Dynamics of Squirrel Monkey Linear Vestibuloocular Reflex and Interactions with Fixation Distance

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Telford, Laura, Scott H. Seidman, and Gary D. Paige. Dynamics of squirrel monkey linear vestibuloocular reflex and interactions with fixation distance. J. Neurophysiol. 78: 1775-1790, 1997. Horizontal, vertical, and torsional eye movements were recorded using the magnetic search-coil technique during linear accelerations along the interaural (IA) and dorsoventral (DV) head axes. Four squirrel monkeys were translated sinusoidally over a range of frequencies (0.5-4.0 Hz) and amplitudes (0.1-0.7 g peak acceleration). The linear vestibuloocular reflex (LVOR) was recorded in darkness after brief presentations of visual targets at various distances from the subject. With subjects positioned upright or nose-up relative to gravity, IA translations generated conjugate horizontal (IA horizontal) eye movements, whereas DV translations with the head nose-up or right-side down generated conjugate vertical (DV vertical) responses. Both were compensatory for linear head motion and are thus translational LVOR responses. In concert with geometric requirements, both IA-horizontal and DV-vertical response sensitivities (in deg eye rotation/cm head translation) were related linearly to reciprocal fixation distance as measured by vergence (in m⁻¹, or meter-angles, MA). The relationship was characterized by linear regressions, yielding sensitivity slopes (in deg · cm⁻¹ · MA⁻¹) and intercepts (sensitivity at 0 vergence). Sensitivity slopes were greatest at 4.0 Hz, but were only slightly more than half the ideal required to maintain fixation. Slopes declined with decreasing frequency, becoming negligible at 0.5 Hz. Small responses were observed when vergence was zero (intercept), although no response is required. Like sensitivity slope, the intercept was largest at 4.0 Hz and declined with decreasing frequency. Phase lead was near zero (compensatory) at 4.0 Hz, but increased as frequency declined. Changes in head orientation, motion axis (IA vs. DV), and acceleration amplitude produced slight and sporadic changes in LVOR parameters. Translational LVOR response characteristics are consistent with high-pass filtering within LVOR pathways. Along with horizontal eye movements, IA translation generated small torsional responses. In contrast to the translational LVORs, IA-torsional responses were not systematically modulated by vergence angle. The IA-torsional LVOR is not compensatory for translation because it cannot maintain image stability. Rather, it likely compensates for the effective head tilt simulated by translation. When analyzed in terms of effective head tilt, torsional responses were greatest at the lowest frequency and declined as frequency increased, consistent with low-pass filtering of otolith input. It is unlikely that IA-torsional responses compensate for actual head tilt, however, because they were similar for both upright and nose-up head orientations. The IA-torsional and -horizontal LVORs seem to respond only to linear acceleration along the IA head axis, and the DV-vertical LVOR to acceleration along the head’s DV axis, regardless of gravity.

INTRODUCTION

The vestibuloocular reflex (VOR) generates compensatory eye movements that help maintain binocular fixation on targets in space during head motion. There are two classes of VOR, each governed by different vestibular end organs. The angular VOR (AVOR) is driven by the semicircular canals in response to head rotations, whereas the linear VOR (LVOR) is driven by the otolith organs in response to linear head accelerations. The latter is the focus of this report.

During the past decade, important advances have occurred in our understanding of the LVOR, largely due to the recognition of two key considerations that govern LVOR response properties. The first is that the otolith organs, and peripheral afferents that innervate them, respond equally well to two kinds of linear acceleration, those produced by head tilt relative to gravity and those generated by head translation. This physical property (Einstein’s equivalency principle) makes otolith input inherently ambiguous and presents a problem because the ocular responses required to compensate for tilt and translation differ. For example, head roll-tilt requires compensatory torsion of the eyes (ocular counterrolling), whereas interaural (IA) head translation, which produces nearly the same otolith stimulus, requires horizontal rotation of the eyes to maintain a stable image. Although selective processing of input from multiple afferents with different directional sensitivities might help resolve the ambiguity under constrained conditions, this cannot resolve the general problem (Holly and McCollum 1996). Further, such complex processing does not seem to occur in the LVOR. Both horizontal and torsional responses occur simultaneously in response to either IA acceleration or roll-tilt (Paige and Tomko 1991a; Paige et al. 1995), and neither type of LVOR systematically changes with head orientation relative to gravity. In short, the two LVORs behave as if responding exclusively to IA acceleration.

An alternative solution to otolith response ambiguity can be achieved largely by a central parsing of linear accelerations on the basis of frequency content (Gueldry 1974; Mayne 1974). In this scheme, tilt pathways select for static and low-frequency accelerations, while translation pathways select for high-frequency inputs. This solution is harmonious with natural behavior. Translational accelerations are typically transient or high frequency (e.g., during walking or running) and are never continuous, whereas tilt often is prolonged (e.g., lying down). Studies of LVOR function support a frequency-selective scheme but with considerable overlap between functions. For example, although IA acceleration generates both tilt (torsion) and translational (horizontal) responses simultaneously, the two are governed by different frequency-dependent dynamics (Paige and Tomko 1991a). In general, translational LVORs behave with high-pass dynamics and include horizontal responses to IA mo-
tion, vertical responses during dorsoventral (DV) motion, and complex responses to nasooccipital motion. In contrast, tilt-LVORs behave with low-pass characteristics and include torsional eye movements during IA motion (equivalent to head roll-tilt) and vertical responses during nasooccipital motion (equivalent to head pitch-tilt). However, the precise dynamic characteristics and interactions between the different LVORs as a function of both the frequency and amplitude of head acceleration remain unexplored. This study quantifies LVOR dynamics and linearity during head translations limited to the IA and DV axes, focusing on a high-frequency range associated with natural linear motion.

A second important consideration is that the kinematic requirements of compensatory responses to head translation, but not tilt, depend on fixation distance. This is particularly critical in frontally-eyed bifoveate species such as primates. To maintain binocular foveal fixation on targets in space, the LVOR must accommodate for the shifting geometric relationship between the eyes and the target. During head translation orthogonal to the line of sight, the ideal ocular response is inversely proportional to fixation distance. Thus little or no eye movement is required during translation when fixating a distant target, but progressively larger ocular responses are required to maintain fixation as the target nears.

Several studies have shown that translational LVOR responses indeed are modulated by fixation distance, particularly during transient or high-frequency motion where visual or contextual influences are minimal (Busettini et al. 1994; Paige 1989; Paige and Tomko 1991b; Paige et al. 1996a; Schwarz and Miles 1991). The central signal responsible for this modulatory influence is linked closely to a command related to binocular vergence (Paige 1991; Paige and Tomko 1991b; Snyder et al. 1992) and, to some extent, accommodation of the intraocular lens (Schwarz and Miles 1991). The frequency and amplitude-dependent limitations of the vergence or accommodation influence remain to be explored. This study extends previous work by providing a direct and systematic quantification of response dynamics and linearity of the translational LVOR while taking the kinematic requirements of binocular fixation distance into account.

METHODS

Subjects and surgical preparation

Experiments were performed using four male squirrel monkeys (Saimiri sciureus) weighing 0.75–1.0 kg. All procedures were done in accordance with guidelines established by an internal review board. Surgical preparation has been described in detail previously (Paige and Tomko 1991a). Briefly, ocular search coils for eye movement recording and a head-fixation bolt for painlessly positioning and fixing the head, were implanted using aseptic technique under inhalation anesthesia (isoﬂurane). A 6.4-mm-diam stainless steel bolt, flattened along the shaft, was ﬁxed to the back of the skull using dental acrylic and stainless steel screws that were inverted and anchored in keyhole slots. The flat surface of the bolt was positioned parallel to the horizontal canal plane. After a lateral canthotomy and conjunctival peritomy, a prefabricated Tellon-in- sulated stainless steel wire coil (12-mm diam, 3 turns; Cooner AS631) was sutured to the sclera in the frontal plane of each eye, and a smaller (8 mm, 4 turn) coil was sutured to the globe laterally and close to the sagittal plane of the right eye. Twisted-pair leads from each coil exited the eye temporally and were routed subcuta-
FIG. 1. Apparatus used to generate linear motion profiles. The translational axis consisted of a 1.2-m-long linear sled (T) mounted on top of an angular rate table (R). A carriage attached to the sled supported a superstructure that contained several angular positioning axes (P1–P3), which were used to place subjects in different orientations relative to the sled’s motion axis and to gravity. P1 allowed the cantilevered arm of the superstructure to be oriented orthogonal (as shown in Fig. 1) or parallel to the linear sled. The primate chair was held in a second angular positioning axis (P2) that was used to manually fix the subject in any yaw position relative to the cantilevered arm. An angular positioning axis (P3) was servo-controlled and was oriented earth horizontally. It was used to alter and fix the subject’s orientation relative to gravity.

TABLE 1. Stimulus parameters

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<th>Frequency, Hz</th>
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extinguished for intervals lasting several seconds, yielding several alternating light-dark periods. Large vergence angles generally were maintained only briefly in darkness after presentation of visual targets, but the repeated light-dark transitions produced a sufficient number of cycles over a large range of vergence angles.

Data analysis

HARMONIC ANALYSIS. Binocular horizontal and vertical, and monocular torsional eye position signals (5 total), as well as sled and on/off light sensor signals, were sampled at 200 Hz by an IBM-compatible computer and stored for off-line analysis (Telford et al. 1996). During analysis, the software defined individual cycles by identifying zero-crossings of the stimulus. All eye position signals were digitally differentiated and smoothed to yield eye velocities. For 4.0-Hz stimuli, a large number of cycles were available that were saccade-free. These were selected for analysis, whereas those containing saccades were discarded. At lower frequencies, saccades were removed from eye-velocity records using an interactive paradigm that performed an iterative least-squares sinusoidal fit and windowing procedure. For all frequencies, individual cycles across all five ocular response signals were selected simultaneously and subjected to harmonic analysis on a cycle-by-cycle basis. To ensure that translatational LVOR responses were not influenced by vision, we included only complete cycles that began $\approx 250$ ms after the lights were extinguished. Least-square fits at the fundamental frequency then were used to calculate sensitivity [peak slow phase eye velocity (in deg/s)/peak linear head velocity (in cm/s); reducing to deg/cm], phase (phase of eye velocity relative to phase of head velocity), and mean eye position over each cycle and for all five ocular response signals. The right eye was used as the reference for all further analysis and figures, with the important exception that mean vergence was calculated as the difference between left and right mean horizontal eye position for each cycle.

KINEMATICS OF THE LVOR. To assess the influence of fixation distance on LVOR responses, vergence angle was linked with sensitivity and phase measures on a cycle-by-cycle basis. Vergence is expressed in meter angles (MA), the reciprocal of fixation distance. For example, 1 MA would be required for binocular fixation of a target located 1 m away, and 2 MA would be required for a target at 0.5 m. This unit provides a form of vergence normalization that allows direct comparisons between different subjects and species regardless of head size and ocular separation (1.7 cm in squirrel monkeys).

Figure 2 illustrates the geometry of compensatory LVOR responses to linear motion along the DV (shown) or IA head axes. The ideal LVOR response ($\theta_i$) is determined by the magnitude of the head translation ($z$) and the target distance ($d$) according to the following derivation

$$\theta_i = \tan^{-1} \frac{z}{x}$$

from which an ideal sensitivity ($S_i$) can be derived, given that $x = d \cos \theta_i$

$$S_i = \frac{\partial \theta_i}{\partial z} = \frac{1}{1 + \left( \frac{z}{x} \right)^2} \frac{1}{d} \cos \theta_i$$

For small angles, $\cos \theta_i \approx 1$, and therefore $S_i \approx 1/d$ (in rad/m). Converting units

$$S_i = 0.57 \frac{1}{d} \approx 0.57 \cdot \frac{v}{v}$$

where $v$ is vergence in MA, and $S_i$ is in deg/cm.

Equation 3 demonstrates a simple linear relationship between ideal LVOR sensitivity ($S_i$) and vergence (MA), governed by a scale factor of $0.57 \times \text{cm}^{-1} \cdot \text{MA}^{-1}$. Actual LVOR response sensitivities ($S$) indeed demonstrate a similar linear relationship with vergence (Paige 1991; Paige and Tomko 1991a; Schwarz and Miles 1991).

Analysis proceeded in steps by which sensitivities and phases for each of the five response signals were first combined into 1 MA bins from 0 to 10 MA and then subjected to regressions to produce best fit lines to the data, yielding sensitivity slopes (typically $<0.57 \times \text{cm}^{-1} \cdot \text{MA}^{-1}$), intercepts (response sensitivity at 0 MA vergence), and phase angles as a function of vergence. The number of cycles represented in each bin varied as a function of frequency and vergence. At 4 Hz, dozens of cycles were available at lower vergences, declining to typically 4–10 at the highest vergences. At 0.5 Hz, typically 4–10 cycles were available at the lowest vergence bins, but we could not usually obtain data at $>4$ MA of vergence. This is because large vergence angles are maintained only briefly in darkness and tend to drift toward a modest value of $\sim 1$ MA (Telford et al. 1996). Sufficiently stable vergences could be achieved up to $\sim 4$ MA for the 2 s required to cover a cycle at 0.5 Hz, and several such cycles could be obtained after repeated presentations of targets. The same holds for 1 Hz. In contrast, at 2 and 4 Hz, even briefly held vergences were sufficient to link high vergences with LVOR response cycles. Because vergence could change during a cycle, presumably modulating LVOR performance accordingly, cycles were excluded if large and erratic changes in vergence occurred midcycle. Shifts in vergence otherwise presented little problem, because the relationship between vergence and LVOR response amplitude is linear (Paige and Tomko 1991b; Schwarz and Miles 1991). Within-cycle shifts in vergence are matched by shifts in sensitivity within the cycle, and both parameters are derived from the entire cycle. One caveat is that changes in LVOR sensitivity precede shifts in actual vergence angle (Paige and Tomko 1991b; Snyder et al. 1992), and indeed this factor might distort results. Quantification of the precise latency difference has proven problematic, but the difference averaged only 49 ms in the study by Snyder et al. (1992). Any influence of this small difference would appear in the noise (standard deviations) of averaged binned data presented and plotted below. Errors due to latency differences between vergence and LVOR responses are small and cannot account for the robust interaction observed between them.

SIGN CONVENTION. Results are presented with reference to a sign and axis convention used previously (Paige and Tomko 1991a,b). Three cardinal axes of the head are used to describe linear motion, designated $X$ (nasooccipital; positive out the front of the head), $Y$...
LVOR responses were more robust at higher frequencies. However, for plots. Ocular responses are traditionally 180° out-of-phase to head rotations and translations but are represented here as 0° to depict the expected compensatory behavior.

RESULTS

General observations

LVOR response sensitivities during IA and DV translation were generally largest at the highest stimulus frequency of 4.0 Hz. Examples of eye movements from one subject during IA and DV translation at 4.0 Hz, 0.2 g peak acceleration, are shown in Figs. 3 and 4, respectively. IA head translations with the head in the UP orientation generated large smooth conjugate responses (shown only for the right eye) in the horizontal plane (Fig. 3B) that were compensatory for head motion (Fig. 3A). Vertical ocular responses were effectively absent (Fig. 3C), but small torsional responses were recorded (Fig. 3D; see legend). A similar response pattern was observed during IA translation with the head oriented NU. During DV motion with the head NU or RD (NU orientation shown in Fig. 4), conjugate vertical (Fig. 4C) responses were generated, but horizontal (Fig. 4B) and torsional (Fig. 4D) responses in darkness were typically negligible (see Fig. 4 legend).

For IA (Fig. 3) and DV (Fig. 4) head translations, the primary compensatory ocular responses, IA-horizontal and DV-vertical, respectively, were modulated strongly by fixation distance, as measured by vergence angle. The high vergence associated with near fixation typically was initiated in the light (bold bars above Figs. 3A and 4A). When the light was extinguished, vergence gradually declined to ~1 MA, the typical ‘dark vergence’ in squirrel monkeys (Telford et al. 1996). IA-horizontal and DV-vertical ocular responses were large when vergence was high and declined as vergence decreased. This effect was most apparent at high frequencies of stimulation. In the sections that follow, the interaction between vergence angle and stimulus frequency is considered in detail for each axis of head translation, followed by an assessment of LVOR response linearity.

Influence of stimulus frequency and fixation distance on LVOR responses

IA-HORIZONTAL LVOR. Figure 5 shows sensitivity and phase of the IA-horizontal LVOR in one monkey as a function of vergence at each of the four stimulus frequencies and with peak head acceleration fixed at 0.2 g. The apparent linear relationship between LVOR response sensitivity and vergence generally was quantified using linear regressions for all subjects. Results are exemplified in Fig. 5 as fine lines, whereas the equations for these lines are listed in the key in the form, \( S = m v + b \), where \( m \) and \( b \) correspond to the sensitivity slope and intercept of the least-square fit, respectively, and \( v \) is vergence in MA. The bold lines in Fig. 5 illustrate the ideal LVOR sensitivity (0.57v + 0; see METHODS, Eq. 3) as a function of vergence required to stabilize the point of binocular fixation in space. For all subjects and for both UP and NU head orientations, sensitivity slopes (\( m \) in deg·cm\(^{-1} \cdot \text{MA}^{-1} \)) were near zero at 0.5 Hz but increased with increasing stimulus frequency. The coefficients of determination (\( r^2 \) values, which indicate the proportion of variation explained by the linear regression model) of the least-square fits were large and increased with increasing frequency (\( r^2 \) ranged from 0.62 to 0.94 over the 0.5–4.0 Hz range of frequencies in all subjects), suggesting that responses were more robust at higher frequencies. However, even the sensitivity slope at 4.0 Hz was only slightly greater than half the ideal response.

The point where the sensitivity versus vergence functions intersect the y axis (see Fig. 5, sensitivity) provides an extrapolation of the LVOR response to zero vergence. This sensitivity intercept (like slope) increased with increasing stimulus frequency in all animals, despite the fact that no LVOR response is required at zero vergence. Note that a positive intercept results in sensitivities closer to ideal across the vergence range than if the intercept was zero (see discussion).

Response phases also are shown in Fig. 5 as a function of vergence angle. Positive values represent phase leads relative to the ideal of zero (bold traces), whereas negative values indicate phase lags. All IA-horizontal responses led head velocity, but these leads were greatest at the lowest frequencies. The fine traces for phase represent averaged values across all vergence angles at each frequency, because phase was not systematically or consistently modified by vergence. This was true for DV-vertical responses as well (see below).

IA-horizontal response sensitivities were further processed by averaging slopes and intercepts from regression equations across all monkeys and acceleration amplitudes and then plotting parameters as a function of stimulus frequency. Phases simply were averaged across all vergences, subjects, and acceleration amplitudes. Averaging across stimulus amplitudes is justified by the nearly linear performance of the LVOR over a broad range of peak accelerations (detailed below). The results are presented in Fig. 6. The majority of the variance in IA-horizontal LVOR parameters (error bars depict standard deviations) is due to between (not within) subject differences. This also holds for DV-vertical responses as a function of frequency and for both reflexes as a function of stimulus amplitude (see section on linearity below).

The data were analyzed statistically by a two-way repeated-measures analysis of variance (ANOVA; 2 head orientations and 4 stimulus frequencies) performed on each of three LVOR response parameters (sensitivity slope, intercept, and phase). Average sensitivity slopes were positive at all frequencies and increased significantly with increasing frequency \( F_{1,9} = 29.57, P < 0.001 \); where the df correspond to (4 frequencies – 1) and (4 frequencies – 1) × (4 sub-
FIG. 3. Raw ocular responses from 1 subject showing horizontal (B), vertical (C), and torsional (D) eye movements (right eye) during IA translation with the head upright (UP) at 4.0 Hz (0.2 g peak head acceleration). Head velocity is shown in A. At the beginning of the trial, the subject was shown a near visual target in the light (bold bar above A). Once a large vergence angle (bold trace in A) was elicited, the lights were extinguished and vergence declined gradually to near 0. Gap in the vergence trace corresponds to a saccadic eye movement along with a blink (B–D), which would have been removed during data analysis. Note the robust horizontal response and its apparent modulation by vergence. A small torsional response also is seen (noisy and variable in this case) but is not so clearly related to vergence.

Data in Fig. 6 also were used to evaluate potential differences in the IA-horizontal LVOR as a function of head orientation. Sensitivity slopes and phases did not differ significantly between the NU and UP head orientations, and although sensitivity intercepts recorded with the head NU were significantly lower than those in the UP orientation ($F_{1,3} = 13.54, P < 0.001$), the difference was small.

IA-TORSIONAL LVOR. In addition to the large horizontal LVOR responses observed during IA head translation, small torsional responses (IA-torsional LVOR) were generated simultaneously at all frequencies (see Fig. 3 for an example...
FIG. 4. Raw responses from a single subject showing horizontal (B), vertical (C), and torsional (D) ocular responses (right eye) during DV translation with the head nose-up (NU) at 4.0 Hz (0.2 g peak head acceleration). Bold bars above the head velocity trace in A indicate when the target was visible. Vergence angle is represented by the bold trace in A. Note the prominent vertical response and its relationship with vergence. Interestingly, just before the initial target is extinguished, a brief horizontal and torsional response is seen (corresponding to a ~0.1° ocular excursion). These are sporadic, occur also with the light off, seem most prominent at high vergences, and are not always locked with the stimulus frequency. They remain mysterious, but add noise (variance) to the data set.

at 4.0 Hz). Figure 7 (top) shows mean torsional sensitivities from three subjects (torsional data were unavailable from the fourth subject due to lateral coil failure) as a function of vergence angle. Results from the UP and NU head orientations have been averaged because a three-way (head orientation, stimulus frequency, vergence angle) within-subjects ANOVA indicated that results from UP and NU orientations did not differ significantly (see DISCUSSION). Sensitivities were not significantly modulated by vergence angle, in marked contrast to IA-horizontal responses, which were highly dependent on vergence (see Figs. 5 and 6).

In contrast to sensitivity slope, the IA-torsional response phase (not shown) was highly variable; some responses were in phase with head velocity, whereas others were out of phase. Response phase was not systematically influenced by either stimulus frequency or vergence angle. The generally small IA-torsional sensitivities probably account for the variable phase; as the signal-to-noise ratio is reduced, phase becomes increasingly variable and eventually becomes meaningless.

It has been suggested previously that IA-torsional responses are compensatory not for head translation but rather for the effective head tilt (roll) associated with IA acceleration (Paige
Horizontal Response to IA Translation

Nose-Up

- 4.0 Hz: $S = 29y + .46$
- 2.0 Hz: $S = 16y + .43$
- 1.0 Hz: $S = 12y + .14$
- 0.5 Hz: $S = 0.0y + .23$

Upright

- $S = 32y + .42$
- $S = 19y + .38$
- $S = 10y + .22$
- $S = 0.03y + .09$

FIG. 5. Horizontal response sensitivities and phases for 1 subject during IA translation at 0.2 g peak head acceleration in the UP and NU head orientations plotted as a function of vergence angle. Here and in Fig. 8, responses have been averaged into 1 meter angle (MA) bins of vergence, and each point represents a mean value at its corresponding mean vergence within the bin. Error bars represent standard deviations within bins. Fine lines in the sensitivity graphs represent first-order linear regressions. Equations for these regressions appear in the key in the form, $S = m y + b$, where $m$ is the slope of the line and $b$ is the $y$ intercept. Fine lines and the values in the key in the lower graphs represent phases ($\phi$) averaged across all vergence angles. By convention, a compensatory response corresponds to a phase of 0° as shown here and in other figures. Note that phases have been omitted for the 0–1 MA bin for the 2 lowest frequencies. This is because phase becomes highly variable if not meaningless when response sensitivity is near 0 (a signal-to-noise problem). Bold lines in all panels show ideal response properties based on geometric considerations.

and Tomko 1991a). To address this perspective, Fig. 7 (bottom) shows torsional sensitivities replotted in terms of tilt gain ($G$; torsional eye position/effective head roll position) using the following equation

$$G = \frac{S \cdot a \cdot 981 \text{ cm/s}^2}{\text{tun}^{-1} (a) \cdot (2\pi f)^2}$$

where $a$ is stimulus acceleration (0.3 g for all frequencies in Fig. 7, and gravitational acceleration, $g$, is 981 cm/s²). Data have been averaged across all vergence angles and are plotted as a function of stimulus frequency. Tilt gains were generally small (<0.05) but showed a clear frequency-dependence, declining with increasing frequency.

**DV-VERTICAL LVOR.** Vertical responses during DV translation closely resembled IA-horizontal responses and were analyzed in the same way. Figure 8 shows DV-vertical LVOR response sensitivities and phases plotted as a function of vergence for two head orientations (NU and RD) from the same subject represented in Fig. 5. Regressing sensitivity against vergence revealed sensitivity slopes and intercepts that generally increased with increasing stimulus frequency. Responses for this particular subject in the NU orientation were unusual in that the LVOR response at 1.0 Hz was atypically small; the remaining subjects demonstrated larger responses at 1.0 than at 0.5 Hz. The coefficients of determination of the least-square linear fits increased with increasing stimulus frequency ($r^2$ values in both head orientations were 0.28 at 0.5 Hz and ranged between 0.86 and 0.97 for the remaining stimulus frequencies). Response phases (Fig. 8) for the two head orientations generally led head velocity, though small lags were sometimes observed at 4.0 Hz in this and other subjects in the RD orientation at small vergence angles.

Figure 9 shows DV-vertical sensitivity slopes, intercepts, and phases for both the NU and RD head orientations averaged across subjects. Figure 9 is in the same form as Fig. 6, facilitating a direct comparison between DV-vertical and IA-horizontal LVOR response properties. The DV-vertical sensitivity slope ($F_{3,9} = 18.78$, $P < 0.001$), intercept ($F_{3,9} = 5.70$, $P < 0.05$), and phase ($F_{3,9} = 17.29$, $P < 0.001$) were all significantly influenced by stimulus frequency. Sensitivity slopes and intercepts increased with increasing frequency while phase lead declined. Results were nearly the same for the two head orientations. However, the sensitivity slope was significantly larger when the head was in the RD orientation than when NU ($F_{1,3} = 73.30$, $P < 0.005$). Intercepts and phases were statistically indistinguishable for the two head orientations.

**Linearity of LVOR responses.** In previous sections, LVOR response properties were analyzed as a function of frequency for two different head orientations relative to gravity during both IA and DV motion. Response linearity was not considered, and responses from all acceleration amplitudes were pooled. We now directly assess potential amplitude-dependent nonlinearity in the IA-horizontal and DV-vertical LVORs over a broad range of stimulus intensities. Mean sensitivity slopes, intercepts, and phases are illustrated in Fig. 10 as a function of peak head acceleration at each stimulus frequency and for both IA and DV motion. Responses from the two head orientations for each motion axis have been pooled. The mean sensitivity...
To this point, the IA-horizontal and DV-vertical LVORs have been treated separately, despite their similarity in performance and common theoretical goal (Eqs. 1–3). The data set underlying Fig. 10 provides a convenient means to quantify the similarity between the two. A three-way repeated-measures ANOVA was performed (stimulus amplitude, motion axis, and frequency) on each response parameter (sensitivity slope, intercept, and phase). Because the two lowest stimulus frequencies could be run only up to 0.4 g due to limitations in sled length (see Table 1), statistical comparisons were performed only for the first four amplitudes. Note that these accelerations differ slightly at each frequency (Table 1), but the values are sufficiently close for this purpose. Analysis of the effect of motion axis (IA vs. DV) revealed only a modest statistical significance for phase lead, which proved greater for the DV-vertical than the IA-horizontal LVOR ($F_{1,6} = 13.54, P < 0.05$). As in the previous analysis, all three response parameters were significantly influenced by stimulus frequency.

Perhaps the LVOR displays an amplitude-dependent non-

slope and intercept both remain flat or increase slightly as stimulus amplitude rises, while phase generally declines.

To quantify LVOR nonlinearity, regressions of each response parameter (sensitivity slope, intercept, and phase) on peak head acceleration were performed for each monkey and at the two frequencies (2 and 4 Hz) at which the translational LVOR is most robust and where the broadest range of stimulus amplitudes were available. The mean and variance of the regression slopes then provide a convenient measure of nonlinearity. The decline in phase with increasing stimulus amplitude proved statistically significant at both frequencies and for both axes of motion ($P < 0.025$ for DV vertical at 2 Hz and $P < 0.001$ for the others). In contrast, the only significant nonlinearity among sensitivity parameters was an increase in DV-vertical sensitivity slope with rising stimulus amplitude at 4 Hz ($P < 0.025$). Note that the amplitude-dependent effects observed actually constitute improvements in compensatory LVOR performance as peak head acceleration rises, not deteriorations.

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**Fig. 6.** Mean sensitivity slopes, intercepts, and phases in response to IA translation in the UP (●) and NU (■) head orientations plotted as a function of stimulus frequency. Data from all acceleration amplitudes have been pooled. Positive phase values represent leads, whereas negative values are lags. Error bars represent standard deviations between subjects.

**Fig. 7.** Mean torsional sensitivities during IA translation (responses in amplitude at 4 Hz ($P < 0.025$). Note that the amplitude-dependent effects observed actually constitute improvements in compensatory LVOR performance as peak head acceleration rises, not deteriorations.
Vertical Response to DV Translation

**Nose-Up**

- 4 Hz: $S = 22v + 32$
- 2 Hz: $S = 20v + 36$
- 1 Hz: $S = 20v + 16$
- 5 Hz: $S = 30v + 09$

**Right-Side Down**

- $S = 21v + 34$
- $S = 31v + 14$
- $S = 07v + 22$
- $S = 06v + 04$

**FIG. 8.** Vertical response sensitivities and phases for a single subject during DV translation at 0.2 g peak head acceleration with the head in the NU and RD orientations, plotted as a function of vergence angle (averaged into 1-MA bins) as in Fig. 5. Error bars represent standard deviations within bins. Fine lines represent first-order linear regressions for sensitivity and average values for phase, whereas the bold lines show ideal response properties.

DISCUSSION

**Overview**

This study characterizes the dynamics of LVOR responses during high-frequency sinusoidal linear translations in the squirrel monkey. Several important variables that influence the LVOR are quantified, including the frequency and amplitude of stimulation, binocular fixation distance, and head orientation relative to the axis of motion and to gravity. These experiments extend the work of Paige and Tomko (1991a,b), which provided an initial characterization of squirrel monkey LVOR function in three orthogonal axes of head translation. Two classes of LVOR were described. The first, the translational LVOR, maintains binocular foveal fixation on targets in space during linear motion. Translational LVORs include horizontal responses to interaural head motion (IA-horizontal), vertical responses to dorsoventral motion (DV-vertical), and complex (horizontal and vertical) responses to nasooccipital motion. Translational LVORs are modulated by fixation distance, in accordance with geometric requirements. The second class of LVOR includes torsional responses during IA motion (IA-torsional) and vertical responses during nasooccipital motion. These responses cannot be compensatory for translation because they do not maintain image stability during linear motion and are therefore visually destructive. Instead, they are best characterized as tilt responses.

The fact that translational and tilt responses occur simultaneously, as is the case for horizontal and torsional responses during IA motion, reflects a fundamental ambiguity in otolith input; otolith responses cannot distinguish between linear accelerations due to head-tilt relative to gravity and those
generated by translation. However, the oculomotor responses required to compensate for tilt and translation differ. A partial resolution of this ambiguity is to parse linear accelerations according to their frequency content (or persistence), such that high-frequency (transient) stimuli are registered as translation and low-frequency (prolonged) accelerations as tilt (Guedry 1974; Mayne 1974). This concept has received experimental support (Angelaki and Hess 1996b; Paige and Tomko 1991a) and is consistent with results reported here.

Several factors have impeded a comprehensive understanding of LVOR function. First, although the modulatory influence of fixation distance (vergence) on LVOR performance had been quantified, its frequency dependence was unknown. Previous studies limited translational stimuli to either single high-frequency sinusoids (3.0–5.0 Hz) (Paige 1989, 1991; Paige and Tomko 1991b), transients (Busettini et al. 1994; Schwarz and Miles 1991), or frequencies <2.0 Hz (Oas et al. 1992; Shelhamer et al. 1995; Skipper and Barnes 1989). Second, the translational LVOR often has been studied without directly measuring vergence (Busettini et al. 1994; Israël and Berthoz 1989; Oas et al. 1992; Paige 1989; Skipper and Barnes 1989). Third, the linearity of the LVOR had remained unexplored. In summary, the previous literature provides an incomplete depiction of LVOR response dynamics.

The current study addresses these shortcomings and systematically quantifies a subset of translational and tilt LVOR responses as a function of stimulus frequency and amplitude, binocular fixation distance (as measured by vergence angle), and head orientation relative to the axis of motion and to gravity. A high-frequency bandwidth (0.5–4 Hz) was selected to focus on the physiological range of translational, rather than tilt, responses. Translational LVOR responses (IA-horizontal and DV-vertical) were shown to be influenced strongly and systematically by stimulus frequency, consistent with high-pass dynamics, as well as binocular fixation distance (vergence). Although the influence of head orientation relative to gravity, acceleration amplitude, and motion axis on some LVOR response parameters were statistically significant, the effects were generally small and largely idiosyncratic. Tilt LVOR responses (IA-torsional) also were influenced strongly by stimulus frequency, but, in contrast to translational responses, behaved with low-pass dynamics. Further, the IA-torsional responses, unlike translational responses, were not systematically modulated by fixation distance.

**Influence of stimulus frequency and fixation distance on the LVOR**

**TRANSLATIONAL LVOR.** A linear relationship between translational LVOR response amplitude and reciprocal fixation distance is now well established for both IA-horizontal (Busettini et al. 1994; Paige and Tomko 1991b; Paige et al. 1996a; Schwarz and Miles 1991), and DV-vertical (Paige 1989, 1991; Paige and Tomko 1991b) responses. This relationship is expressed conveniently as regressions of response sensitivity on vergence angle. The modulation of the LVOR by vergence then is given by the slope, whereas the intercept represents the LVOR response at zero vergence. Our findings suggest that both the slope and intercept are frequency dependent and have similar dynamics. Both are lowest at 0.5 Hz and increase dramatically with increasing frequency. Note that the influence of frequency and vergence on the LVOR are independent. At a given frequency, there is a quantifiable influence of vergence on LVOR sensitivity, and at a particular value of vergence, there is a quantifiable influence of frequency.

Like sensitivity, LVOR response phase is also dependent on stimulus frequency. Responses displayed a large lead at the lowest frequency, which declined to near zero by 4.0 Hz. However, in contrast to sensitivity, phase is generally insensitive to fixation distance. Taken together, the frequency-dependent characteristics of the translational LVOR are consistent with the operation of a high-pass filter within LVOR pathways, along with a multiplicative influence by a signal related to vergence, as modeled previously (Paige and Tomko 1991b) and reformulated below.

Given a more complete understanding of LVOR response dynamics and the modulatory influence of fixation distance,
we now can resolve much of the controversy that exists in the literature. Studies employing acceleration transients (Busettini et al. 1994; Schwarz and Miles 1991) and high-frequency sinusoids (>2.0 Hz) (Paige 1989, 1991; Paige and Tomko 1991b; Paige et al. 1996a) have demonstrated that binocular vergence angle plays a substantial role in the modulation of LVOR function, whereas those using stimuli of modest frequency content (≤2.0 Hz) have shown a weak or minimal influence (Oas et al. 1992; Shelhamer et al. 1995). Given the remarkably high-pass dynamics of the LVOR, these seemingly disparate findings are actually quite compatible.

What is the signal that conveys information about fixation distance and modulates LVOR sensitivity? Because modulation of LVOR responses can occur in darkness, candidate signals cannot be visually based. Signals related to accommodation of the intraocular lens and vergence angle have been proposed (Hine and Thorn 1987; Paige 1989; Post and Leibowitz 1982; Schwarz and Miles 1991; Snyder et al. 1992). Both could provide appropriate signals related to fixation distance, even in darkness, because they largely reflect signals underlying motor behavior. Hine and Thorn (1987) used spherical lenses and base-out wedge prisms to independently vary accommodation and vergence demand, and concluded that the modulation of AVOR gain as a function of fixation distance is linked closely with changes in vergence but not accommodation. Paige (1989, 1991) employed similar optical techniques and likewise observed that changes in DV-vertical LVOR sensitivity are linked closely with vergence angle, but not accommodation demand. These studies employed human subjects. Monkeys may behave somewhat differently, because accommodation has been shown to influence the IA-horizontal LVOR (Schwarz and Miles 1991), although less strongly and consistently than vergence. The distinction may have little practical relevance, however, because accommodation and vergence typically operate together during natural behavior.

If signals related to vergence play a role in the modulation

### TABLE 2. Mean translational LVOR response parameters

<table>
<thead>
<tr>
<th>Frequency</th>
<th>Sensitivity slope (deg·cm⁻¹·MA⁻¹)</th>
<th>Sensitivity intercept (deg/cm)</th>
<th>Phase (deg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5</td>
<td>0.03 ± 0.03</td>
<td>0.06 ± 0.04</td>
<td>42 ± 28</td>
</tr>
<tr>
<td>1.0</td>
<td>0.08 ± 0.05</td>
<td>0.12 ± 0.08</td>
<td>38 ± 18</td>
</tr>
<tr>
<td>2.0</td>
<td>0.23 ± 0.08</td>
<td>0.24 ± 0.19</td>
<td>24 ± 9</td>
</tr>
<tr>
<td>4.0</td>
<td>0.31 ± 0.11</td>
<td>0.48 ± 0.29</td>
<td>10 ± 9</td>
</tr>
</tbody>
</table>

Values (expressed as means ± SD) are averaged across subjects, head orientations, motion axes, and acceleration amplitudes. LVOR, linear vestibuloocular reflex.
of VOR responses, it is unlikely that this signal is an afferent input from extraocular muscles or even an efference copy of the same. This conclusion was reached by Snyder et al. (1992) after examining the time course of shifts in VOR response amplitude as compared with changes in vergence angle when monkeys shifted gaze between targets at different fixation distances. Changes in the VOR preceded those in vergence angle by 49 ms on average (reaching ~200 ms in the extreme case).

Although the stimulus used (eccentric rotation) stimulated both the AVOR and LVOR, qualitative observations on translational LVOR responses alone (Paige 1991; Paige and Tomko 1991b) provide confirmation. The signal responsible for modulating the VOR is presumably a central premotor, or “motor command,” signal shared by both the VOR and vergence systems. Its source remains undetermined.

Other influences, such as the context of target motion, also may influence the VOR (Barr et al. 1976). In the human LVOR, Paige et al. (1996a) found that tracking an imaginary earth- or head-fixed target in darkness increases or decreases LVOR sensitivity, respectively, in a vergence-dependent fashion. However, unlike the effect of vergence, this motion context influences the LVOR only at relatively modest frequencies of sinusoidal motion (<2.0 Hz) and thus resembles the dynamic limitations of smooth pursuit.

How well does the translational LVOR match its kinematic requirements (see Methods, Eqs. 1–3)? Because IA-horizontal and DV-vertical LVORs are geometrically the same, differing only in the axis of head motion and ocular response plane, the behavior of these two reflexes also should be the same. Indeed, only subtle differences in IA and DV responses were observed, and both behaved nearly linearly over a broad range of acceleration amplitudes. Although amplitude-dependent changes in some response parameters proved statistically significant, the effects were generally small and somewhat idiosyncratic. At 4 Hz, where the translational LVOR is most robust, response sensitivity rose slightly, whereas phase lead declined. If anything, this tendency constitutes an improvement in LVOR response as acceleration increases. In addition, as head orientation relative to gravity is irrelevant for the translational LVOR on theoretical grounds (Paige and Tomko 1991a,b), no measurable influence of head orientation was expected and indeed no systematic differences were observed.

The most notable disparity between observed LVOR responses and ideal geometry proved to be the influence of vergence, even at 4.0 Hz where the effect was maximal. The ideal LVOR has a sensitivity slope of 0.57°·cm⁻¹·MA⁻¹, whereas observed slopes at 4.0 Hz averaged 0.31°·cm⁻¹·MA⁻¹ across head orientations and motion axes (Table 2) or 54% of the ideal value. Another departure from ideal geometry is the presence of a measurable LVOR response when binocular fixation distance is infinitely far (vergence = 0). The functional utility of this sensitivity intercept, which also exists in humans (Busettini et al. 1994; Paige et al. 1996a), is unclear. One explanation (Paige and Tomko 1991b) is that it confers enhanced image stabilization over a broader range of fixation distances than if the intercept were zero. Although an LVOR response at zero vergence generates inappropriate retinal slip when fixating distant targets, the actual retinal slip velocities are small and typically under the threshold of oscillopsia (Paige and Tomko 1991b). However, the intercept effectively raises the response sensitivity (adds a fixed value) at all vergence angles. This facilitates stabilization of visual objects within the subject’s haptic space. For example, in Figs. 5 and 8, the regression lines for the LVOR at 4.0 Hz cross the geometrically ideal response line at ~1.7 MA of vergence. This corresponds to a fixation distance of 60 cm. Thus the translational LVOR behaves nearly perfectly for targets at this distance. That would not be the case in the absence of a positive sensitivity intercept; the LVOR would perform suboptimally for all fixation distances short of infinity.

The presence of the intercept incurs little cost but serves to match LVOR behavior more closely with the ideal over a broad range of fixation distances.

At frequencies <4.0 Hz, the point at which sensitivity regression lines cross the ideal shifts to lower vergence values. Thus at low frequency, only very distant targets can be stabilized with the LVOR alone. However, this does not pose a functional problem because visual following mechanisms can take over for a failing LVOR at these lower frequencies (Paige et al. 1996a). The interaction between visual following mechanisms and the AVOR is similar, except that a broad overlap exists in their frequency bandwidths. The effective bandwidth of the AVOR is extended by roughly an order of magnitude lower in frequency than that of the LVOR (see Paige et al. 1996a).

The real mystery may be why the AVOR performs well over such an extended low-frequency range despite the ability of visual mechanisms to track and stabilize images. TILT LVOR. Small torsional responses were observed during IA head translation, confirming earlier observations by Lichtenberg et al. (1982) and Paige and Tomko (1991a). It has been suggested that IA-torsional responses are compensatory for head tilt and not translation (Paige and Tomko 1991a). Recall that the otoliths respond to both tilt and translation, and thus tilt responses may be generated in addition to translational responses during linear motion. Tilt angle is equivalent to the resultant sum of the gravitational and translational accelerations (or “gravito-inertial force”). When expressed in terms of tilt-gain, torsional responses demonstrate a clear decline as frequency increases from 0.5 to 4 Hz, as described previously (Paige and Tomko 1991a). The data in squirrel monkeys extend those from the human experiments of Lichtenberg et al. (1982), who examined torsional responses across a lower frequency range (0.1–1.0 Hz). Unlike the translational LVOR, there is no geometric requirement for tilt responses to be modulated by changes in fixation distance. This expectation was confirmed experimentally.

One interesting caveat concerning the IA-torsional LVOR is the absence of an influence of head orientation relative to gravity. With the head in the UP orientation, IA acceleration is equivalent to head roll-tilt, but with the head NU, IA acceleration should combine with gravity to yield an effective head yaw. The appropriate tilt response should be torsional with the head UP and horizontal with the head NU. This does not occur. Responses are always torsional and do not differ between the two head orientations. Thus the IA-torsional LVOR, a presumed tilt response, is not compensatory for actual head tilt. Instead, the response is governed only by linear acceleration along the IA axis, not the actual angle of gravito-inertial force. The IA-torsional response is best described as a “quasi-tilt” response, which is equivalent to a true tilt response only when the head is in the UP orientation assumed during most natural behavior (Paige and Tomko 1991a).
A recent study by Merfeld et al. (1996) in humans obtained slightly different results. IA-torsional responses to sinusoidal oscillations at 0.35–1.0 Hz exhibited low-pass dynamics as in monkeys. However, response amplitudes were smaller in the NU than in the UP orientation. The difference was attributed to a central process that calculates changes in gravito-inertial force explicitly and responds accordingly. However, the difference in response between the two head orientations was small and, more importantly, was insufficient to shift the response plane appropriately for the different head orientations. It is unclear why the brain would evolve an elaborate mechanism for such a small part of the overall response. There are at least two alternative explanations. First, a change in response amplitude could result from a static influence of otolith origin, such that IA-torsional response amplitude is altered by head orientation. Second, the perception of motion may differ depending on orientation, and this could induce potential changes in context that, in turn, might modify eye movement responses at modest frequencies, as occurs in the IA-horizontal LVOR (Paige et al. 1996a).

**Labyrinthine origin of the LVOR**

LVOR responses presumably are driven by otolith inputs. Human subjects with defective labyrinths do not have such responses (Bronstein and Gresty 1988; Israël and Berthoz 1989; Tokita et al. 1981). Furthermore, peripheral afferents from squirrel monkey semicircular canals do not respond to linear accelerations (Goldberg and Fernández 1975; Somps et al. 1994). That LVOR responses are derived from labyrinthine input is supported further by a monkey that underwent successive labyrinthectomies (Paige et al. 1996b), thereby abolishing all LVOR and AVOR responses.

LVOR responses to IA and DV motion presumably are mediated by separate otolith organs, specifically the utriculus and sacculus, respectively. This is based on directional response sensitivities (polarization vectors) of otolith afferents in squirrel monkeys (Fernández and Goldberg 1976a). Linear accelerations directed along the IA head axis primarily activate afferents that innervate hair cells in the utriculus, whereas DV accelerations primarily stimulate those from the sacculus. Given the similarity of IA-horizontal and DV-vertical responses, it is likely that inputs from these two end organs are processed in a similar fashion to generate translational LVOR responses. That afferent (Fernández and Goldberg 1976b) and LVOR response dynamics differ fundamentally signifies that dynamic central processing of otolith inputs must be performed.

**Model of the LVOR**

The fundamental response characteristics of the LVOR are schematized in a model shown in Fig. 11. Its structure is deliberately simple but is sufficient to account for most attributes of LVOR behavior reported above. Although a single otolith input and a single ocular output is an oversimplification, the extension to a bilateral otolitic input, along with a binocular output, as described previously (Paige and Tomko 1991b), is straightforward. Similarly, although this model describes responses to IA motion, generalization to other motion axes requires only simple modifications. For example, DV acceleration would stimulate saccular afferents, the inputs of which would be processed by the DV-vertical translational LVOR pathway but without a tilt pathway. Motion along the nasocipital axis would actuate both translational and tilt pathways. The tilt pathway (effective pitch-tilt) would drive vertical eye movements, whereas the translation pathway (more complex than that shown in Fig. 11) would drive vergence and gaze-dependent horizontal and vertical ocular responses (Paige and Tomko 1991b). Although the existence of tilt and translation pathways in the model is supported by experimental findings, these are not the only otolith influences on the oculomotor system (Angelaki and Hess 1996b). They are, however, the LVOR reflexes recorded in the frequency bandwidth of this experiment.
Key features of the model in Fig. 11 are as follows. IA head acceleration is transduced by the utriculus with different IA-responsive afferents conveying opposing signs depending on the polarity of the hair cell populations innervated. Recent evidence suggests that opposing responses in the cat saccular function in a push-pull fashion to yield a single directionally selective signal in the vestibular nuclei (Uchino et al. 1996). At this early stage of investigation of the LVOR, a simple head acceleration input is used without dynamic elements. The ocular plant is likewise simplified. Head acceleration input is split into two functional pathways corresponding to the translational and tilt LVORs. The tilt pathway is the simpler of the two and requires a low-pass filter and amplitude scaling ($G_{\text{tilt}}$) to convert head acceleration into effective head roll-tilt (an angular position signal), which is passed directly to the oculomotor system to drive torsional eye position. Because the input is IA acceleration, actual head orientation relative to gravity is irrelevant, as observed experimentally, and the term quasi-tilt LVOR can be used to describe this response more accurately.

The translational LVOR pathway is more complex. Initial stages of processing include an integration of head acceleration and high-pass filtering. Different neuronal processes potentially could yield the same result (Angelaki and Hess 1996a; Raphan et al. 1996). Ultimately, however, the outcome is a high-pass signal proportional to head velocity. The high-pass process is necessary to account for the fact that persistent head acceleration, as occurs routinely when the head is tilted, does not produce continuous nystagmus or erroneous perceptions of translation. The filtered head velocity signal then is sent through a subpathway with a gain element ($G_{\text{trans}}$), and on to the oculomotor system where it is integrated again (the "oculomotor integrator") and passed to the horizontal extracocular muscles. This subpathway underlies the sensitivity intercept observed in LVOR behavior. The filtered head velocity signal also is passed through a different gain element ($G_{\text{trans}}^{\text{int}}$) and multiplied by a signal proportional to "vergence command". This subpathway underlies the observed LVOR sensitivity slope. The processed signal also is passed to the oculomotor system through its classic integrator to drive horizontal eye position.

An alternative structure to account for LVOR sensitivity slope and intercept would be for the vergence command signal to include a positive DC offset without the second pathway. A vergence command of zero then would drop the reflex to a nonzero value. To achieve zero output would require a binocular divergence equal to the offset. This alternative view is not far-fetched and can be best understood by examining Figs. 5 and 8. If the vergence ($x$) axis of the graph were extended to the left, imagine that the various regression lines might intersect near a common point, corresponding to some measurable divergence angle where sensitivity reaches zero.

The model of Fig. 11 raises two important concerns. First, what are the characteristics of the model’s dynamic elements? The simpler tilt pathway contains a low-pass filter that may be modeled as a one-pole element in the form, $1/(sT_{\text{trans}} + 1)$, where $T_{\text{trans}}$ is the time constant, and $s$ is the Laplace complex frequency. The data are simulated adequately by this simple element, as are those of Lichtenberg et al. (1982). However, with the aid of additional preliminary data at low frequencies (Paige et al. 1995), we estimate $T_{\text{trans}}$ to be $\sim 2$ s (corner frequency of 0.08 Hz), and gain, $G_{\text{trans}}$, to be $\sim 0.4$. Both are substantially larger than values reported before (Lichtenberg et al. 1982). The translation pathway contains a "leaky" integrator that may be expressed in the form, $[T_{\text{int}}/(sT_{\text{int}} + 1)]$, where $T_{\text{int}}$ is the time constant. This is in series with a high-pass filter that may be modeled in the form, $[sT_{\text{trans}}/(sT_{\text{trans}} + 1)]$, where $T_{\text{trans}}$ is the time constant. The combination of the leaky integrator and high-pass filter accounts for the fact that a simple shift in head tilt, equivalent to an acceleration step, does not generate persistent nystagmus or perceptions of constant translation. One implication is that the translational LVOR should undergo a 180° phase lead as stimulus frequency shifts from high to low. Experimental support is provided by LVOR studies (Angelaki and Hess 1996b; Borel and Lacour 1992) that employ frequencies less than our 0.5-Hz lower bound; phase leads indeed undergo a roughly 180° shift with decreasing frequency. Empirically estimated model parameters, $T_{\text{trans}} = 0.25$ s, $T_{\text{int}} = 0.05$ s, $G_{\text{trans}} = 0.4$, and $G_{\text{int}} = 0.5$, approximate LVOR sensitivity quite well (Fig. 12). However, predicted phase leads are greater than those recorded experimentally, indicating either dynamic nonlinearity or complexities in the LVOR that remain unclear. These evolving issues will be explored further in on-going studies that include a broader frequency range (Paige et al. 1995).

A second and more fundamental concern is, if IA translation stimulates both translational and tilt pathways to simultaneously...
generate translational and tilt LVORs, does dynamic tilt likewise generate both responses? The answer is confounded by the high-pass nature of the translational LVOR and by an overwhelming AVOR response that occurs during rapid head tilt. However, given translational LVOR dynamics as expressed in the model, a rapid head tilt of 14°, corresponding to a 0.25 g acceleration, should yield a brief (<1 s) response of only 2–3° at dark vergence. This could be lost easily within the larger AVOR response during transient head roll-tilt. However, we recently have confirmed that both horizontal and torsional responses occur during low frequency dynamic roll tilts as well as IA translations (Paige et al. 1995). The horizontal component presumably reflects the IA-horizontal LVOR operating well below its physiological frequency range.

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