

Human Vestibuloocular Reflex and Its Interactions With Vision and Fixation Distance During Linear and Angular Head Movement

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Paige, Gary D., Laura Telford, Scott H. Seidman, and Graham R. Barnes. Human vestibuloocular reflex and its interactions with vision and fixation distance during linear and angular head movement. *J. Neurophysiol.* 80: 2391–2404, 1998. The vestibuloocular reflex (VOR) maintains visual image stability by generating eye movements that compensate for both angular (AVOR) and linear (LVOR) head movements, typically in concert with visual following mechanisms. The VORs are generally modulated by the “context” in which head movements are made. Three contextual influences on VOR performance were studied during passive head translations and rotations over a range of frequencies (0.5–4 Hz) that emphasized shifting dynamics in the VORs and visual following, primarily smooth pursuit. First, the dynamic characteristics of head movements themselves (“stimulus context”) influence the VORs. Both the AVOR and LVOR operate with high-pass characteristics relative to a head velocity input, although the cutoff frequency of the AVOR (<0.1 Hz) is far below that of the LVOR (~1 Hz), and both perform well at high frequencies that exceed, but complement, the capabilities of smooth pursuit. Second, the LVOR and AVOR are modulated by fixation distance, implemented with a signal related to binocular vergence angle (“fixation context”). The effect was quantified by analyzing the response during each trial as a linear relationship between LVOR sensitivity (in deg/cm), or AVOR gain, and vergence (in m⁻¹) to yield a slope (vergence influence) and an intercept (response at 0 vergence). Fixation distance (vergence) was modulated by presenting targets at different distances. The response slope rises with increasing frequency, but much more so for the LVOR than the AVOR, and reflects a positive relationship for all but the lowest stimulus frequencies in the AVOR. A third influence is the context of real and imagined targets on the VORs (“visual context”). This was studied in two ways—when targets were either earth-fixed to allow visual enhancement of the VOR or head-fixed to permit visual suppression. The VORs were assessed by extinguishing targets for brief periods while subjects continued to “fixate” them in darkness. The influences of real and imagined targets were most robust at lower frequencies, declining as stimulus frequency increased. The effects were nearly gone at 4 Hz. These properties were equivalent for the LVOR and AVOR and imply that the influences of real and imagined targets on the VORs generally follow low-pass and pursuit-like dynamics. The influence of imagined targets accounts for roughly one-third of the influence of real targets on the VORs at 0.5 Hz.

INTRODUCTION

The vestibuloocular reflex (VOR) produces eye movements that compensate for head movements to maintain visual image stability. The VOR is compensatory for both

angular (AVOR) and linear (LVOR) head movements, as required by the challenges of natural behavior. The VORs typically operate together with visual following mechanisms to achieve the common goal of preserving stable images of targets in space.

The VORs are modulated by the “context” in which head movements are made. There are three classes of contextual influences known to operate in the VOR. First, VOR performance depends on the characteristics of the head movement itself (“stimulus context”), notably its frequency and intensity. Both the AVOR and LVOR operate with high-pass characteristics relative to a head velocity input, although with different physiological operating ranges (Paige 1996). The lower cutoff frequency of the AVOR is <0.1 Hz, whereas that of the LVOR is ~1 Hz. Both perform well at high frequencies that exceed the capabilities of visual following. The fastest continuous visual tracking system in primates is smooth pursuit. Its low-pass performance characteristics allow accurate target tracking that is limited to relatively low frequencies, below ~2 Hz. Thus visual–vestibular interactions (VVI) operate in complementary fashion to maintain target fixation across a broad range of stimulus frequencies, with each modality contributing most where the other fails.

A second contextual influence on the VOR is the ambient state of binocular fixation during head movements (“fixation context”). Although the general goal of all VORs is to maintain a stable retinal image, in primates (including humans) this goal can be further refined—eye movements serve to stabilize binocular fixation on targets in space and therefore maintain a stable bifoveate image. The geometry of eye and head movements in relation to binocular fixation of targets then becomes critical for understanding both the goals and performance characteristics of the reflex. For a given head movement, the VOR must compensate for both its rotational and translational components to maintain binocular target fixation. Proper compensation for the translational component is governed by target distance, or more accurately, fixation distance (how far away the 2 eyes are looking). Because the eyes are typically looking at a target, fixation and target distance are usually the same. Restricting attention to horizontal LVOR responses during interaural (IA) linear head motion, the ideal compensatory response is inversely proportional to fixation distance. If fixating a target far away, little or no eye movement is required, but, as fixation distance declines, ocular responses must progressively increase in amplitude. The LVOR indeed operates in

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this fashion, although imperfectly (Baloh et al. 1988; Paige 1989; Paige and Tomko 1991b; Schwarz and Miles 1991; Skipper and Barnes 1989). The source of fixation distance information underlying LVOR modulation remains controversial. Experimental manipulations of binocular vergence angle and accommodation (focus) of the intraocular lens reveal that vergence angle is the key variable related to VOR amplitude modulation in humans (Hine and Thorn 1987; Paige 1989, 1991), and accommodation plays a parallel but less robust role in rhesus monkeys (Schwarz and Miles 1991). It is not vergence angle per se but rather an as-yet unidentified "vergence command" signal that modulates the LVOR along with generating binocular vergence of the eyes because LVOR changes occur in advance of binocular vergence movements (Paige 1991; Paige and Tomko 1991b; Snyder et al. 1992).

Fixation distance is important in the AVOR as well as the LVOR. This is because the eyes are displaced eccentrically in the head relative to the axis of natural head rotation. This ocular eccentricity results in a small translation of the eyes in space during natural head rotations, and compensatory eye movements must counteract the translational as well as the angular component of motion. Ideally, compensation for the translational component should be inversely proportional to fixation distance, as for the LVOR. The AVOR in fact does include a small modulation related to fixation distance when studied during transient or high-frequency head rotations (Biguer and Prablanc 1981; Paige 1996; Snyder and King 1992; Telford et al. 1998; Viirre et al. 1986). However, studies employing modest frequencies of head rotation reported meager or even the opposite effect on the VOR (Crane et al. 1997; Gizzi and Harper 1996; Shelhamer et al. 1995; Viirre and Demer 1996) in which gain declines rather than increases with decreasing fixation distance. This study reevaluated the controversy in light of our recent finding that the influence of fixation distance on the monkey LVOR behaves with high-pass characteristics governed by a cutoff frequency >1 Hz (Telford et al. 1997). Perhaps the same applies to the AVOR.

A third contextual influence on the VOR is the motion of the visual target, even when the target is imagined in darkness ("visual context"). This phenomenon has been most thoroughly studied in the AVOR (Barnes 1998; Barr et al. 1976; Furst et al. 1987). Recall that the VORs generally operate in conjunction with visual mechanisms that also drive eye movements, primarily the smooth pursuit system given the range of stimulus frequency considered here (0.05–4.0 Hz). VVI is typically studied in two ways, when the visual target is earth-fixed (ef) or moving in tandem with the head (head fixed, hf). In the former case, visual input enhances the VOR, and, in the latter case it suppresses the reflex, regardless of the nature of the head movement (i.e., rotation or translation). A fascinating feature of VVI is the apparent modulation of VOR responses in darkness by the context of imagined target motion relative to the head. That is, simply imagining that a "target" in darkness is ef or hf (changing visual context) results in a VOR enhancement or attenuation, respectively. The influences of real and imagined targets on the VOR behave with similar dynamic limitations that resemble the low-pass (<2 Hz) characteristics of smooth pursuit (Barnes 1993; Collewijn 1985; Paige

1994). Although the LVOR has been studied under different conditions of VVI and visual context (Baloh et al. 1988; Israël and Berthoz 1989; Oas et al. 1992; Shelhamer et al. 1995; Skipper and Barnes 1989), none measured fixation distance while also addressing LVOR behavior in the critical high-frequency range of head movements where the reflex is most robust.

In this study, the human LVOR during IA head motion was studied as a function of frequency and fixation distance. Punctate visual targets at different distances were used to control fixation distance and to provide real visual targets to characterize VVI. Periods of darkness were interspersed with target presentations to assess the role of imagined target motion on the VOR while subjects maintained "fixation" on previously viewed targets in the dark. Finally, the experiment was repeated during horizontal head rotations to assess the same variables and contextual influences on the more widely studied AVOR. These experiments combine all three contextual influences under common laboratory conditions and over a frequency bandwidth (0.5–4.0 Hz) that matches an important region of change in both the LVOR and smooth pursuit. A preliminary report has been published (Paige et al. 1996).

METHODS

Subjects

Nine normal human volunteers between the ages of 21 and 49 participated in these experiments. Four participated in related experiments, and the remaining subjects were naïve. All were free of past or present neurological, ophthalmologic, otologic, systemic, or traumatic disease that could have affected results. All showed normal neuroophthalmologic and neurootologic function on clinical examination (performed by Paige), with particular attention toward assuring normal corrected visual acuity, stereopsis, visual fields, binocular oculomotor control, binaural hearing, and vestibular function. In addition, all subjects tested normally on pure-tone audiometry and vestibular caloric testing. The experimental procedures described were all performed in accordance with the 1964 Declaration of Helsinki and with the approval of an internal Research Subjects Review Board.

Eye movement recording and calibration

Horizontal and vertical eye movements were recorded binocularly with a dual charge-coupled device camera system (El-Mar, Toronto). The system consists of two cameras mounted on a goggle frame together with infrared (IR)-emitting diodes on both sides of each eye. The cameras view the eyes with the aid of half-silvered mirrors positioned below and in front of each eye but without impinging on the visual field necessary to view all targets in these experiments. The system tracks the motion of two IR reflections as well as the computed center of the pupil at 120 Hz and generates analog outputs proportional to horizontal and vertical eye position binocularly with a sensitivity of $\sim 0.2^\circ$ over a $\pm 25^\circ$ range. The method is established and compares well with others (DiScenna et al. 1995; Paige et al. 1996).

Calibrations were initially performed directly by the El-Mar system while subjects fixated targets 1.4 m away by using 5° steps horizontally and vertically around 0° (defined as eye level in the midsagittal plane). Posthoc calibrations corrected for vergence relative to each subject's interocular distance and for geometric distortions caused by the forward ocular eccentricity in the head. An additional level of calibration was performed based on the pre-

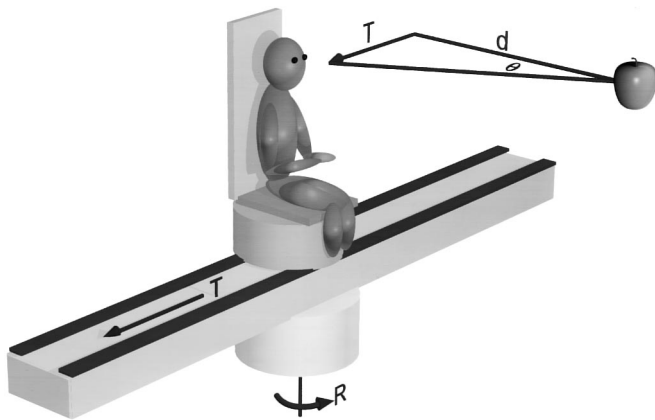


FIG. 1. Schematic of the sled/rotator device with a subject positioned for interaural (IA) translation or earth-horizontal rotation (R). The geometric requirements for an ocular response (angle) to translation (T) while the subject fixates a target (apple) at distance, d , is illustrated here and described further in the text.

sumption of accurate and stable fixation during 0.5- and 1-Hz trials in the presence of eye targets (Crane et al. 1997; Furst et al. 1987; Kasteel-van Linge and Maas 1990; Paige 1994). Mean scale factors derived from these trials were then used to adjust responses from other trials. Although refractive correction cannot be worn during recordings, refractive blur does not affect oculomotor performance tasks appreciably (Post et al. 1979; Van den Berg and Collewyn 1986), and our experience is in concert with this contention.

Stimulus presentation and apparatus

CHAIR AND MOTION CONTROL. A multiaxis sled/rotator (Contraves USA and JA Design, Pittsburgh, PA) was used to present all motion profiles (see Fig. 1). Subjects sat in a custom test chair with their heads securely fixed by a rigid bite bar of dental impression compound over a steel plate molded to each subject's bite. This tight interface between head and chair is as rigid as can be achieved practically and is essential if stimulus control is to be maintained during high-frequency motion. The chair with subject was mounted on a motorized linear sled riding on precision linear bearings and driven by a lead screw (1.1 m total excursion) connected to a DC motor by a timing belt. This mechanical drive was chosen over other methods because of its remarkable ability to faithfully generate high frequencies (including 4 Hz) of translation at high peak accelerations ($\leq 0.5 g$), despite a ~ 400 -lb. payload. The sled, chair, and subject were in turn mounted on a motorized angular base axis (peak torque, 325 ft-lb.) that performed all rotational trials.

Translational trials were limited to the head's IA axis, while rotational trials were limited to the head's horizontal (yaw) plane. IA translation trials consisted of sinusoidal oscillations at 0.5, 1.0, 2.0, and 4.0 Hz, with a peak head acceleration of 0.2 g (where $g = 981 \text{ cm/s}^2$) for all but 0.5 Hz, where peak acceleration was reduced to 0.1 g . This was necessary to limit translational excursion to the useful range of eye movement recording while subjects viewed the nearest earth-fixed target. In addition, trials were performed over a range of amplitudes, including 0.1, 0.2, 0.3, and 0.4 g , but at a fixed frequency of 4 Hz, to assess the linearity of the LVOR and VVI. Rotation trials included the same frequencies of oscillation (0.5–4 Hz) but with a peak head velocity of $20^\circ/\text{s}$. Table 1 lists the stimulus characteristics used in these experiments.

MECHANICAL CONSIDERATIONS. Motion control in complex mechanical systems entails potential difficulties. How accurately does

the motion profile of the head follow the desired control signal? The question can be parsed into two aspects, the mechanics of the sled/rotator device and the linkage between the device and the head. To assess the former, mechanical tests were performed for all stimulus parameters with a three-axis linear accelerometer (Entran EGAL3 12S-10D) and three-axis angular rate sensor (Watson Industries, Eau Claire, WI) mounted on the head-holder/bite-bar apparatus of the chair. Inaccuracies arose with increasing stimulus frequency (worst at 4 Hz). These were limited primarily to a lag in IA translation during linear trials caused by the sled's drive mechanism and a lag in yaw during rotation trials caused by chair compliance. Motion along or around axes outside the primary stimulus proved inconsequential. Correction factors for stimulus amplitude and phase were propagated throughout data analyses. These adjustments ensured an accurate depiction of motion at the bite bar.

The linkage between the bite bar and the head proved more difficult to assess. The custom bite bar provides the most rigid linkage practical. However, frequency-dependent uncoupling of the head from the bite bar likely existed as the teeth could rock slightly at high frequency, even when severely clenched around a custom fitted bite. We measured the head independently of the bite bar by securing a single-channel Watson rate sensor to the bony structures of the nose and medial orbit. The difference between the motion of the head relative to the head holder proved negligible during rotation trials. The most important error was a small yaw of the head during the highest frequencies of IA translation. However, we measured $< 1^\circ/\text{s}$ (or 0.03°) peak head yaw at 4 Hz and slightly more at 2 Hz. This small rotation would be largely counteracted by a robust AVOR at high frequencies and have only a small influence on results. Similarly, a small concurrent head roll produces negligible effects on horizontal eye movements.

Like the mechanical considerations related to head motion, concerns also exist in recording eye movements because the recording device is coupled to the head through its own mechanical linkage. The camera system consists of a rigid goggle mounted on an adjustable assembly that is tightly attached to the head both circumferentially and over the calvarium. A large nasal bridge and dense conforming foam at the temples provided additional rigidity. The eyes and paraorbital structures were continuously monitored on a CRT (~ 5 image). Motion of head landmarks would indicate uncoupling between the head and the goggle. We could discern no movement of the goggle relative to the head during any stimulus conditions with the exception of 4-Hz translation trials in which a small roll (but not horizontal) motion of the goggle was detected in

TABLE 1. Stimulus parameters

Linear Motion				
Frequency, Hz	Peak acceleration		Peak velocity, cm/s	Peak position, cm
	g	cm/s ²		
0.5	0.10	98.1	31.2	9.94
1.0	0.20	196.2	31.2	4.97
2.0	0.20	196.2	15.6	1.24
4.0	0.20	196.2	7.8	0.31
Angular Motion				
Frequency, Hz	Peak acceleration, deg/s ²	Peak velocity, deg/s	Peak position, deg	
0.5	62.8	20	6.37	
1.0	125.7	20	3.18	
2.0	251.3	20	1.59	
4.0	502.7	20	0.80	

some subjects. No influence of this on reported horizontal VOR responses could be attributed to mechanical uncoupling of the goggle from the head.

CONDITIONS OF VVI. Translational (LVOR) and rotational (AVOR) trials were studied under two conditions of VVI, 1) when targets were ef to allow visual enhancement of the VORs and 2) when targets were hf to permit visual suppression of the VORs. For each condition, targets were extinguished periodically to record the VORs in darkness. However, subjects were instructed to continue "fixating" the imagined hf (ihf) or ef (ief) targets. Thus trials were always paired, including ef/ief and hf/ihf forms, for both translational and rotational trial sets. This yielded a total of four trial types: ef/ief-LVOR, hf/ihf-LVOR, ef/ief-AVOR, and hf/ihf-AVOR. All stimulus characteristics were performed for each of these trial types.

For all trial types and stimuli presented, responses were recorded while subjects viewed or imagined targets at different distances. This allowed us to quantify the relationship between response properties and fixation distance. Different methods were used to present visual targets depending on whether these targets were hf or ef. All hf targets were produced by a chair-fixed laser-diode that projected a 0.2° spot guided by an x - y galvanometer (General Scanning, Watertown, MA) above the head onto one of two ef screens. These screens (5×120 cm) were oriented parallel to the sled at 20 and 135 cm from the eyes and were separated by a small vertical displacement centered at eye level. Slight vertical deviations of the projected target then changed its distance instantly. ef targets were numerical light-emitting diodes (LEDs) mounted centrally on the same screens and at the same distances described previously, with a third LED mounted 45 cm from the eyes and centered vertically at eye level. The numerals were scaled to maintain roughly the same 0.2° size. In general, targets were roughly aligned with primary gaze of the right eye, which also served as the reference eye for all data analysis.

The sequence of trial presentations varied among subjects; translations were performed first for some and second for others. The order of hf/ihf and ef/ief trials as well as stimulus frequency also varied within translation and rotation series.

Two procedural concerns are noteworthy. First, we avoided assessing the "default" VOR (e.g., during mental arithmetic) because it is never quite clear what a given subject imagines during the task (perhaps an image of hf numbers?). Second, maintenance of vergence in darkness, although imperfect, is not a critical factor. In a set of control trials at 4 Hz, we attempted to modulate vergence in four subjects while they 1) "fixated" imagined ef near targets (as described previously), 2) maintained a tone whose pitch was linked to vergence performed voluntarily in darkness, or 3) followed ef arthropomorphic cues (i.e., the subject's thumb in darkness). Results with these different methods proved indistinguishable. All demonstrated the same clear relationship between LVOR amplitude and vergence. None proved universally advantageous in maintaining vergence in darkness over all subjects.

Data collection and analysis

HARMONIC ANALYSIS. All stimulus generation and data acquisition was performed by an IBM-compatible Pentium PC and custom software (Telford et al. 1997, 1998). Binocular horizontal and vertical eye position, chair angular velocity, sled linear velocity, and target ON/OFF signals were analog filtered (≤ 50 Hz) and sampled at 100 Hz. During analysis individual cycles were identified with a timing record produced by the stimulus generator within the software. At 2.0 and 4.0 Hz, a large number of cycles were available that were saccade-free, regardless of fixation conditions (e.g., ef vs. hf). These were selected for analysis, whereas those containing saccades were discarded. Analysis was performed on

position traces at these high frequencies to avoid digitization noise, especially given the small response amplitudes recorded. At lower frequencies, eye position signals were first digitally differentiated and smoothed to yield eye velocities. Saccades were more frequent, particularly during hf/ihf-AVOR and ef/ief-LVOR trials. These saccades were identified and removed from eye velocity records with an iterative least-squares sinusoidal fit and windowing procedure (Ebisawa et al. 1988; Paige and Sargent 1991a), replacing gaps with the corresponding portions of the sinusoid fit to each cycle. An initial fit "by eye" was performed on each cycle, with a $50^\circ/\text{s}$ inclusion window around the fit. Subsequent fits (the fundamentals from Fourier analysis) and window reductions (scaled by residual root-mean-square noise) for each cycle rapidly converged on stable desaccaded cycles after two to three iterations. Saccades comprised a small proportion of each cycle and were removed only from the 0.5- and 1-Hz trials, as noted previously.

In the previous process, individual cycles across all ocular response records (both eyes, horizontal and vertical) were selected and subjected to harmonic analysis on a cycle-by-cycle basis. To ensure that ocular responses were not influenced by sudden transitions, such as shifts in target distance or switching targets on or off, we excluded cycles containing transitions and those that began within 250 ms thereafter. The sinusoidal fits from harmonic analysis were then used to calculate response parameters for each cycle and for each response trace. For translational trials, these included sensitivity [peak 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 the cycle. For rotatory trials, gain [peak eye velocity (in deg/s)/peak angular head velocity (in deg/s)] replaced sensitivity, whereas other parameters remained as described. For all further analysis and for figures, horizontal responses of the right eye were used as the reference, with the important exception that mean vergence was calculated as the difference between left and right mean horizontal eye position for each cycle. Vertical traces were only used to ensure that subjects fixated the targets presented and did not vary excessively during responses. Finally, cycles were grouped into ef, ief, hf, and ihf conditions for each frequency.

To assess the influence of fixation distance on ocular responses, vergence angle was linked with sensitivity (or gain) and phase measures on a cycle-by-cycle basis. Vergence is expressed in meter-angles (MAs), the reciprocal of fixation distance (in units of m^{-1}). For example, one MA would be required to fixate a target 1 m away, whereas two MAs would be required for a target 0.5 m away. This unit provides a form of vergence normalization that allows direct comparisons between different subjects and species regardless of head size and ocular separation (6.4 cm on average in humans).

GEOMETRIC CONSIDERATIONS. *Overview.* The kinematic requirements for ocular responses to head rotation and translation can be directly calculated to provide a reference for comparison with actual VOR response measures. To maintain fixation on hf targets, no eye movement is required regardless of stimulus characteristics. In contrast, for ef targets, the ideal response differs between rotation and translation trials, according to the following kinematic requirements.

Kinematics of the LVOR. During translational motion, both the eyes and head move precisely in tandem, and the ideal LVOR response to maintain fixation on an ef target depends on fixation distance (Paige and Tomko 1991b; Telford et al. 1997). Figure 1 illustrates the geometry of compensatory LVOR responses to IA head translation. For small angles, the ideal LVOR response (θ_i) is determined by the magnitude of the head translation (T) and the target distance (d) according to the relation

$$S_i = 0.57 \cdot \frac{1}{d} = 0.57 \cdot v \quad (1)$$

where v is vergence (in MA) and S_i is sensitivity (in deg/cm).

Equation 1 demonstrates a simple linear relationship between ideal LVOR sensitivity (S_i) and vergence (v), governed by a scale factor of $0.57^\circ/\text{cm}/\text{MA}$. Actual LVOR response sensitivity (S) indeed demonstrates a similar linear relationship with vergence (Busetini et al. 1994; Paige 1991; Paige and Tomko 1991b; Schwarz and Miles 1991; Telford et al. 1997), and this forms the basis of our quantitative assessment of LVOR performance.

Kinematics of the AVOR. If the eye were positioned over the axis of rotation, the ideal AVOR response to rotation when fixating an ef target would be unity; that is, eye rotation would match head rotation, but in the opposite direction. However, because the eyes are displaced anteriorly in the head, small ocular translations are generated when the head rotates (Biguer and Prablanc 1981; Hine and Thorn 1987; Paige 1996; Viirre et al. 1986). The magnitude of the ocular response required to compensate for this translational component depends on fixation distance. When fixating far away, the required AVOR gain remains unity, but increasingly larger gains are needed as fixation distance declines. The ideal gain, G_i , required to maintain binocular fixation is a function of both ocular eccentricity from the axis of rotation, r (in m), and fixation distance as determined by vergence angle, v (in MA). This geometric relationship between gain, vergence, and ocular eccentricity (Telford et al. 1998) can be approximated for small angles of rotation by the equation

$$G_i = r \cdot v + 1.0 \quad (2)$$

During natural (head-centered) head rotation, $r = 0.08$ m in humans, but this distance was in practice extended by ~ 0.03 m because of the mechanics of the bite-bar apparatus used to hold the head.

Sign convention. Results are presented with reference to a sign and axis convention used previously. IA head translation is considered positive when motion is out the right ear, and head rotation is considered positive when motion is rightward (or clockwise as observed). Eye rotation is considered positive for rightward horizontal and upward vertical responses. Ocular responses are 180° out-of-phase to head rotations and translations but by convention are presented here relative to 0° to depict the expected compensatory behavior.

QUANTITATIVE ANALYSIS OF RESPONSE PERFORMANCE. Data analysis proceeded in steps. Gains (AVOR) or sensitivities (LVOR) and phases for each stimulus condition and frequency were first distributed into vergence bins centered around the value required for each target distance. Vergences tended to cluster closely around these points even in darkness and only wandered on occasion in darkness after viewing the nearest targets, and then only in some subjects (see Fig. 2). Linear regressions were then performed on the data, yielding slopes (response parameters as a function of vergence) and intercepts (response at 0 MA vergence), in concert with the form of *Eqs. 1* and *2*. The number of cycles represented in each bin varied slightly as a function of frequency. Typically, 5–10 cycles were available at 0.5 Hz at each vergence and viewing condition, rising to 15–25 cycles at 4 Hz. Because vergence could change during a cycle, presumably modulating VOR performance accordingly, cycles were excluded if large and erratic changes in vergence occurred midcycle. This was rare, and in any case shifts in vergence presented little problem because the relationship between vergence and VOR response amplitude is linear (Busetini et al. 1994; Paige and Tomko 1991b; Schwarz and Miles 1991; Telford et al. 1997). Within-cycle shifts in vergence are matched by shifts in response amplitude 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 1991; Paige and Tomko 1991b; Snyder et al. 1992), and perhaps this factor might distort results.

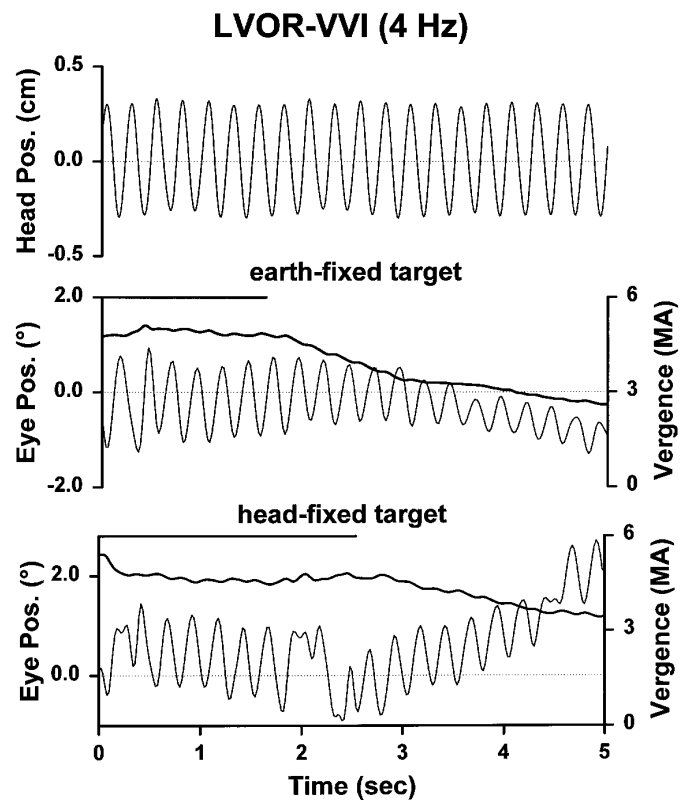


FIG. 2. Raw records of horizontal eye movement responses (*middle and bottom sets of traces*; all digitally smoothed) to translation at 4 Hz (oscillating trace in top set) from one subject while attempting to fixate a visible earth-fixed (ef, *middle records*) or head-fixed (hf, *bottom records*) target (thick bar above response records indicates that the target is on) and when instructed to maintain fixation on imagined targets in darkness. The responses (thin oscillating traces; axes labeled on the left) display evidence of modulation associated with changes in vergence (thick traces; axis labeled on the right), plotted in meter angles (MA, in m^{-1}). Because all targets were roughly aligned with the right eye, vergence was generated almost entirely by the left eye, and the average position of the right eye remained relatively stable.

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 (SDs) of averaged binned data presented and plotted. Errors caused by latency differences between vergence and VOR responses are small and cannot account for the robust interaction observed between them. In general, the results of all regressions proved precise regardless of VVI condition and frequency; the SE of the coefficients (slope and intercept) typically remained <0.02 and only rarely (and idiosyncratically) exceeded 0.03.

MECHANICAL AND GEOMETRIC CONCERNS. To what extent would the mechanical variables raised above (coupling of the motion stimulus and of the eye tracker to the head) affect experimental results? A key point is that all mechanical influences that we measured tend to increase with rising stimulus frequency, and all would produce fixed artifacts at any given frequency. In analysis, they would result in erroneous response intercepts. No such artifact would disturb the measured influence of visual targets or vergence on ocular responses, and these are the key parameters of interest in this report.

Equations 1 and *2* quantify ideal response properties during head translation and rotation. However, they are simplifications of the kinematic requirements for maintaining binocular fixation

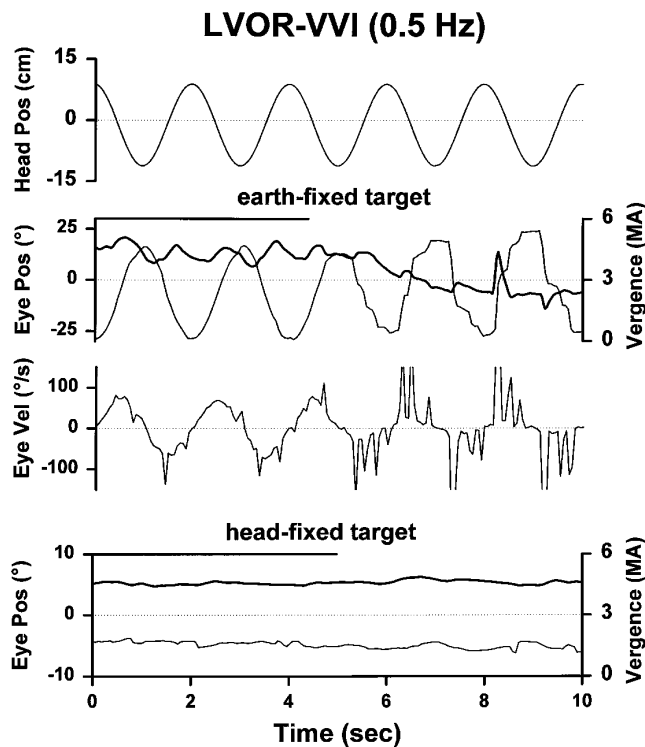


FIG. 3. Raw records of horizontal eye movement responses to translation at 0.5 Hz, displayed as in Fig. 2.

on targets at different distances and apply when eye movement responses are small. These simplifications become less accurate as ocular responses increase, and this in turn occurs as frequency or fixation distance declines. This is a negligible concern for AVOR trials because head rotation travels only 6.4° peak even at 0.5 Hz, and response deviation from an ideal sinusoidal response is minuscule, as is any error in gain. Translation trials entail a greater departure from the simplified geometry embodied in Eq. 1. However, this is a practical concern only for the stimulus with the largest excursion (9.94-cm peak at 0.5 Hz) and closest target (20 cm), and only when subjects fixate ef targets. This stimulus requires an ocular response of 26° peak excursion that follows a tangential, not a sinusoidal, relationship with head translation. However, even under this extreme condition, a sinusoidal fit to the ideal waveform yields a peak excursion error of $<1\%$ and harmonic distortion of $<2\%$. Other stimulus conditions entail far smaller errors, and these represent inconsequential influences on findings.

Another factor that is relevant primarily to translation trials is that they produce changes in ideal fixation distance along with small distortions in waveform (Crane et al. 1997). Again, this concern is inconsequential for all but the largest excursions and the closest ef target. Ideal vergence during head oscillation varies during the cycle at twice the stimulus frequency and with an average over the cycle (recall that the average is used in analysis) that is 10% less than the 5.0 MA required for the initial target distance of 20 cm. This error drops precipitously as peak head translation or vergence declines. The phenomenon appears in some raw vergence records, especially those in Fig. 3 (ef/ief-LVOR at 0.5 Hz). Small oscillations in vergence records at 4 Hz (e.g., Fig. 2) also include a component due to small unavoidable differences in calibration between the right and left eye movement signals. This is especially true when vergence is large, and therefore requires large adductions of the left eye while the right eye remains roughly fixed (recall that targets were roughly aligned with the right eye).

RESULTS

LVOR and VVI during head translation

LVOR RESPONSES RELATED TO FIXATION OF EARTH-FIXED TARGETS. Examples of raw eye movement responses during head translation at 4 Hz are shown in Fig. 2. The stimulus (*top trace*) required to achieve 0.20-g peak acceleration at 4 Hz is quite small in excursion (see Table 1). A portion of the response record during an ef/ief trial from one subject is illustrated in the middle set of traces. Response amplitude varies considerably in relationship with vergence angle. Initially (*far left* in the diagram) the nearest target LED is on (thick bar above traces), and vergence is large (thick trace). The ocular response (thin oscillating eye position trace) is initially large in amplitude. This represents a portion of the trial under ef conditions. When the target is extinguished (at ~ 1.5 s), vergence gradually declines in darkness, as this particular subject is unable to maintain near fixation in the absence of visual feedback. The shift in vergence is accompanied by a gradual decline in response amplitude.

A comparable record during 0.5-Hz translation is presented in Fig. 3. Note the smooth and large amplitude response and large vergence when the near target is on (initial 5 s), reflecting accurate continuous fixation. After the target is extinguished, the character of the response changes dramatically. Most of the response amplitude in the eye position trace is now provided by saccades, as the subject imagines tracking the target in darkness (ief condition). The smooth and presumably vestibular-driven component of the response is markedly reduced, as best visualized in the eye velocity trace.

From records such as those in Figs. 2 and 3, plots of LVOR response sensitivity against vergence for each cycle were derived. Figure 4 shows examples from trials at 4 and 0.5 Hz for both the ef (target on; open circles) and ief (dark; filled circles) conditions. The plots are from the same records as those of Figs. 2 and 3. The clumping of responses over many cycles, especially when the targets were on (ef conditions), corresponds to vergence angles for the three target distances employed. The spread of values for high vergence in darkness (ief) reflects this subject's inability to maintain vergence after the nearest target was extinguished (see Figs. 2 and 3).

The relationship between response sensitivity and vergence was roughly linear across subjects and for all frequencies and conditions, as expected based on ideal response kinematics (Eqs. 1 and 2) as well as past experience (Busetini et al. 1994; Paige and Tomko 1991b; Telford et al. 1997). Linear regressions provided a convenient means of characterizing response properties. The solid lines in Fig. 4 represent the geometrically ideal relationship, calculated to have a slope of $0.57^\circ/\text{cm}/\text{MA}$ and an intercept of $0^\circ/\text{cm}$ at 0 MA of vergence, regardless of frequency. The dotted and broken lines show the regression results for the ef and ief conditions, respectively. Several observations are derived from these plots. First, there is a substantial positive intercept under both ef and ief conditions at 4 Hz. Second, the sensitivity slope for the ef condition is greater than that for ief and closer to the ideal at both frequencies. Third, the sensitivity slope in darkness (ief) at 0.5 Hz is considerably reduced, and farther from ideal, than that at 4 Hz. This last observation

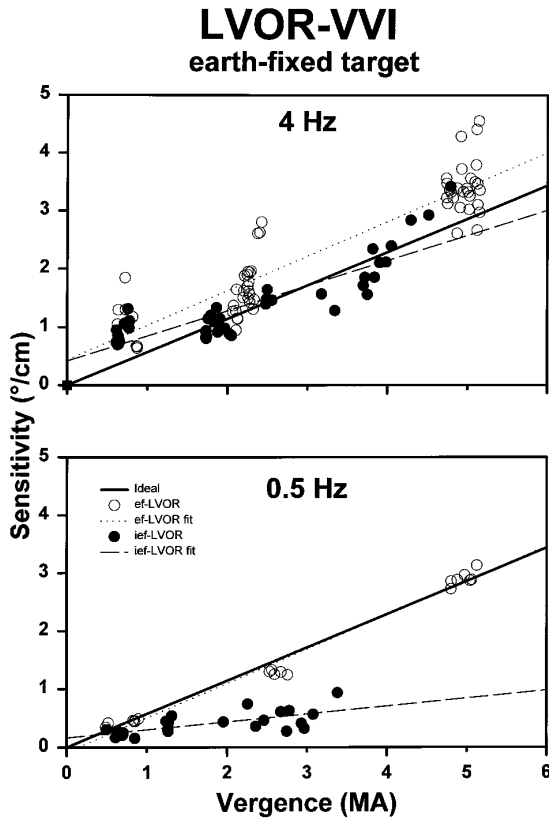


FIG. 4. Linear vestibuloocular reflex (LVOR) response sensitivity (deg/cm), plotted as a function of vergence on a cycle-by-cycle basis, at both 4 Hz (top plot) and 0.5 Hz (bottom plot). Open circles depict when the ef target was on, and closed circles indicate when the target was off (imagined fixation in darkness, or ief condition). The thick solid lines illustrate ideal response properties based on geometric predictions, and the dotted (ef) and dashed (ief) lines show best-fit lines to the data. Note the markedly reduced slope of the ief slope at 0.5 Hz compared with 4 Hz and the presence of a small response sensitivity at 0 MA vergence (response intercept) in all but the ef condition at 0.5 Hz.

is apparent in the raw records of Figs. 2 and 3 and illustrates the failure of the LVOR to adequately drive smooth eye movements at even modest frequencies. This was true despite the context of an imagined ef target. That this context actually existed during responses is apparent in Fig. 3, as the subject employed saccades to supplement the LVOR and more closely approximate the goal of maintaining fixation stability during translation (Israël and Berthoz 1989).

We now focus on LVOR and VVI response characteristics as a function of frequency across all subjects. Figure 5 shows mean (and SD) sensitivity slope, intercept, and phase as a function of frequency across all subjects and for all conditions (ef, ief, hf, and ihf). Values for the slopes and intercepts were derived from linear regressions, as described previously. Unlike sensitivity, phase did not display a systematic relationship with vergence and are therefore expressed in Fig. 5 as averages (and SDs) across vergences for each condition.

In the ef condition, the average sensitivity slope at 0.5 Hz ($0.57 \pm 0.04^\circ/\text{cm}/\text{MA}$) closely matched the ideal but declined to $0.32 \pm 0.16^\circ/\text{cm}/\text{MA}$ as frequency increased to 4.0 Hz. In darkness (ief conditions), the sensitivity slope was relatively low ($0.15 \pm 0.09^\circ/\text{cm}/\text{MA}$) at 0.5 Hz but

climbed with rising frequency to reach $0.24 \pm 0.12^\circ/\text{cm}/\text{MA}$ at 4 Hz. Slope values in darkness (ief conditions) were generally less than those obtained with the target on (ef), even at 4 Hz ($P < 0.05$; paired *t*-test). Phase under ef conditions hovered near 0° across the frequency range but developed a lead in darkness (ief) of $10\text{--}22^\circ$. Interestingly, the mean response intercept (sensitivity at 0-MA vergence) at 0.5 Hz maintained a modest value of $+0.14 \pm 0.15^\circ/\text{cm}$ for the ief condition (in darkness), rising to $+0.30 \pm 0.25^\circ/\text{cm}$ as frequency climbed to 4 Hz. In contrast, the intercept remained indistinguishable from $0^\circ/\text{cm}$ with the target on (ef) at 0.5 Hz, rising to $+0.50 \pm 0.23^\circ/\text{cm}$ at 4 Hz. The intercept displayed large variances between subjects and conditions at the highest frequencies.

LVOR RESPONSES RELATED TO FIXATION OF HEAD-FIXED TARGETS. Response characteristics were assessed in the presence of real and imagined head-fixed targets (hf and ihf). Examples of raw ocular responses are illustrated in Figs. 2 and 3 (lowest set of traces), corresponding to 4- and 0.5-Hz trials, respectively. At 4 Hz (Fig. 2), there is little apparent distinction between responses under hf and ef conditions or between ihf and ief conditions, so long as differences in vergence are taken into account. The presence of a near hf

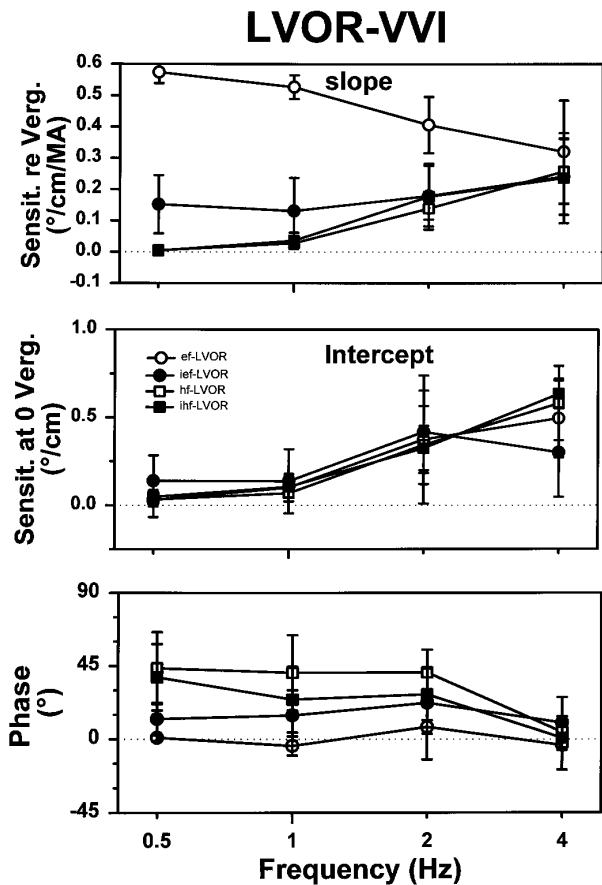


FIG. 5. Mean LVOR sensitivity slope (response sensitivity as a function of vergence), intercept (response sensitivity at 0 vergence), and phase, plotted as a function of stimulus frequency for all conditions of target motion (see key). Error bars depict SDs. The ideal response for ef/ief conditions would be a slope of $0.57^\circ/\text{cm}/\text{MA}$, an intercept of $0^\circ/\text{cm}$, and a phase angle of 0° . For hf/ihf conditions, the ideal slope would also be zero.

target simply cannot reduce the LVOR response driving the eyes. Subjectively, all subjects reported strong oscillopsia under these conditions. In contrast, all subjects were able to overcome the LVOR at 0.5 Hz (Fig. 3) and in general had little difficulty suppressing eye movements during either hf or ihf conditions. The LVOR was completely suppressed in the presence of real targets and was barely perceptible after targets were extinguished.

These response characteristics are evident in the averaged data of Fig. 5. Both sensitivity slope and intercept were indistinguishable from 0 at 0.5 Hz. However, as frequency increased, the slope for both the hf and ihf conditions climbed to values that were indistinguishable from those obtained in the ief condition at 4 Hz. Only the slope under ef conditions was somewhat higher than the others (though only significantly so relative to ief; $P < 0.05$). The same qualitative characteristics held for the intercept. Corresponding phases displayed large leads ($44 \pm 22^\circ$ for hf; $38 \pm 20^\circ$ for ihf) at 0.5 Hz, declining with increasing frequency to $1-4^\circ$ at 4 Hz. Response phases under ihf conditions were significantly less than hf phases only at 1 ($P < 0.01$) and 2 Hz ($P < 0.025$).

A direct comparison between ef and hf conditions is useful. For both sensitivity slope and phase, differences between ef and hf (compare open circles with open squares in Fig. 5) were greatest at 0.5 Hz ($P < 0.001$; paired t -test, for both slope and phase separately), where fixation of real targets was maintained nearly perfectly in both cases. The difference declined, however, as frequency increased, becoming statistically insignificant by 4 Hz. This suggests a loss of visual influence on eye movements at high frequency. The same qualitative characteristics applied to differences between ief and ihf conditions in darkness. Differences were statistically significant for sensitivity slope only at 0.5 Hz ($P < 0.005$) and 1 Hz ($P < 0.05$) and for phase only at 0.5 Hz ($P < 0.005$). This suggests that the influence of imagined target motion, like that of real visual targets, is limited to modest frequencies.

RESPONSE LINEARITY AS A FUNCTION OF STIMULUS INTENSITY. In addition to quantifying LVOR-VVI response characteristics as a function of frequency, we assessed the influence of stimulus intensity at 4 Hz, where the LVOR is most robust. A subset of four subjects participated. Sinusoidal head translations were generated at 0.1-, 0.2-, 0.3-, and 0.4- g peak head acceleration over all conditions of VVI (ef, ief, hf, and ihf) and all target distances. Analysis proceeded as described previously. Linear regressions revealed no significant influence of stimulus amplitude on response parameters (slope, intercept, or phase). Most notably, sensitivity slope varied by $<8\%$ across the range of stimulus amplitude for all conditions and in no systematic or significant manner.

In addition to considerations of response linearity, the intensity-series data provided a better opportunity to reevaluate potentially subtle differences between different VVI conditions at 4 Hz than the 0.2- g data described previously, simply by virtue of the larger number of observations entailed. After pooling all four stimulus amplitudes within and across the four subjects, sensitivity slopes averaged $0.29 \pm 0.03^\circ/\text{cm}/\text{MA}$ for ef, $0.20 \pm 0.01^\circ/\text{cm}/\text{MA}$ for ief, $0.15 \pm 0.05^\circ/\text{cm}/\text{MA}$ for hf, and $0.15 \pm 0.02^\circ/\text{cm}/\text{MA}$ for ihf condi-

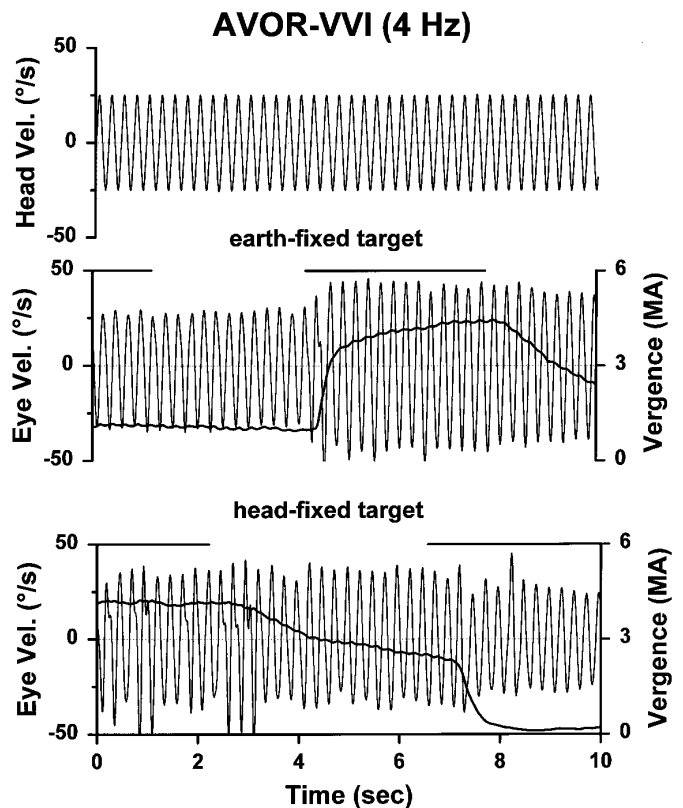


FIG. 6. Raw records of horizontal eye movement responses to head rotation at 4 Hz, displayed as in Fig. 2 and from the same subject.

tions. These values revealed significant differences in sensitivity slope between ef and all other conditions ($P < 0.001$; paired t -tests), confirming the impression derived earlier from Fig. 5. The difference between ief and ihf also proved significant ($P < 0.01$).

AVOR and VVI during head rotation

AVOR RESPONSES RELATED TO FIXATION OF EARTH-FIXED TARGETS. The entire experiment described previously was repeated with head rotation as the stimulus instead of head translation. All attributes of VVI condition (ef, ief, hf, and ihf) and target distance were identical, and the same subjects were used. A key element of this part of the study is that AVOR-VVI data were processed exactly as were LVOR-VVI data, including the analysis of the influences of binocular vergence, stimulus frequency, and VVI condition. Consider the raw eye velocity response to 4-Hz rotation shown in Fig. 6 (*middle record*). The subject is initially fixating the middle target and maintains vergence quite well after the target is extinguished (at ~ 1 s). The response amplitude is likewise maintained. After the near target is presented at ~ 4 s, vergence suddenly climbs, accompanied by an obvious increment in response amplitude. This persists after the target is once again extinguished, and gradually declines as vergence tapers off beyond 8 s. These qualitative characteristics resemble comparable responses seen during head translations (Fig. 2), but the modulation by vergence is less pronounced during rotation.

Differences between AVOR-VVI and LVOR-VVI re-

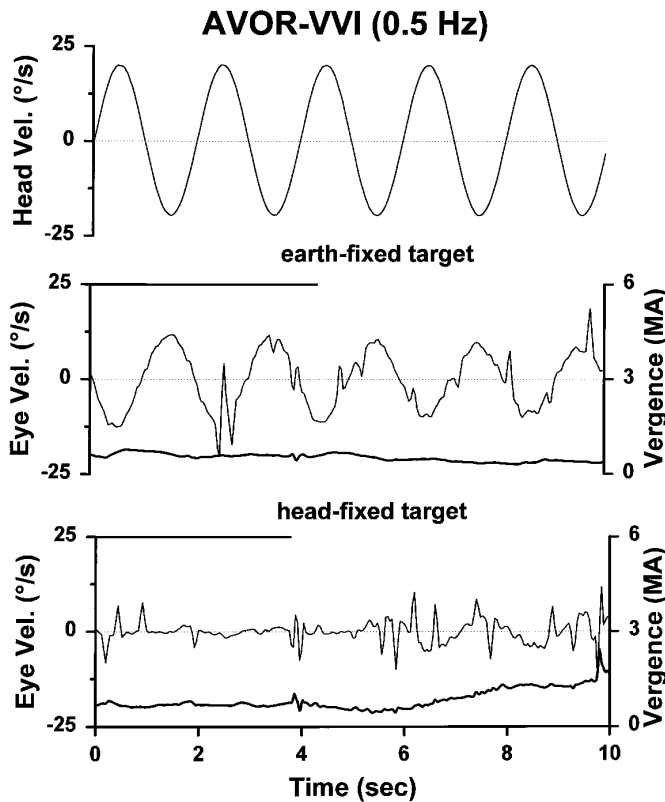


FIG. 7. Raw records of horizontal eye movement responses to head rotation 0.5 Hz, displayed as in Fig. 2.

sponses are more striking at 0.5 Hz. In general, smooth ocular responses to head rotation in darkness (both ief and ihf) are much greater in amplitude than those to translation, presumably reflecting the more robust AVOR than LVOR at modest frequencies (compare Fig. 7 with Fig. 3). After viewing an ef target, the response in darkness continues as a nearly unaltered smooth sinusoidal waveform. This is in contrast to the highly saccadic character of translation responses at 0.5 Hz.

Analysis of AVOR-VVI responses proceeded identically to that described above for LVOR-VVI trials. The data were parsed by stimulus condition and frequency and subjected to regressions to quantify the influence of vergence on response properties. Instead of sensitivities, rotational responses are expressed in terms of gain change as a function of vergence (slope) and gain at zero vergence (intercept). Figure 8 displays both parameters as well as phase for each condition of VVI (ef, ief, hf, and ihf) as a function of stimulus frequency. The gain intercept most closely resembles traditional measures of AVOR gain and should ideally equal unity when fixating a distant target. Under ef conditions, the gain intercept averaged 0.99 ± 0.03 at 0.5 Hz, rising to 1.11 ± 0.23 at 4 Hz. Unlike translation responses, the intercept in darkness (ief) proved statistically indistinguishable from that in the presence of real targets (ef) at all frequencies (Fig. 8). The influence of vergence on gain (slope) behaved quite differently. Under ef conditions, slope averaged 0.11 ± 0.02 at 0.5 Hz, closely matching the ideal of 0.11. However, values declined gradually with increasing frequency to reach 0.053 ± 0.064 at 4 Hz. These slopes are significantly positive

($P < 0.001$ for all frequencies except 4 Hz, where $P < 0.05$). In darkness (ief), the gain slope at 0.5 Hz averaged -0.036 ± 0.087 , indicating that increasing vergence actually reduced AVOR gain, in contrast to when viewing a real target. As frequency increased, however, the slope gradually rose to cross 0 at ~ 2 Hz and achieved a positive value of 0.036 ± 0.062 at 4 Hz. This value was indistinguishable from that under ef conditions. The ief slopes were sufficiently variable and small at all frequencies as to be insignificant, but the trend from negative to positive as frequency shifted from low to high was robust ($P < 0.01$ for regression slope). Phase angle over the same frequency range remained $\leq 2^\circ$ of 0 for both ief and ef conditions, except at 2 and 4 Hz, where ef phase developed a lag of $-3 \pm 3^\circ$ and $-5 \pm 3^\circ$, respectively ($P < 0.01$).

AVOR RESPONSES RELATED TO FIXATION OF HEAD-FIXED TARGETS. Response characteristics were assessed in the context of hf as well as ef ones. Examples of raw ocular responses are illustrated in Figs. 6 and 7 (lowest set of traces), corresponding to 4- and 0.5-Hz trials, respectively. At 4 Hz (Fig. 6), hf and ihf responses are robust and barely distinguishable from ef and ief conditions. As during translation trials, the presence of a near hf target cannot reduce the vestibular

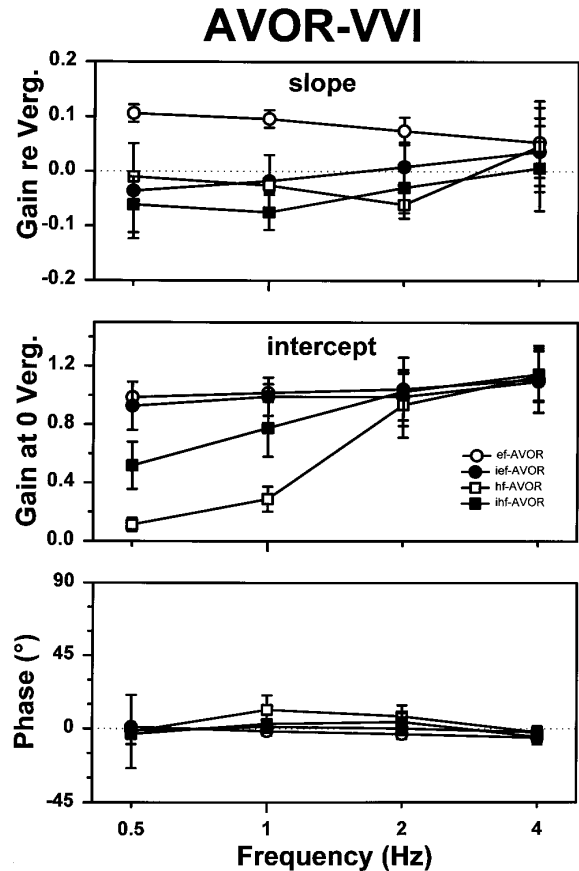


FIG. 8. Mean angular vestibuloocular reflex (AVOR) gain slope (response gain as a function of vergence), intercept (response gain at 0 vergence), and phase, plotted as a function of stimulus frequency for all conditions of target motion (see key). Error bars depict SDs. The ideal response for ef/ief conditions has a slope of 0.11/MA, an intercept of 1.0, and a phase angle of 0° . For hf/ihf conditions, the ideal slope and intercept are 0.

drive to the eyes, and all subjects again reported strong oscillopsia. All subjects were able to overcome the AVOR at 0.5 Hz (Fig. 7) and had little difficulty suppressing most (but not all) of the eye movement response during fixation of an hf target. However, a strong AVOR response appeared promptly when the target was extinguished but still imagined (ihf), although at smaller amplitude than under ief conditions. This is in contrast to the barely visible response seen under comparable conditions during translation trials (Fig. 3, *bottom traces*).

Figure 8 includes hf and ihf response parameters from rotation trials as a function of frequency. The hf gain intercept is small at 0.5 Hz but rises with increasing frequency to meet that of ef responses at 4 Hz. The gain intercept under ihf conditions behaves similarly but displays larger values than for hf conditions at the lowest two frequencies, commensurate with the limited influence of imagined hf targets on the AVOR. Gain slopes are variable and typically negative under both hf and ihf conditions, but the ihf slope reveals a positive trend with increasing frequency ($P < 0.01$ for regression slope). Response phase shows a tendency to lead the head, most noticeably under hf conditions and for the middle two frequencies. Phase generally was not systematically modified by vergence.

DISCUSSION

Overview

The response dynamics of the VOR and its interactions with vision were quantified during both translational and rotational motion (LVOR-VVI and AVOR-VVI). Response characteristics were assessed as a function of three variables known to influence the VORs, all related to the context in which head movements are made. These contextual influences include stimulus characteristics (frequency and amplitude of motion: stimulus context), binocular viewing distance (fixation context), and real or imagined visual target motion (visual context). Stimulus properties directly affect the vestibular input by virtue of both the mechanics of the sensory endorgan and neural processing within VOR pathways. In contrast, the fixation and visual contexts reflect the presumed goal of all VORs, to maintain binocular fixation on targets in space. This goal is determined by the geometric relationship between the position and motion of the eyes relative to their fixated target as well as the potential motion of the target in space. These relationships govern the ocular responses required to maintain stable binocular foveal images during head movements. In this study, common analytic methods were applied to LVOR-VVI and AVOR-VVI responses in part to emphasize their common goals.

Before discussing the three contextual influences on the VOR noted above, let us first address an important general concern—to what extent do the experimental conditions studied here reflect the physiological challenges of natural behavior? First, the VORs were studied in the presence of visual targets and therefore as interactions with visual mechanisms that also drive eye movements, most notably smooth pursuit. Natural activities typically entail such interactions, and objects of interest are encountered that are stationary (ef) or moving through space. The latter might resemble the

experimental hf context, arising when examining objects in our hands while walking or when tracking targets largely with the head. Second, we studied the VORs during sinusoidal motion. Even casual observation reveals that harmonic oscillation is a common attribute of daily activity. Examples include head movements made during natural ambulation (Cappozzo 1981; Demer and Viirre 1996; Grossman et al. 1988; Waters et al. 1973), which predominantly lie within the frequency bandwidth (0.5–4 Hz) employed in this study. Third, most behaviors include combinations of linear and angular motion, with different weightings depending on the activity (e.g., walking entails largely linear head motion). Extensive studies of VOR responses during angular, linear, and combined stimulation in squirrel monkeys revealed that AVOR-LVOR interactions behave linearly (Telford et al. 1996, 1998). The current human investigation limited stimuli to angular and linear motion alone to focus on specific contextual influences on the two classes of VOR. Preliminary (and unpublished) observations suggest that human AVOR-LVOR interactions also behave linearly, as supported by others (Crane et al. 1997).

Influence of stimulus characteristics on VVI

Ocular responses during translational and rotational trials were quantified over the frequency bandwidth, 0.5–4.0 Hz. This limited range was chosen largely because previous experiments in monkeys (Paige and Tomko 1991b; Telford et al. 1997) demonstrated a robust LVOR only during oscillations at >1 Hz or during transient accelerations that resemble high frequencies (Busetini et al. 1994; Schwarz and Miles 1991) but weak responses at more modest frequencies (Telford et al. 1997). In general, the current experiments in humans reflect the same overall characteristics. LVOR responses in darkness (ief and ihf conditions) generally display the greatest sensitivities and smallest phase leads at the highest frequency and show declining sensitivities and rising phase leads as frequency declines toward 0.5 Hz, although with clear influences of other contextual variables. In general, this qualitative behavior replicates findings in squirrel monkeys under similar conditions (Telford et al. 1997) and is characteristic of a high-pass filtering process operating on otolith input. The findings are consistent with the notion that the LVOR operates with distinct frequency-dependent reflexes that include a high-frequency translational LVOR that operates at frequencies >1 Hz and a tilt LVOR that operates most prominently below 0.1 Hz (Paige 1996; Paige and Tomko 1991a). Because our goal was to emphasize translational LVOR reflexes and their interactions with vision, a stimulus bandwidth was chosen that emphasized this reflex. A related frequency parsing scheme seems to hold, at least in part, for motion perception (Glasauer 1995; Guedry 1974; Schöne and Mortag 1968; Walsh 1961). A relevant psychophysical observation is that all subjects in these experiments reported subjective sensations of IA translation and never roll tilt. This is in contrast to low-frequency (≤ 0.1 Hz) linear accelerations in our laboratory with the same device (Seidman and Paige 1996; Seidman et al. 1998), which induced sensations of tilt and not translation. Studies at intermediate frequencies induce combinations of tilt and translation perceptions, commonly referred to as the “Hilltop illusion” (Glasauer 1995).

The dynamics of the LVOR are in dramatic contrast to those of the AVOR, in which gains are less influenced by stimulus frequency (0.5–4 Hz), particularly when subjects imagine ef targets. Thus AVOR responses while subjects imagine ef targets (ief–AVOR) are indistinguishable from those in which real targets are present (ef–AVOR; see Fig. 8), regardless of stimulus frequency. In contrast, the equivalent LVOR responses are considerably reduced under ief compared with ef conditions at lower frequencies (see Fig. 5). This reflects a fundamental difference in dynamics between the LVOR and AVOR. Although both behave with high-pass characteristics, the effective cutoff of the AVOR extends to a much lower frequency (<0.1 Hz) than the LVOR (Paige 1996) by roughly a decade. Further, the low-frequency range of the AVOR is an extended version of the dynamics of its canal afferent input, accomplished by a process commonly called “velocity storage” (Raphan et al. 1979; Robinson 1981), whereas the translational LVOR specifically filters out low-frequency information from its otolith afferent input. This distinction is quite useful during natural behavior and serves to avoid erroneous LVOR responses and perceptions of translation when we simply tilt our heads toward one shoulder, a maneuver that activates IA otolith input as readily as translational accelerations (Paige et al. 1995; Paige and Tomko 1991a). That natural head tilt is registered by a robust canal signal in addition to otolith input does not alter the fact that when the head tilt is completed the canal signal ceases while otolith signals persist, and yet no enduring translational LVOR or perception accompanies this linear acceleration signal. This is why our model of the translational LVOR includes an effective two-pole, high-pass process within its central pathway (Telford et al. 1997).

Influence of binocular viewing distance on VVI

Simple geometric considerations dictate that the ideal VOR must modulate its response amplitude inversely with viewing distance if binocular fixation stability is to be maintained. This is particularly true for the LVOR, in which case the kinematically ideal response to head translation should be entirely dependent on fixation distance. The ideal LVOR sensitivity should equal 0 when fixation distance is infinitely far and should climb progressively as fixation distance declines. This relationship is conveniently quantified by the sensitivity slope parameter (Fig. 5), which relates LVOR response amplitude to binocular vergence, a measure of the eyes’ fixation distance. This relationship indeed holds for the experimentally recorded LVOR. However, the phenomenon is most robust at 4 Hz and declines as stimulus frequency drops. In other words, the influence of vergence on the LVOR is frequency dependent and behaves with high-pass dynamics (Telford et al. 1997). This observation applies to the LVOR in darkness but with a further modulation by the imagined context of target motion; that is, there is an obvious distinction between ief and ihf conditions at lower frequencies. Nevertheless, for both conditions, a clear influence of vergence is apparent at a fixed high frequency and a clear influence of stimulus frequency at a given vergence, as reported in monkeys (Telford et al. 1997). The high-pass properties of the vergence influence helps explain why many

studies, typically employing lower frequencies or “soft” transients, have not witnessed a robust effect, and this in turn emphasizes the need for high-frequency stimuli in quantifying the LVOR.

One common observation among LVOR studies (Busetini et al 1994; Paige 1991; Paige and Tomko 1991b; Schwarz and Miles 1991), including this one, is the presence of a response at zero vergence, as quantified by the sensitivity intercept parameter. This response when binocular fixation distance is infinitely far is clearly not required to maintain stable fixation. Indeed, any response under these conditions actually generates retinal image slip. We previously suggested (Paige and Tomko 1991b) that this positive intercept serves a useful purpose. In effect, the intercept shifts the entire relationship between vergence and response amplitude upward. This positive intercept allows the LVOR to approach ideal performance over a wider range of fixation conditions than if the intercept were zero. This concept is exemplified in Fig. 4, which includes the best-fit line segment (slope and intercept) to the data along with the ideal (slope of 0.57°/cm/MA and intercept of 0°/cm). In this subject, note that in the ief case at 4 Hz the regression line intersects the ideal at ~3 MA of vergence, indicating a fixation distance of 33 cm. This intersection corresponds to perfect reflex performance; that is, the LVOR response exactly matches requirements to maintain binocular fixation on a point 33 cm from the eyes. For this particular subject, the ef–LVOR response at 4 Hz lies entirely above the ideal across the measured range of vergences but is idiosyncratic to this individual. On average, the point of perfect fixation stability occurs somewhere between 33 and 73 cm at 4 Hz across all conditions, including real or imagined ef and hf targets. Thus the LVOR seems optimized to maintain fixation stability at roughly arm’s length. In addition, the error that accumulates as vergence extends from this distance in either direction remains quite small. Note that if the intercept were zero ideal performance would exist only when fixating infinitely far targets and would progressively deviate below the ideal as vergence increased. This would be especially troublesome at 4 Hz because the sensitivity slope is just 61% of ideal even when the LVOR is visually enhanced by a real ef target, and just 46% in darkness. Curiously, the LVOR performance in darkness observed in this study is considerably better than previously reported in the human LVOR (Busetini et al. 1994; Paige 1989, 1991). Again, the difference is likely due to the remarkable frequency dependence of the LVOR, including its vergence influence. Even a shift from 3 to 4 Hz provides a noticeable augmentation of LVOR response sensitivity.

Another provocative observation is that the LVOR maintains a positive intercept even at low frequencies, including 0.5 Hz. This is true even in darkness under conditions in which subjects imagine a hf target, which would tend to suppress the response. Indeed, under ihf conditions the sensitivity slope at 0.5 Hz (vergence influence) is gone, and the intercept remains a small but significant positive value. This implies that some LVOR sensitivity exists at 0.5 Hz (and presumably below), which remains unmodulated by vergence. The same was observed in the squirrel monkey LVOR (Paige et al. 1995; Paige and Tomko 1991b; Telford et al. 1997). Recent recordings of the human (unpublished

observations) and monkey (Paige et al. 1995) translational LVOR at frequencies <0.5 Hz confirm this supposition.

The influence of fixation distance applies to the AVOR as well as to the LVOR. This is true because the eyes are positioned anteriorly in the head relative to the axis of natural head rotation. The eccentricity of the eyes in the head is responsible for a small translational component of ocular motion in space whenever the head rotates. Proper compensation for this translational component, as for the LVOR, depends on fixation distance. The effect is small given that the ocular translations produced by head rotations are small, but are nevertheless quantifiable. The appropriate parameter is the gain slope shown in Fig. 8. In contrast, the gain intercept corresponds to the more traditional measure of AVOR response amplitude, and this parameter reflects compensation for the strictly angular component of head rotation.

There are several concerns of relevance to AVOR–VVI. First, under the simplest and most ideal of circumstances, rotation while subjects fixate a real ef target, the gain slope closely matches the ideal of 0.11 at modest frequencies, commensurate with an ocular eccentricity from the rotation axis of 0.11 m in this study. The gain slope declines with increasing frequency to nearly match that of AVOR responses in darkness, as observed in LVOR–VVI responses. Gain slope behaved quite differently when subjects imagined ef targets in darkness. Although a small (but not statistically significant) positive slope was recorded at 4 Hz, in concert with previous reports with transient stimuli (Biguer and Prablanc 1981; Snyder and King 1992; Viirre et al. 1986), the slope declined systematically as frequency decreased, to yield negative numbers at the lowest frequencies. This latter phenomenon was reported by others (Crane et al. 1997; Shelhamer et al. 1995; Viirre and Demer 1996). Thus AVOR gain was modulated by vergence in different directions depending on the frequency of the stimulus. At low frequency vergence had a detrimental effect on AVOR gain, whereas at the highest frequency AVOR amplitude climbed slightly with rising vergence. The overall increasing trend in gain slope with increasing frequency resembles a comparable finding in human LVOR–VVI responses and in the monkey LVOR (Telford et al. 1997).

What might explain the negative AVOR gain slope observed at lower frequencies? Recall that geometric considerations require a positive relationship between vergence angle and gain. One provocative possibility is that vergence is associated with an increase in tonic (or average) discharge rates in oculomotor neurons driving both the lateral and medial rectus, even when the observed eye is stationary and convergence is accomplished entirely by the other eye. This notion has received neurophysiological support (Gamlin et al. 1989; Maxwell and King 1992). The outcome would presumably be reflected as a balanced increase in muscle torque on the eye, without a change in its ambient eye position. This effective co-contraction would produce an increase in stiffness and/or resistance, which in turn might result in smaller response amplitudes for the same stimulus. Thus, as vergence increases and mechanical stiffness or resistance rises, response amplitudes presumably decline, resulting in a negative gain slope. Such a change in plant dynamics would be expected to behave in a frequency-dependent manner; specifically, high frequencies would be less influenced

than low, as observed experimentally. Why is gain slope negative at low frequencies in the AVOR while sensitivity slope is always positive in the LVOR? Presumably, vergence-dependent changes in ocular mechanics would hold regardless of the particular vestibular reflex, but, because the LVOR is more dramatically influenced by vergence, the effect is presumably masked, resulting in a generally positive slope, although always suboptimal.

Recall that rotational stimuli were routinely performed with subjects displaced slightly forward from their intended axis of rotation by ~ 3 cm. This means that a small LVOR component is contained within our AVOR responses. To what extent did this factor influence results? Both qualitatively and quantitatively, response characteristics of Fig. 8 prove to be overwhelmingly driven by the AVOR and its interactions with vision. This conclusion was solidified after we calculated the LVOR component based on the LVOR–VVI response characteristics of Fig. 5 and then subtracted the calculated LVOR from the combined responses, presuming linearity of AVOR–LVOR interactions (Crane et al. 1997; Telford et al. 1996, 1998). In general, the outcome reduced the gain slope by ~ 0.01 across the frequency bandwidth and the intercept by only 2% at 4 Hz, declining to negligible values at the lowest frequency.

Influence of real and imagined visual targets on VVI

The presence of real or imagined visual targets has been known to influence AVOR response properties for decades (Barnes 1993; Barr et al. 1976; Furst et al. 1987; Jell et al. 1988). AVOR–VVI responses reported here replicate earlier findings, but response properties are expressed in a non-traditional manner. Gain is parsed into an angular response component at 0 vergence (gain intercept) and a vergence-dependent response component (gain slope) that compensates for ocular translations in the head during natural rotation. Nevertheless, conclusions remain the same. The influence of hf and ef real visual targets is always greater than their imaginary equivalents. The effect is generally most pronounced at low frequency and declines systematically as frequency rises.

Response properties are nearly indistinguishable across conditions of visual context at 4 Hz and become progressively more discernible as stimulus frequency declines. In general, the influences of real and imaginary targets on AVOR–VVI properties behave with low-pass characteristics that closely resemble those of smooth pursuit (Barnes 1993; Jell et al. 1988; Paige 1994). The same properties and conclusions apply to LVOR–VVI responses. The major difference between AVOR and LVOR driven responses is the generally more robust AVOR than LVOR at lower frequencies. This is due to the vastly different high-pass dynamics of the two reflexes. One result is that AVOR responses to rotation under ief conditions closely follow those under ef conditions at all frequencies, whereas LVOR responses to translation under ief and ef conditions are close only at high frequency and separate as frequency declines.

An interesting manifestation of this difference appears in the raw records of the AVOR and LVOR at 0.5 Hz (Figs. 7 and 3, respectively). Under ief conditions the AVOR displays a smooth and large-amplitude response that is nearly

indistinguishable from the *ief* response. In contrast, the *ief*-LVOR response is heavily supplemented by saccades, as reported by others (Baloh et al. 1988; Israël and Berthoz; Skipper and Barnes 1989). The smooth component of the response, presumably related to vestibular (LVOR) input, is meager at best. The same applies during *ief*-AVOR trials, but because the AVOR is so much more robust than the LVOR at, for example, 0.5 Hz, there is little need to invoke saccades along with the AVOR to maintain fixation stability; the AVOR performs sufficiently well that the overall response remains smooth. The situation reverses when considering *ihf* conditions for the same 0.5-Hz head oscillation. Whereas the LVOR requires little suppression to dampen its weak output at this low frequency, the more robust AVOR persistently drives the eyes away from the imagined *hf* target, and subjects must evoke saccades to repeatedly correct for the VOR-driven fixation errors. None of this occurs at 4 Hz, where any saccadic strategy would prove counterproductive given the small ocular excursions involved and the unacceptably long latency of saccade production relative to the 250-ms period of head oscillation.

One way of describing the *ief*-LVOR response at 0.5 Hz is that overall eye *position* rather admirably tracks the imagined *ef* target relative to head translation, including both smooth LVOR and saccadic components of the response strategy. In contrast, eye *velocity* poorly tracks target velocity. This is not unlike the behavior of smooth pursuit when tracking a real target under predictable conditions, in which the target is unexpectedly extinguished, only to reappear later. The smooth (accurate eye velocity tracking) component is rapidly abolished during such moments and is replaced by a saccadic strategy that attempts to maintain overall eye position on the estimated position of the target in space. However, eye velocity remains near zero except during saccades. In essence, smooth pursuit itself disappears and is replaced by a saccadic strategy based on a cognitive impression of target position. We indeed demonstrated this in control experiments on several subjects during pursuit trials at 0.5 Hz in which the target was periodically blanked, as in our VVI paradigms. The ability to predict and “track” imagined targets presumably underlies the combined smooth and saccadic character of *ief*-LVOR responses (e.g., Fig. 3).

An interesting controversy exists in the VVI literature regarding the mechanism behind the influence of imagined targets; that is, does the context of target motion reflect a linear combination of VOR and smooth pursuit (or pseudopursuit), or is there also a direct influence on the VOR's neural pathways? The controversy is founded on a discrepancy in VVI responses that depends on whether steady-state harmonic or transient stimuli are applied. The presence of *hf* targets during brief transients directly reduces AVOR response performance by ~30% in humans (Huebner et al. 1992) and monkeys (Cullen et al. 1991), but not during sinusoids (Paige 1994), as replicated here at 4 Hz. The same is true in the LVOR. The reason remains mysterious. Potentially, steady-state sinusoids reduce suppression of the VOR at high frequency by degrading fixation. The VOR never quite matches kinematic requirements at 4 Hz and therefore experiences persistent image slip under steady-state conditions. Studies with transient stimuli never operate under the same conditions and therefore represent a more

idealized situation where fixation and image stability are initially quite well preserved before the head is perturbed. Perhaps a transient applied during high-frequency oscillation would provoke no greater change in VVI response properties than the steady-state response alone.

What is the source of the visual contextual signal (imagined target motion in darkness) that modulates VOR performance? Perhaps the system utilizes the vestibular input itself through a shared pathway with smooth pursuit downstream from its visual input. This would account for the remarkable similarity between the dynamics of pursuit and that of imagined context on the AVOR and LVOR (Barnes 1993; Paige et al. 1996). Similarities extend to other response attributes, such as eye velocity oscillations (ringing) during both pursuit and *hf*-AVOR, and the phenomenon of prediction (Barnes 1993). Perhaps smooth pursuit really represents a multisensory tracking system for which vision is the primary, but not the only, driving stimulus to the system. If so, to what extent are vestibular signals available to this mechanism? We can use LVOR-VVI and AVOR-VVI recordings at 0.5 Hz to generate a reasonable estimate. The difference in peak eye velocity between *ef* and *hf* responses reflects the direct visual influence on eye movements (smooth pursuit) during both translational and rotational motion. Similarly, the difference between *ief* and *ihf* reflects the influence of imagined target motion (pseudo-pursuit). The ratio of the two differences [(imagined)/(real)] provides an estimate of the desired answer. This ratio was calculated for both translational and rotational trials at 0.5 Hz and over a range of vergence angles between 0 and 5 MA. The ratios for angular and translational trials closely overlapped as a function of peak eye velocity and were therefore pooled. The ratio dropped systematically with increasing peak eye velocity from roughly 45% at 20°/s to 31% at 85°/s. Such high eye velocities were achieved during translational trials when subjects viewed or imagined the nearest target. Overall, and acknowledging the amplitude-dependent nonlinearity, the influence of imagined target motion (pseudo-pursuit) on the VOR generally accounts for roughly one-third of the influence of real targets (true smooth pursuit).

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