is more closely synchronized with head velocity than when rotating about an earth-vertical axis.

TABLE 6

Responses of two subjects to ultra-low-frequency sinusoidal stimulation. Gain and phase ($^\circ$) for each subject are shown

Gain	EVAR frequency		OVAR frequency	
	0.0025 Hz	0.005 Hz	0.0025 Hz	0.005 Hz
Subj 1	0.10	0.24	0.14	0.15
Subj 2	0.10	0.27	0.20	0.31
Phase				
Subj 1	129°	74°	51°	43°
Subj 2	94°	74°	25°	30°

DISCUSSION

The results of the present study show that when stimulus conditions are such that the otolith signals vary with time, this changing otolith signal can interact with the horizontal semicircular canal VOR to produce either a lengthening or a shortening of the apparent VOR time constant. Specifically, when the dominant time constant of the horizontal VOR is estimated from per-rotatory yaw velocity trapezoid responses, the time constant is shortened for OVAR trials, suggesting that the simultaneous otolith signal has led to a reduction of velocity storage. This is true despite the fact that the same dynamic otolith signal is simultaneously producing the horizontal “bias component” of the OVAR response.

In contrast, when the rotational stimulus consists of extremely-low-frequency sinusoidal yaw stimuli (0.01 Hz and below), the resulting horizontal eye velocity is closer in phase to the head velocity, as though the dynamic otolith stimulus is helping to produce a more faithful representation of head motion.

No direct comparison has been made previously between responses to constant-velocity OVAR and responses to sinusoidal OVAR. However, several published observations indicate that our results are consistent with those of previous investigators. Wall and Furman (1989) reported a shortened time constant in humans during constant velocity rotation using 90° off-vertical tilt. The data reported herein extend these results to much smaller tilt angles (10° – 30°) and confirm that the effect is seen at multiple rotational velocities. This observation regarding the VOR time constant could not be made in monkeys because the bias component is so large that there is effectively no exponential decay of slow-component velocity. The reduction in phase lead that we observed during sinusoidal rotation was noted by Benson (1974) during earth-horizontal axis rotation. Our results extend this observation by showing the effect is robust across a large sample and

FIG. 3. Model for semicircular canal and otolith organ estimation of head velocity. The otolith organ system estimates head velocity from the (moving) gravity vector; this contribution sums with that from the semicircular canals and feeds into the velocity storage system, here represented as a positive feedback loop through a leaky integrator. The effect of a tilted rotation axis is to reduce by one third the gain of this feedback loop.

that the reduction in phase lead becomes more pronounced at very low frequencies of rotation.

For linear systems, steady-state and transient responses are directly comparable and can be estimated from one another. The discrepancy in results from sinusoidal trials (OVAR responses are more like the velocity stimulus) and velocity trapezoid trials (OVAR responses are less like the velocity stimulus) in this study suggests that some nonlinear process may be taking place in the interaction between semicircular canal and otolith organ signals.

To investigate the underlying basis for our results, we constructed a model of the horizontal vestibulo-ocular reflex that includes semicircular canal–otolith organ interaction (Fig. 3) and examined the model's response to a velocity step and to sinusoidal stimuli. We assume that the labyrinth provides two independent estimates of head velocity, one directly via the semicircular canals, and another indirectly through the otolith organ system's analysis of the changing orientation of the gravity vector during OVAR. During EVAR, we assume the otolith organ system estimates a head velocity of 0 (due to the unchanging gravity vector). The semicircular canal contribution to this estimate of head velocity is a cascade of a high-pass filter with a time constant of 6 s, representing the semicircular canal fluid dynamics, and an adaptation operator with a time constant of 80 s. During OVAR, we assume that the otolith organ system (through central neural processing) can compute an accurate estimate of head velocity, which is then low-pass filtered with a time constant of 5 s, representing the “build up” of the horizontal bias component observed during OVAR. Several investigators have modeled the neural processing that might produce such OVAR estimates of head velocity (Hain 1986; Raphan and Schnabolk 1988; Merfeld et al. 1993). These two estimates are then summed and fed through a “velocity storage” loop, here represented by a positive feedback loop through a leaky integrator that, with a gain of 0.75, has the net effect of lengthening the dominant VOR time constant from 6 to 16 s. When the head is tilted, as during OVAR, the gain of the velocity storage loop

FIG. 4. Response of model shown in Figure 3 to a velocity step of 60°/s (per-rotatory response). The EVAR response is dashed, the OVAR response is a solid line. Note that the model predicts both a nonzero per-rotatory offset (“bias” component) for OVAR and a shorter time constant for the OVAR response (9.5 s) than for the EVAR response (16 s). Parameter values used: $g_0 = 0.05$; $g_c = 0.6$; $k_{vs} = 0.75$; $t_c = 6$ s; $t_0 = 5$ s; $t_a = 80$ s. The gain of the velocity storage loop, k_{vs} , is reduced to 0.5 for nonzero Rotation Axis Tilt (i.e., during OVAR).

is reduced by a third to account for the decreased efficacy of velocity storage during tilt.

Figure 4 shows the behavior of this model when tested with a velocity step. As expected from the design of this simple model, the EVAR response, when fit with a single exponential decay, has a time constant of 16 s and decays to 0, while the OVAR response has a shorter time constant (8.7 s) and exhibits a nonzero offset, i.e., a “bias” component. This behavior is consistent with the per-rotatory responses reported in this study (compare Fig. 4 with Fig. 1).

When the same model is stimulated with sinusoids, the model shows similar responses to EVAR and OVAR stimuli at frequencies above about 0.01 Hz, but the responses begin to diverge, particularly in the phase of the response, at lower frequencies (Fig. 5). The EVAR response at the lowest frequencies has a significantly larger phase lead than does the OVAR response. We have plotted the data summarized in Tables 4–6 on the same set of axes in Figure 5 for comparison.

FIG. 5. Bode plot of the frequency response of model shown in Figure 3 (parameters are identical to those of Fig. 4). As in Figure 4, the EVAR response is a dashed line, the OVAR response is a solid line. Superimposed on the model response are the gains and phases recorded from our subjects. For frequencies at 0.01 Hz and above, responses are shown as mean $\pm$ one standard deviation, while at the lowest two frequencies, the data from the two subjects are plotted directly. EVAR responses are indicated by X's, and OVAR responses are indicated by squares.

Our model, though simple, accounts for the observation, during OVAR, of the apparent reduction of velocity storage during velocity trapezoid (constant velocity) rotation and the paradoxical "improvement" of the response during sinusoidal rotation. The model suggests that even though velocity storage is less effective during OVAR (and therefore contributes minimally to making the response "closer to velocity"), the contribution by the otolith organs to the estimate of head velocity during the sinusoidal stimulation more than compensates for the reduction of velocity storage. The remarkable agreement between our experimental data and our model simulations, especially during the ultra-low-frequency sinusoidal rotations, further emphasizes the importance of including otolith signals in models of the VOR.

ACKNOWLEDGMENTS

The authors thank Anita Lieb and Timothy Schumann for their technical assistance. This work was supported by NIH grants Nos. DC01791, DC03417, and DC02421.

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