Ocular Motor Responses to Abrupt Interaural Head Translation in Normal Humans

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Ramat, Stefano and David S. Zee. Ocular motor responses to abrupt interaural head translation in normal humans. J Neurophysiol 90: 887–902, 2003. First published April 2, 2003; 10.1152/jn.01121.2002. We characterized the interaural translational vestibulo-ocular reflex (tVOR) in 6 normal humans to brief (~200 ms), high-acceleration (0.4–1.4g) stimuli, while they fixed targets at 15 or 30 cm. The latency was 19 ± 5 ms at 15-cm and 20 ± 12 ms at 30-cm viewing. The gain was quantified using the ratio of actual to ideal behavior. The median position gain (at time of peak head velocity) was 0.38 and 0.37, and the median velocity gain, 0.52 and 0.62, at 15- and 30-cm viewing, respectively. These results suggest the tVOR scales proportionally at these viewing distances. Likewise, at both viewing distances, peak eye velocity scaled linearly with peak head velocity and gain was independent of peak head acceleration. A saccade commonly occurred in the compensatory direction, with a greater latency (165 vs. 145 ms) and lesser amplitude (1.8 vs. 3.2 deg) at 30- than 15-cm viewing. Even with saccades, the overall gain at the end of head movement was still considerably undercompensatory (medians 0.68 and 0.77 at 15- and 30-cm viewing). Monocular viewing was also assessed at 15-cm viewing. In 4 of 6 subjects, gains were the same as during binocular viewing and scaled closely with vergence angle. In sum the low tVOR gain and scaling of the response with viewing distance and head velocity extend previous results to higher acceleration. A saccade commonly occurred in the compensatory direction, with a greater latency (165 vs. 145 ms) and lesser amplitude (1.8 vs. 3.2 deg) at 30- than 15-cm viewing. Even with saccades, the overall gain at the end of head movement was still considerably undercompensatory (medians 0.68 and 0.77 at 15- and 30-cm viewing). Monocular viewing was also assessed at 15-cm viewing. In 4 of 6 subjects, gains were the same as during binocular viewing and scaled closely with vergence angle. In sum the low tVOR gain and scaling of the response with viewing distance and head velocity extend previous results to higher acceleration.

INTRODUCTION

Motion of the head can impede clear vision of objects of interest in the environment. Head movement is detected by the labyrinthine sensors, and the eyes rotate to compensate for both rotations and translations of the orbits. Two vestibulo-ocular reflexes (VOR) generate the compensatory response: the angular VOR (aVOR), using information about angular motion from the semicircular canals, and the translational VOR (tVOR) using information about linear motion from the otoliths. During all natural head movements both reflexes cooperate to stabilize images on the retina. Many experimental paradigms have been developed to test the reflexes separately and to investigate their interaction. The interaural tVOR has been extensively studied in monkeys in response to interaural sinusoidal oscillations (Angelaki et al. 2000; Paige and Tomko 1991a; Telford et al. 1997), eccentric rotations (Snyder and King 1992; Telford et al. 1998), and brief head translations (Angelaki and McHenry 1999; Schwarz and Miles 1991). These studies found that the interaural tVOR in the monkey elicits a short-latency (12 ms) compensatory response, with high-pass filter dynamics and a sensitivity that scales linearly with the inverse of target distance (Paige and Tomko 1991b; Schwarz and Miles 1991; Snyder and King 1992).

The interaural tVOR has also been investigated in humans in response to linear sinusoidal motion (Paige et al. 1998; Shelnhammer et al. 2000), sinusoidal eccentric rotation (Bronstein and Gresty 1988; Crane et al. 1997; Gresty et al. 1987; Paige et al. 1998), and to abrupt, steplike stimuli but usually at a relatively low acceleration (Busettini et al. 1994; Gianna et al. 1997, 2000; Lempert et al. 1998). Somewhat higher accelerations (0.5g) were used in recent studies (Aw et al. 2003; Crane et al. 2003; Tian et al. 2002a,b).

The eye movement required to achieve optimal visual stabilization in response to both rotational and translational movement of the head depends on the position of the target relative to the fovea of the eyes of the subject. Close targets require an increase in the amplitude of the eye movement and some degree of disconjugacy between the two eyes to minimize motion of images on the fovea of both eyes during head movement. The effect of target distance on the human tVOR has been studied during natural activities (Crane and Demer 1997; Moore et al. 2001), during combinations of unpredictable transients of linear and angular accelerations delivered through off-center rotation (Crane and Demer 1998), during lateral steps at relatively low head accelerations (Busettini et al. 1994; Gianna et al. 2000), and, most recently, to abrupt translations (Aw et al. 2003; Crane et al. 2003; Tian et al. 2002a,b).

The aim of the present study was to characterize further the response of normal human subjects to an abrupt transient interaural stimulus, at very high accelerations (>1.4g), which might mimic head motion that can occur with a perturbation of the head during movement of the body. The goal was to study the eye movement response to a stimulus that placed challenging demands on the translational VOR, analogously to the brief, high acceleration head “thrust” stimulus that makes demands on the angular VOR (Halmagyi and Curthoys 1988). Here, we focused not only on the analysis of the first part of the eye movement response, which is commonly considered

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“open-loop”, given that no visual feedback about performance is yet available to modify the initial response, but also on the overall functional capabilities of the reflex, including the use of saccades, by examining the degree of compensation achieved by the time the head stops moving. We also examined the effects of viewing distance for near targets, and the influence of monocular versus binocular viewing. An abbreviated and preliminary report of a portion of the results of this investigation was presented in a conference proceedings (Ramat and Zee 2002).

**METHODS**

*Patients and normal subjects*

Responses to interaural translations of the head were evaluated in 6 normal subjects (ages between 19 and 36 yr, 2 women, 4 males) with normal vestibular function and no eye movement abnormalities. All subjects gave informed consent before participating in the experiment. The protocol was approved by the Joint Committee on Clinical Investigation of The Johns Hopkins University School of Medicine.

*Recording of eye and head movements*

The movements of both of the eyes and the head were recorded around all three axes of rotation (horizontal, vertical, and torsional) using the magnetic field search coil method (1 m3 cubic coil frame) with dual coil annuli. The output signals of the coils were filtered with a single-pole RC analog filter with a bandwidth of 0–90 Hz, and then sampled at 1 kHz with 12-bit resolution. Head rotations were sensed with a search coil embedded in the bite bar. System noise was limited to 0.1°. Data were stored on disc for later off-line analysis using Matlab (Mathworks, Natick, MA). Further details of the calibration and eye movement recording procedures can be found in Bergamin et al. (2001).

Translational (and also rotational head movements) were recorded through a 6-degrees-of-freedom miniBIRD device (bandwidth of 144 Hz, manufactured by Ascension Technology) that determines the position and orientation of a receiver with respect to a transmitter. The receiver was embedded in the bite bar worn by the subject (as was the head search coil), whereas the transmitter was fixed in space at a distance of about 35 cm from the subject. The bite bar prevented any concurrent rotation of the head around the yaw axis that might have led to a confounding, compensatory slow phase for angular motion. The position resolution of the miniBIRD device was 0.5 mm RMS and the rotation resolution was 0.1° RMS, at 30 cm from the transmitter (manufacturer’s specification). Static position accuracy was 1.8 mm RMS averaged over a range of ±75 cm in any direction. Translational head motion also was recorded with a linear accelerometer attached to the bite bar; the resulting signal was sampled at 1 kHz. The accelerometer signal was used to detect the onset of head motion as well as to confirm the accuracy of the translational signal recorded by the miniBIRD device.

The head of the subject was precisely centered in the field coils, using 2 space-fixed, horizontally and vertically oriented laser beams emanating from the location of the zero-position light-emitting diode (LED), so that the center of the interpupillary line coincided with the center of the field coils and the interpupillary line was parallel to the earth horizontal. The position recorded by the miniBIRD device when the subject was centered in the fields was considered as the reference position for measures of both angular and linear head movement. Instantaneous head position provided by the miniBird device during head translation was used for the computation of ideal eye movements (see **ANALYSIS OF RESPONSES**).

To deliver quasi-reproducible translational stimuli along the interaural axis we developed a “head sled” device (Ramat et al. 2001), which has the advantage of a low inertia compared with whole body sleds. The head sled device consists of two Plexiglas plates that can be connected together and tightened on the sides of the head of the subject. Padding material is inserted between the ears of the subject and the Plexiglas plates for comfort. Two square section rods are rigidly attached to the external sides of the two plates providing the guide rail for the motion of the device, which can slide en bloc along the subject’s interaural axis.

*Viewing conditions*

In the experimental trials the subjects were asked to fix on an LED target while they were translated along the interaural axis. The LED remained illuminated throughout the trial. The room was otherwise dimly illuminated. Trials were performed at 2 viewing distances with the LED at 15 and at 30 cm in front of the eyes of the subject. Viewing distances were measured from the external canthi of the eyes, a landmark approximating the location of the center of rotation of the globe. Each trial began with the LED aligned with the midsagittal plane of the subject. For the near target condition we recorded responses both in monocular (REV and LEV) and in binocular (BEV) conditions. For the 30 cm target only BEV data were acquired. Stimuli were delivered with random timing and direction so the subject could not anticipate the stimulus.

*The stimuli*

The stimuli were delivered manually by translating the head abruptly to produce a step-like change of head position along the interaural axis. A superposition of the head position traces in one subject (S1) is shown in Fig. 1. The head movements had an average duration of 190 ms, and a peak head velocity of about 25 cm/s, which occurred on average 86 ms after the onset of the head movement. The acceleration profiles, shown in the bottom panel of Fig. 1, were of a consistent shape with a shorter and sharper acceleration period and a longer and smoother deceleration time. The description of the whole population of head stimuli delivered to all subjects is as follows: median (90% confidence interval) duration of the overall head movement, 191 (131 to 300) ms; overall amplitude 2.5 (1.9 to 3.1) cm; peak head velocity, 25 (19 to 36) cm/s occurring on average 86 (65 to 104) ms after the onset of head motion and reaching an average peak acceleration of 0.71g (0.43 to 1.25g). We found no significant differences in the stimulus parameters (duration, peak velocity, time of peak velocity) among the different experimental conditions (P > 0.15).

To characterize the stimuli better we evaluated the frequency content of head motion. Because each “head heave” stimulus represents a transient signal having a finite length, given that it was sampled at a finite frequency (1 kHz), we computed the energy spectra of our head acceleration data using a padding and windowing technique suggested by Harris (1998). The resolution of the spectrum computed with this approach was 0.12 Hz. The cosine window technique introduces distortion at frequencies of the order of the reciprocal of the length of the data segment (1/8192 = 10^-4 Hz) but these are below the range of interest for our analysis.

For all subjects the stimulus had a relatively wide spectrum, showing energy content at frequencies exceeding 10 Hz, often extending ±20 Hz. After the main peak all spectra showed a linear fall off with a slope of approximately −2, therefore confirming the steplike nature of the movement.

*Analytical techniques*

**CALCULATION OF EYE MOTION.** Rotation matrices were generated using the calibration values of the eye and head coils, and then transformed into rotation vector coordinates (Bergamin et al. 2001). The angular positions of each eye coil (relative to spatial coordinates) were calculated from the rotation vectors. To calculate the angular
velocity trajectories, a 5th-order 100-Hz low-pass finite impulse response (FIR) filter was first applied to the rotation matrices. The resulting data were differentiated using a 5th-order REMEZ (Matlab) FIR filter, designed to differentiate $\pm 40$ Hz and to low-pass filter the data above 100 Hz. The differentiated data were then used with the undifferentiated, filtered rotation matrices, to calculate angular velocity (Hepp 1990). To calculate the angular acceleration trajectories, the angular velocity data were differentiated with the same 5th-order REMEZ combination differentiator and low-pass filter.

**Calculation of Head Motion.** To calculate the motion of the head we used six coordinates describing the position and the orientation of the head of the subject with respect to the fields: 3 angles from the bite bar coils, describing head orientation with respect to the magnetic fields, and 3 linear coordinates from the miniBIRD receiver in the bite bar, describing the position of the subject with respect to the earth-fixed coordinate system originating from the transmitter. Based on the knowledge of the instantaneous position of the head in space and of the visual target, we were able to compute the instantaneous ideal position of each eye in the orbit needed to maintain perfect fixation of the visual target, following the technique detailed in Ramat et al. (2001).

**Analysis of Responses.** Ideal eye position was computed from the 6-column data matrix representing the instantaneous position and orientation of the bite bar, the position of the target (measured directly during the initial steady fixation of the near target without head motion), and the two anatomical measurements required for the computation: the orthogonal distance between the miniBird receiver and the outer canthi of the eyes and the interpupillary distance. Ideal and recorded eye positions were defined to be zero at the beginning of each trial, and eye movements from that initial position were compared with the ideal movement.

To evaluate the influence of head motion within the fields outside of the volume in which they are homogeneous, we mounted the eye coils on a Styrofoam model of the head, and secured the simulated head in the head sled and on the bite bar. We then recorded eye and head coil signals from the Styrofoam model during translations of the head sled of the same amplitude as during the actual recordings from subjects. The translation of the head coil within the fields accounted for an apparent head rotation of at most 0.5° when the head was translated to a position 3.0 cm away from the center of the fields. The effect was much smaller in the eye rotation traces ($\pm 0.2^\circ$ in the eye moving away from the center of the fields) because the eyes are located closer to the geometrical center of the magnetic fields. The error in our position gain measurements introduced by artifacts related to head movement in the magnetic fields is at most 2% ($0.15^\circ$ at the time of gain measurements).

To test the coupling of the head of the subject with the bite bar holding the sensors, and thus for our measurements of head motion, we performed a control experiment during which one search coil was attached to the forehead of the subject during head translations. We then compared any yaw-axis rotation recorded by the search coil on the forehead with that recorded by the search coil embedded in the bite bar. Taking into account the artifact related to the motion within the fields, we found that there was a maximum transient head rotation lasting $\leq 10$ ms and peaking at 0.1° for accelerations of 1.5g.

We computed the ideal behavior of the tVOR and evaluated its performance as the ratio of recorded/ideal eye movement. This ratio, which subsequently will be referred to as gain, was evaluated with respect to both position and velocity. We computed a position gain as the ratio of the recorded to the ideal amplitude of the movement of the eye between the beginning of head motion and the specific time of interest. A first position gain was computed at the time of peak head velocity (PHV) and a second value at the end of the head movement (END). Trials containing a saccade (identified by visual inspection of eye velocity traces) occurring before peak head velocity were excluded from the analysis for the PHV gain measures. However, all trials containing saccades that finished before the end of the head movement were considered in the computation of the gain relative to the end of the movement of the head (END). The first position gain value at peak head velocity was used to quantify the performance of the slow-phase response; the second position gain value at the end of the head movement provided insight into the functional performance of the entire tVOR response.

A velocity gain was also computed as the ratio of the maximum recorded eye velocity to the maximum ideal eye velocity. Trials
containing a saccade occurring before peak eye velocity were excluded from the analysis for the velocity gain measures.

For the analysis here we only used trials in which the maximum value of linear acceleration, before peak velocity was reached, exceeded 0.4 g. We examined individual eye traces and gain values for each subject in both binocular and monocular viewing experiments. Intrasubject responses were assessed based on the performance of each eye with respect to its corresponding ideal performance. Intersubject comparisons in binocular viewing experiments were performed based on the cyclopean eye (computed as the average of the right and left eyes), whereas in monocular viewing trials only the viewing eye was considered. Mean traces were always computed using the average of the 2 eyes (cyclopean trace). All figures are reported in terms of means (± SD) or in terms of the population’s median value and the extremes of a 90% confidence interval (i.e., the 5th and 95th percentile of the population).

Statistical significance of the results was assessed using the Wilcoxon rank sum test and the analysis of variances (ANOVA) test. Unless otherwise indicated, results were considered to be significant at $P < 0.05$.

ONSET OF HEAD MOVEMENT. Because the stimuli were imposed manually, the onset of head motion had to be inferred from the head movement recordings. Because different amounts of noise can influence the traces at different times, and because the modes of onset of the manually imposed stimuli were not identical, the onset of head movement could not be detected satisfactorily with a 3SD technique (Bush and Miles 1996). With a greater amount of noise the SD increases; this moves the threshold for detecting the onset of movement to higher values. If these measures are used for aligning the eye movement data for further averaging, the (different) ordinate values at which the eye traces exceed the threshold are aligned to the same relative time, thus altering the average. Therefore we detected the onset of head movement using a fitting technique, which weighs a larger amount of data by considering also the evolution of the stimulus after the onset of head motion. The onset of the head movement was thus estimated by using a piecewise fitting function as described in the APPENDIX. Overall, we only used trials for computing mean traces in which there was a total amplitude of head translation between 1.8 and 3.0 cm, a peak value of head acceleration between 0.4 and 1.4 g and any saccadic correction had to occur after the time of peak head velocity.

Eye movements were recorded using the magnetic search coils technique; head movements were quantified using both a miniBird device and an accelerometer. To control for the different dynamic responses related to the different physical principles on which these transducers are based, and for the different processing of their signals, we performed an experiment analogous to the mechanical armature experiment described by Crane et al. (2003). Thus the sensor-bearing hite bar (see Recording of eye and head movements) was attached to one extremity of a 40-cm-long pivoting arm so that it was situated in the center of the coil frame. A rotation of $\alpha$ rad of the search coil would thus correspond to a translation of $40 \times \sin(\alpha)$ cm. We simultaneously recorded the output of our sensors after an abrupt movement of the free tip of the arm and compared it to determine intrinsic delays. We found that the delay between the accelerometer and both the coil and the miniBird signal ranged between 2 and 5 ms.

LATENCIES. Any analysis of tVOR latency must consider the methodological uncertainties of determining the onset of eye and head movement. The limitations of the 3SD technique become especially evident when trying to compare latencies of responses to different stimuli, as is the case for the different viewing distances in our experiments. If there is no difference in the amount of noise that is superimposed on the response, then the threshold value identified by this technique will remain unchanged for the different experimental conditions. The lesser geometrical requirements of further viewing distance, however, causes that threshold value to be reached later.

Accordingly, we determined latencies using mean traces computed by aligning the recorded trials based on the onset of head translation (see above) and then averaging the ocular responses. Also, for two reasons, the onset of the eye movement could not be determined on a trace-by-trace basis using the same function-fitting technique we had used on mean traces to detect the onset of head motion. The use of the same fitting function would assume linearity of the entire tVOR from the otoliths to the ocular motor plant, and, based on visual inspection, the first part of the eye movement response did not clearly conform to a quadratic function.

The traces used for this analysis are thus the result of a double-averaging process: first the averaging of the right and left eyes for the computation of the cyclopean trace, then the averaging across trials. This process reduces the influence of noise (ambient and biological) on the eye movement recordings by substantially improving the signal-to-noise ratio. Latencies were thus calculated by detecting the onset of eye movement using a 3SD approach on the average eye movement traces computed on each subject and aligned based on stimulus onset as described above. When this averaging technique was applied to sets of simulated trials—produced through a mathematical model in which band-limited white noise was added to the output of a third-order system—it consistently provided a closer approximation to the correct onsets than the 3SD technique applied on individual traces.

ONSET OF RESPONSE MODULATION BY VIEWING DISTANCE. To determine the onset of viewing distance modulation we compared the mean eye position trace for the 15- and the 30-cm viewing distance conditions. The intrinsic variability of the manually imposed stimuli was a concern in the computation of the mean traces because the time course and amplitudes may have been different. Taking into account stimulus variability by normalizing the responses with respect to the ideal eye movement, however, would implicitly normalize the data with respect to viewing distance, thereby possibly biasing our measurements. An alternative would be normalization with respect to head translation, but such scaling also assumes linearity. Our aim was to try to minimize the data processing before the comparison of the response, yet obtain reliable results by making an appropriate comparison.

Our analysis of latency differences was limited to the first 80 ms after the onset of the head movement. Over such a time span, we computed the mean $[m(t)]$ and the SD $[sd(t)]$ traces of the head translation by pooling the 15- and the 30-cm viewing conditions. Then, for each viewing distance, we selected the most representative head movement trajectories as those trials that fell within 1SD from the mean for all but a maximum of 5 samples. In other words, we selected the trials for which the head translation $[h(t)]$ satisfied the relationship $m(t) - sd(t) \leq m(t) + sd(t)$ for every $t$ except for at most 5, between the onset of the head movement and 80 ms later. For each viewing distance, only the eye movements recorded in response to the selected stimuli trials were considered for computing means and SDs.

For each subject, the two resulting mean traces were then compared and the time when the 15-cm viewing mean trace crossed the line determined by the sum of the 30-cm mean and its SD was considered to be the onset of viewing distance modulation of the reflex. The reduction in noise level by the averaging process yields traces that allow meaningful comparisons even for the very small movement of the eyes occurring early in the response. The onsets as identified at the crossing of the SD line, however, are almost certainly an overestimation of the true value (see Fig. 6).

RESULTS

We now present the results in three sections based on viewing conditions and target distance: both eyes viewing with the target at 15 cm, both eyes viewing with the target at 30 cm, and monocular viewing with the target at 15 cm.
Both eyes viewing at 15-cm distance

GENERAL DESCRIPTION. The ocular response to the translation of the head began with a slow eye movement that started \(19 \pm 5\) ms (mean \(\pm\) SE, all subjects) after the head began moving, with the range among subjects being 15 to 29 ms. A faster, position-correcting saccade (which we hereafter call a saccade), in the same direction as the slow phase, began, on average (considering all subjects, all trials containing a corrective saccade), about 145 ms after the onset of the movement of the head and usually took the eyes back toward the target (Fig. 2, A and C) because the initial slow phase was undercompensatory. The timing of this first saccade showed great intersubject variability with means (\(\pm\) SD) ranging from 108 to 29 ms. The amplitude of the saccade was also variable (range 2.3 to 3.8) and averaged 3.2 \(\pm 1^\circ\) (overall group mean \(\pm\) SD). A final saccade was sometimes made near or just after the end of the head movement to correct for any residual position errors.

Position gains (amplitude of the response/amplitude of the ideal response) were computed at two different times in the response: at the time of peak head velocity (PHV), and at the end of the head movement (END). For the PHV calculations, trials in which a saccade was triggered before the time of peak head velocity were discarded from the position gain computations; the number of trials accepted for analysis ranged between 85 and 100% in 5 of 6 subjects. One subject (S5) tended to produce earlier saccades, so that only 45% of the trials from this subject were used for the PHV. Velocity tVOR gain was measured as the ratio of the peak recorded slow-phase eye velocity over the peak ideal eye velocity.

Figure 2 also shows that the eye movement response—both the slow phases and the saccades—were disconjugate, as expected from the geometrical requirements (as reflected in the ideal traces) to compensate for the pattern of head motion. Examining quantitatively the difference in the performance of the two eyes, individual eye asymmetries in PHV gains were statistically significant in only 2 subjects (i.e., one or the other eye performing better for one head movement direction). Only one subject (S6) showed a statistically significant eye preference (i.e., the same eye performing better in both directions of head movement).

The first 100 ms of the responses for each subject are shown in light gray in Fig. 3, in which each trace reflects the average of the two eyes (cyclopean trace) and was aligned with the onset of the head movement (vertical black bar). For each subject the thicker black line represents the average of the individual recorded responses. The thick dashed line represents the average of the corresponding individual ideal responses.

The time at which peak head velocity occurred was in the first 100 ms of the response in over 90% of all trials. The time of peak eye velocity occurred on average (all subjects, all trials), 13 (\(\pm 9\)) ms after the time of peak head velocity. For subjects 2, 4, and 6 (right panel) the eye movement response was smooth; for subjects 1, 3, and 5 (left panel), in some trials there were discrete accelerations in the position traces after the time of peak head velocity. They represent small saccades.

Table 1A summarizes the medians (5th and 95th percentiles) of position gains computed at the time of peak head velocity and of velocity gains (peak eye velocity/peak ideal eye velocity) for head movements in both directions. Viewing was binocular and the target at 15-cm distance. In spite of some variability, the slow-phase component of the tVOR was consistently undercompensatory, with an overall mean position gain at PHV of about 0.40, and median (90% confidence interval) of 0.38 (0.25 to 0.62) when pooling all the data (both directions) from each subject. Velocity gains were significantly greater than position gains, averaging 0.53 with a median (90% confidence interval) of 0.52 (0.35 to 0.73), when considering all trials, all subjects. Finally, we asked whether there were significant abduction-adduction asymmetries in either the

![Figure 2. Examples of tVOR response during 15-cm viewing (A and C) and during 30-cm viewing (B and D) from subject S5. Each panel shows right and left eye data and corresponding ideal traces. A and B: eye displacement. C and D: eye velocity. Note different y-axis scales for 15- and 30-cm viewing. Note that both slow phases and saccades are both undercompensatory and appropriately disconjugate. [A modified from Ramat and Zee (2002) with permission.]](https://www.jn.org/)

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FIG. 3. Average eye movement traces for each subject at 15-cm viewing, BEV (both eyes viewing). Light gray: individual eye movement traces; thick black: average eye movement trace; thick dashed: average ideal trace. Vertical line at 20 ms shows head movement onset. Thicker vertical line shows eye movement onset computed on average traces. Abrupt inflections in eye movement traces occurring after peak head velocity are small saccades.
PHV position gains or the velocity gains. With the exception of one subject in one direction, there were none.

In the computation of the position gains at the end of the head movement (END), the responses including a saccade that finished before the time of completion of the head movement were included. About 9% of trials were discarded from this analysis because a saccade was ongoing at the time of the gain measurement. The average gain computed by pooling all subjects and head movement directions was, as expected, higher than the earlier gain indicators, with a mean value of 0.65 and a median (90% confidence interval) of 0.68 (0.33 to 0.89). The gain computed at the end of the head movement was significantly greater than the gain at the time of peak head velocity in all subjects. In 5 of 6 subjects these gains were above 0.5, but even so, still undercompensatory (Fig. 4).

The two position gains for 15-cm viewing trials are shown in Fig. 4, where, for each subject, the left bar is the PHV gain and the right bar represents the END gain values.

We also investigated how eye velocity scaled with head velocity using a linear regression of peak eye velocity on peak head velocity. We found significant correlations ($r^2$ ranging from 0.35 to 0.76) in 9/12 conditions (6 subjects, 2 directions). On the other hand, the gain of the response and peak head acceleration showed significant correlations ($r^2 > 0.2$) in only 3/12 conditions, and in 2 cases the gain increased slightly with head acceleration and in the other it decreased. Taken together these results suggest that eye velocity largely scaled linearly with head velocity, without showing saturation, and the gain did not depend on head acceleration. A representative example of the relationship between peak eye velocity and peak head velocity is shown for one subject in Fig. 5.

The relationship between the time of peak head velocity and the time of peak eye velocity was also investigated. The correlation coefficients averaged 0.72 and ranged between 0.51 and 0.87. The average delay of time of peak eye velocity with respect to peak head velocity was 0.13 (0.09, 0.16) seconds.

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### TABLE 1. Subject-by-subject gains during 15- and 30-cm viewing (recorded/ideal) median and 90% confidence interval for head movements to the left and to the right

<table>
<thead>
<tr>
<th>Subject</th>
<th>Pos Gain to Left</th>
<th>Pos Gain to Right</th>
<th>Vel Gain to Left</th>
<th>Vel Gain to Right</th>
</tr>
</thead>
<tbody>
<tr>
<td>S1</td>
<td>0.39 (0.32, 0.56)</td>
<td>0.39 (0.23, 0.46)</td>
<td>0.45 (0.53, 0.80)</td>
<td>0.40 (0.30, 0.82)</td>
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<tr>
<td>S2</td>
<td>0.49 (0.22, 0.66)</td>
<td>0.48 (0.34, 0.85)</td>
<td>0.55 (0.52, 0.71)</td>
<td>0.69 (0.58, 0.95)</td>
</tr>
<tr>
<td>S3</td>
<td>0.32 (0.23, 0.37)</td>
<td>0.34 (0.28, 0.45)</td>
<td>0.55 (0.48, 0.83)</td>
<td>0.58 (0.34, 0.79)</td>
</tr>
<tr>
<td>S4</td>
<td>0.38 (0.29, 0.53)</td>
<td>0.47 (0.31, 0.58)</td>
<td>0.57 (0.43, 0.89)</td>
<td>0.64 (0.41, 0.95)</td>
</tr>
<tr>
<td>S5</td>
<td>0.36 (0.24, 0.80)</td>
<td>0.37 (0.30, 0.61)</td>
<td>0.59 (0.35, 1.01)</td>
<td>0.42 (0.49, 1.44)</td>
</tr>
<tr>
<td>S6</td>
<td>0.34 (0.21, 0.39)</td>
<td>0.31 (0.24, 0.42)</td>
<td>0.37 (0.39, 0.49)</td>
<td>0.37 (0.33, 0.40)</td>
</tr>
</tbody>
</table>

**A:** 15-cm viewing. Median (5th; 95th percentiles) for the cyclopean eye at time of PHV for each subject in each direction. Columns, left to right, are: subject, position gain in head movement to left, position gain in head movement to right, velocity gain in head movement to left, velocity gain in head movement to right.

**B:** 30-cm viewing. Median (5th; 95th percentiles) for the cyclopean eye at 30 cm for each subject in each direction. Columns are the same as in A.

![Fig. 4. Position gains at 15-cm viewing in each subject. PHV: gain when peak head velocity is reached; END: gain at end of head movement (actual/ideal; medians and error bar extending between 25th and 75th percentiles).](image)
respect to time of peak head velocity was 13 ms and ranged between 9 and 20 ms.

Both eyes viewing at 30-cm distance

The pattern of response while viewing a target 30 cm in front of the eyes was qualitatively similar to that for the 15-cm target (Fig. 2, B and D). The onset of the eye movement occurred with an average latency (±SE) of 20 (±12) ms, which was not significantly different ($P = 0.47$) than for the 15-cm viewing distance (18 ± 5 ms). The saccadic correction occurred with an average latency (considering all subjects, all trials containing a corrective saccade) of 165 ± 60 ms, which was significantly higher ($P < 0.01$) than the saccadic latency in the near viewing experiments (145 ms). Saccadic amplitudes were significantly lower for 30-cm than for 15-cm viewing ($P < 0.01$), averaging $1.8 ± 0.7°$.

Figure 6 compares the velocity and the END position gains measured for the 15- and 30-cm targets.

The average PHV position gain was 0.38 with a median value of 0.37 (0.15 to 0.62). These gain values, though, were not significantly different from those recorded at corresponding times in the responses while viewing the 15-cm target. The mean position gain at END for all subjects was 0.74 [median 0.77 (0.39 to 1.07)] which was significantly higher than during 15-cm viewing. Even so, on a subject-by-subject basis the increase in gain was significant only for subject S5.

Velocity gains at 30-cm viewing averaged 0.63, with median (90% confidence interval) of 0.62 (0.42 to 0.89), which was significantly higher than that at 15-cm viewing. Even so, on a subject-by-subject basis velocity gains were significantly higher in 30- than in 15-cm viewing in only 2 subjects (S1 and S5).

Eye velocity also scaled with head velocity during 30-cm viewing. Linear regression of peak eye velocity on peak head velocity showed significant correlations ($r^2 > 0.2$) in 8/12 conditions, whereas the correlation between velocity gains and peak head acceleration was significant in only 2/12 conditions.

Figure 5. Linear regression of peak eye velocity (in deg/s) vs. peak head velocity (in cm/s) during leftward and rightward head movements in one subject (S2).
longer latencies for both monocular viewing conditions. Overall, saccadic latencies during monocular viewing ranged from $106 \pm 37$ (S5) to $181 \pm 45$ ms (S2).

Figure 8 shows the comparison of the right eye position gain for right-eye viewing (top) and of the left-eye gain for left-eye viewing (bottom). The median (90% confidence interval) PHV gain for REV and for LEV for all subjects, and with pooling data from different head directions, was 0.28 (0.15 to 0.59) and 0.27 (0.13 to 0.54), respectively. These values were significantly lower than the gains found for the corresponding eye in binocular viewing conditions ($P < 0.01$). Half of the subjects showed significantly greater gains for adduction (temporal to nasal) of the viewing eye in one or both monocular viewing conditions at PHV, whereas the remaining subjects showed no significant asymmetry.

All subjects showed statistically significant changes in the vergence angle [measured at the onset of the head movement, in meter angles (MA)] between binocular and monocular viewing conditions. The 2 subjects (S2 and S3) who showed the least reduction in gain during monocular viewing at time of peak head velocity (4 and 9%, respectively) also showed the smallest change in vergence angle between BEV and REV or LEV (6 and 20%). Also, the 2 subjects (S1 and S6) whose decrease in gain was the greatest (44% and 35%) were those who showed the largest change in vergence angle (subject S1 showed exophoria in both monocular viewing conditions; subject S6 showed a decrease in vergence angle of 52%). One subject (S4), however, showed an increase (11%) in vergence angle during monocular viewing, although his gain decreased by about 21%.

Figure 9 summarizes the relationship between vergence angle—expressed in meter angles (MA = 1/viewing distance)—and tVOR sensitivity (eye rotation in degrees/head translation in cm) for all subjects in all viewing conditions.

DISCUSSION

The last decade has seen a resurgence in interest in otolith-ocular reflexes and there have been a number of studies of the vestibulo-ocular response to interaural translations of the head both in monkeys (Angelaki and McHenry 1999; Angelaki et al. 2000; Schwarz and Miles 1991; Telford et al. 1997) and in human beings (Aw et al. 2003; Bronstein and Gresty 1988; Busettini et al. 1994; Crane et al. 2003; Gianna et al. 1997; Lempert et al. 1998, 1999; Tian et al. 2002a,b). The stimulus conditions, methods of recording eye movements, and analy-
ical techniques, however, varied considerably from study to study. Our stimulus was a brief, abrupt acceleration of the head (peak acceleration $0.4 - 1.4 \text{g}$), of relatively high-frequency content, which resulted in a “position step.” The subjects were asked to fix on an LED 15 or 30 cm in front of their eyes in a dimly lit environment. We chose this new stimulus profile to place a challenging demand on the translational VOR, analogously to the brief, high-acceleration head thrust stimulus that makes demands on the angular VOR (Halmagyi and Curthoys 1988). Here we focused on both the analysis of the first part of the eye movement response, which is commonly considered “open-loop,” and the performance of the reflex as a whole, including saccades, based on the position of the eyes when the head stops moving.

**Gain of the tVOR**

Our results are in accord with the findings of others in humans that the gain of the initial portion of the tVOR is low, with a functional performance around 35–40% of the ideal for viewing targets at both 15 and 30 cm. These findings appear to be uninfluenced by the presence or absence of a visual target during head motion, at least during the first 100 ms after the onset of the head movement (Tian et al. 2002b). In monkeys, too, the gain of the tVOR is undercompensatory (Angelaki et al. 2000; Schwarz and Miles 1991).

Position gains evaluated at the time of peak head velocity (average time 86 ms) were about 40% of ideal for either binocular or monocular viewing, in agreement with previous results (Gianna et al. 2000) that were obtained at similar times in the response, although with much lower accelerations ($0.08$ and $0.17 \text{g}$). Slightly higher gains [overall average is $0.53 \pm 0.10$ (±SE)]—but still strikingly undercompensatory—are obtained when measuring the gain as the ratio of peak eye velocity/peak ideal eye velocity (time of peak eye velocity lags time of peak head velocity by about 15 ms).

Similar considerations apply to the gains measured at the end of the head movement (~200 ms after the onset of head motion); even taking into account the corrective saccades, the overall gain still remains undercompensatory.

The gain of the slow-phase component of the tVOR was nearly constant over the range of accelerations (up to a maximum value of $1.4 \text{g}$) tested here. Also, in most subjects there was a good correlation between peak eye velocity and peak head velocity, arguing for a substantially linear relationship between these two variables ($r^2$ range $0.35–0.76$). This finding clarifies some of the uncertainties about the relationship between gain and acceleration raised by Gianna et al. (2000).

**Response modulation with viewing distance**

The sensitivity of the tVOR modulated appropriately with distance and the same relative amount of compensation was achieved in both the 15- and 30-cm viewing distances. In the gain computed at the end of the head movement all subjects but S5 compensated for about the same proportion of the ideal at both viewing distances ($50–80\%$), leading to a larger position error at the end of the head movement for the 15-cm viewing trials. Velocity gains showed a small increase in some subjects for viewing the more distant target (30 cm).

The finding of only small differences in the gain values between the 2 viewing distances indicates that viewing the closer target little changes the relative amount of compensation achieved by the tVOR, at least for the 2 viewing distances tested here. On the other hand, if the overall gain...
is the same, the amount of retinal image motion increases as the target gets closer, implying that functionally, the performance of the tVOR degrades with the proximity of the target. Similarly, the amount of retinal position error at the end of the head movement gets larger for nearer targets, given that the END gains are the same. The results obtained at the viewing distances used in our experiments suggest that the gain of the tVOR is tuned to compensate for a fixed proportion of the head movement (using both slow phases and saccades) and that the reflex modulates appropriately with the different viewing distances to achieve the same amount of relative compensation.

These results differ from those of others (Busettini et al. 1994) who found increasing tVOR gains with increasing viewing distance. Such a difference could be related to the closer targets that we used in our studies. In fact the data published by Busettini et al. (1994) show rapidly increasing tVOR gains primarily associated with the more distant targets used in their study. Taken together the data suggest that tVOR gain is nearly constant for targets that are quite close to the subject. A similar result was shown for monkeys (Schwarz and Miles 1991).

Possible explanations for the low tVOR gain

Why the tVOR has such a low gain, and persistently so, even with changes in viewing distance, is enigmatic. One possible explanation is that head movements made under normal circumstances are usually a combination of rotations and translations with the rotational component dominating. A purely linear, lateral motion of the head (and specifically of the orbits) would be an unusual stimulus to occur naturally, either passively or actively. During standing, walking, and running, head rotations are phase locked to head translations both in the horizontal and vertical planes (Crane and Demer 1997; Demer and Crane 1998, 2001; Demer and Viirre 1996; Imai et al. 2001; Moore et al. 2001; Raphan et al. 2001). Thus, head translation to the left, evoking a rightward eye rotation, is accompanied by head rotation to the right, evoking a leftward eye rotation. With the head rotation to the right there is also a translation of the orbits to the right, as a consequence of their eccentricity with respect to the axis of rotation of the head, which also calls for a leftward eye rotation. Thus stabilization of gaze during motion of the head in most natural circumstances is associated with several and sometimes oppositely directed commands for eye rotation. Thus, the pure, high-
acceleration tVOR, as we have elicited it, may be a circumstance to which the brain has neither a need nor had an opportunity to optimize its performance. Indeed it has been shown that with prolonged exposure to a visual–vestibular conflict, both the human (Hegemann et al. 2000; Shelhamer et al. 2000, 2002), and the monkey (Angelaki et al. 2002; Zhou et al. 2002a,b) tVOR can undergo adaptive adjustment of its gain.

Another possible explanation for the low tVOR gain relates to the geometrical requirements for compensation of a combined rotational–translational motion of the head; these are inherently nonlinear because of the translation of the orbits accompanying each head rotation.1 For the head rotation itself to be useful in stabilizing gaze, the aVOR needs to be suppressed by varying amounts, based on viewing distance (Demer and Viirre 1996). In fact, such subunity aVOR gains are found in all subjects during walking and running on a treadmill while viewing targets at 50 or 500 cm (Demer and Crane 1998). Nevertheless, it has been shown that during walking both the horizontal and vertical aVOR and tVOR interact to achieve gaze stabilization of both near and far targets (Crane and Demer 1997; Demer and Crane 2001; Moore et al. 2001). In the case of the compensation for vertical head motion the slow phase even changes direction, as it should, depending on whether viewing is near or far (Moore et al. 1999; Viirre and Demer 1996). Thus, if the gain of the aVOR is less than ideal [near viewing compensation actually requires the gain of the aVOR to be greater than unity (Viirre et al. 1986)], then the uncompensated portion of the head rotation goes toward reducing the response requirement for the tVOR.

For near-target viewing the required tVOR response decreases with increasing head rotation and with decreasing aVOR gain. Moore et al. (2001) have shown that during walking the amount of yaw head rotation increases with decreasing viewing distance; at 25-cm viewing this was about 2 deg. In this context, the tVOR could be tuned to compensate only partially for head translation to achieve gaze stabilization, the residual error depending on the amount of rotation, the gain of the aVOR, target distance, and eccentricity. Depending on individual motor behavior during natural activities, the tVOR could be tuned to work around a reference percentage of its ideal gain, the value that is observed when the two components of natural head movements are isolated and a response to pure head translation is evoked.

Another, but not mutually exclusive, explanation for the low tVOR gain is that during natural behavior, at least at the higher frequencies of head motion invoked in our experiments, there is a nonlinear combination within the vestibular nuclei of rotational and translational signals, leading to a better overall response than expected from linear summation of the two responses. Some studies of canal and otolith interactions have argued for a linear summation of the responses (Crane and Demer 1999; Paige et al. 1998; Sargent and Paige 1991); others suggest that vestibulo-ocular reflexes are driven by an adaptively controlled nonlinear combination of otolith and semicircular canal vestibular information (Anastasopoulos et al. 1996; Angelaki et al. 2002; Barmack and Pettorossi 1988; Fuhry et al. 2002). It has been suggested that the individual contributions of the peripheral organs can be enhanced or suppressed depending on the presence or absence of other sensory signals. The gain of the tVOR could be increased by the presence of a simultaneous head rotation, and/or the gain of the aVOR could be reduced by the presence of a simultaneous translation.

Furthermore, this complex interaction between the different

![Sensitivity versus MA](http://jn.physiology.org/)

**FIG. 9.** Relationship between tVOR sensitivity (deg/cm) and vergence angle [meter angle (MA)] for all subjects in all viewing conditions. Dashed line represents ideal relationship between sensitivity and vergence angle. Continuous lines connect data points relative to BEV for each subject. Monocular viewing conditions for subject S1 are not shown because viewing distance could not be determined as result of subject’s exophoria. Closed symbols: BEV sensitivity (15 and 30 cm). Open symbols: monocular viewing (REV and LEV) sensitivity. Vertical lines extending above the axis of the abscissa at 3.3 and 6.7 MA indicate ideal vergence angle for 30- and 15-cm viewing, respectively.

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1 Considering the average distance between the orbits and the center of rotation of the head to be R—usually about 10 cm (Viirre et al. 1986)—a CCW head rotation by α deg implies a leftward translation of both orbits by R*sin(α) cm, a translation in depth of the right eye by R*[1 − cos(α)] cm toward the target and an identical translation of the left eye away from the target.

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types of head motion and the crucial role that viewing distance plays in determining what the tVOR gain should be, may make it impossible for the brain to have a correct calibration for every conceivable combination of stimuli that it might face. The vestibular system would then opt for some intermediate working point around which it could modulate the gain depending on any feedback information that becomes available.

The latter argument could also explain the high tVOR gains (~1) reported with distant viewing (Busettini et al. 1994; Gianna et al. 1997). Given that in those conditions compensation for head translation requires a small eye movement, if the brain presets the sensitivity of the tVOR to an estimate average value, then the gain would be too high.

Saccades and tVOR

Both the occurrence and the amplitude of saccades were modulated with viewing distance, confirming that saccades play a fundamental functional role in the overall response. Consistently, we found that the average size of the first saccadic correction with 30-cm target viewing was significantly smaller than that with 15-cm target viewing. The mean amplitude of saccades was reduced by about 44% that roughly corresponds, in an average subject, to the percentage reduction in eye movement requirement for the same amount of head movement when going from a target at 15 cm in front of a subject’s eyes to one at 30 cm (about 48%). Thus as for the slow-phase response, the contribution of saccades to the overall tVOR gain remains at a fixed percentage of the ideal response. This finding suggests a close relationship between the central programming of saccades and the slow-phase response of the tVOR, and may be analogous to the natural symbiosis between the tVOR and the other voluntary eye movement types, vergence and pursuit (Busettini et al. 1994). The functional importance of the saccade is also reflected in the increased amplitude of the saccade when the slow-phase component of the tVOR evoked by a translation toward the side of a labyrinthine lesion is impaired (Ramat et al. 2001).

Finally, we noticed that the latency for saccades was larger (and the amplitude lower) for viewing the 30-cm (165 ms) than for the 15-cm target (145 ms). One interpretation of this finding is that there is a threshold for generating a corrective saccade, perhaps based on an internally created estimate of where the eyes are in the orbit relative to the desired location for fixation of the target of interest (Berthoz et al. 1987). The signals that drive these corrective saccades are most likely generated by internal signals based on vergence angle/target distance, and head motion—rather than by on-line visual error signals—because they occur so early during the response (Tian et al. 2002b).

Latencies in the tVOR

We applied a 3SD approach on mean eye position traces for 15-cm viewing and found that overall tVOR latencies were significantly lower (range 15 to 29 ms) than those reported by other groups. The average eye movement latency at 15-cm viewing was only 18.8 ± 5.3 ms (mean ± SE).

The 3SD approach is commonly used for determining latencies in response to transient stimuli both during the aVOR (Angelaki and McHenry 1999) and during the tVOR (Crane et al. 2003; Tian et al. 2002a). Thus, for comparison, we also evaluated latencies by applying such criteria to both head velocity and eye velocity. We found tVOR latencies averaging (±SE) 36 ± 15 ms, with means ranging 29 ± 12 to 42 ± 13 ms. These results were similar, albeit slightly smaller, than previous observations in the response to pure head translations [42 ms at 15-cm viewing by Tian et al. (2002a), 30 ms at 25-cm viewing by Crane et al. (2003), about 36 ms at 20- and 30-cm viewing by Aw et al. (2003), about 50 ms at 30-cm viewing measured by Gianna et al. (2000), and 34 ms at 110-cm viewing by Bronstein and Gresty (1988)].

A similar technique was used to compare latencies of the eye movement responses at the two viewing distances. The only difference was that for this comparison we needed to take into account the different requirements imposed by the geometry of the two different viewing distances. Each response was thus scaled by the peak ideal eye displacement reached within the first 80 ms from the onset of head motion. Even though this approach assumes the system to scale linearly with viewing distance, it provides a reasonable means for comparing the latencies to different viewing distances. When a 3SD algorithm was then applied to the traces thus normalized, 4 subjects showed negligible (±3 ms) differences in the latencies for the two viewing distances and the means were also very close (18.8 ms at 15 cm vs. 20.3 ms at 30 cm).

Finally, we determined the onset of viewing distance modulation (i.e., the time between the onset of the head movement and when the responses at the 2 viewing distances first differ) by using a mean trace approach, taking into account only the responses evoked by similar head movements. We found that the tVOR response is modulated for viewing distance at least as early as 10 to 24 ms after the onset of the slow-phase response to the head movement (Fig. 6). Our data are compatible with the findings of others that the tVOR slow phases are modulated by viewing distance from close to the onset of the response (Gianna et al. 1997); this is a similar finding to that reported for the aVOR during head thrusts in humans (Lasker et al. 2002).

Taken together these findings suggest that the tVOR may not really be that much slower a reflex than the aVOR. Likewise, the tVOR latency reported here (~19 ms) is closer to that reported for monkeys (~12 ms) (Angelaki 2002; Angelaki and McHenry 1999). The significantly longer latencies recorded in some previous studies may reflect the techniques used to estimate the reflex latency, and the relatively low gain of the reflex; so that the response onset cannot be accurately discerned from the underlying noise using the classic latency detection algorithms. Thus, using our stimulus, we suggest that the tVOR is a short-latency reflex, its latency is independent of viewing distance, and the reflex response is modulated for viewing distance close to the onset of the response.

Monocular versus binocular viewing: abduction adduction asymmetries

During binocular viewing at 15-cm target distance, we found no significant asymmetries between the gains (position and velocity) of the adducting and abducting eyes, with the exception of one subject in one direction. During monocular viewing, the only consistent finding was that some subjects showed a greater response for adducting movements of the viewing
eye, but no subjects showed a greater response for abducting movements of the viewing eye. The comparison of monocular versus binocular viewing conditions showed a reduction of the gain of the tVOR in the monocular viewing responses, but such change was usually accompanied by a reduction in the vergence angle.

Gain modulation and vergence angle

In 4 of 6 subjects we found a good correlation between gain and vergence angle during monocular trials, showing that whenever the vergence angle was not appropriate for the actual target distance (vergence angle was usually lower than required in the monocular viewing trials) the gain of the reflex decreased accordingly. This may be better appreciated in terms of the relationship between the sensitivity of the responses and vergence angle [Fig. 9, correlation coefficients ranging from 0.80 (S5) to 0.99 (S6)]. Although in general these results show sensitivity depending on vergence angle, the results in subject S4 (sensitivity reduction but increase in vergence angle) during monocular viewing indicate that vergence cannot be the sole signal used for gain (or sensitivity) modulation with viewing distance. This interpretation is in accord with the findings of others in response to sinusoidal oscillations (Busettini et al. 1994; Crane and Demer 1997; Shelhamer et al. 1995). The accommodative system, and other cues to distance, also contribute to the perception of distance, although previous studies showed that the role played by accommodation may not be as important in humans as in monkeys (Hine and Thorn 1987; Paige 1991). One explanation is that the gain of the tVOR is preset (Gianna et al. 1997) to a value, taking into account all the information available on target position and eye position, the most relevant of which might be vergence angle. There is some evidence that the vergence modulation is determined by cerebellar circuits (Wiest et al. 2001). In this interpretation even the short latency we found would not preclude the involvement of the cerebellum, given that its role would be carried out before the onset of the movement. Based on the initial vergence angle, cerebellar circuits could preset the gain of the tVOR to some predetermined and presumably optimal value, without prior knowledge of which kind of perturbation (linear, angular, or combined) would need compensation.

To summarize, our results argue for the tVOR being a fast reflex, having a latency on the order of 20 ms, a relatively lower value than previously suggested for humans and closer to values reported for monkeys. As others, we found that the tVOR is heavily undercompensatory when viewing relatively near targets, thus extending this finding to the higher accelerations of our stimulus. Slow-phase peak eye velocity scales linearly with peak head velocity and gain is independent of head acceleration and viewing distance, at least for the stimuli used here. Saccades are also an integral part of the tVOR response and scale with viewing distance in a similar way as does the slow phase.

APPENDIX

Estimate of head movement onset

Each head position trace, between a time preceding the onset of head movement by about 100 ms and the time of peak head velocity, was fit with a piecewise quadratic curve using a nonlinear least squares technique based on the Levenberg–Marquardt minimization algorithm. The fitting curve was composed of a constant value and a quadratic function with an imposed constraint of continuity of the first derivative; this is equivalent to having a switch between the two components at the vertex of the parabola. This point was considered to be the onset of the movement and once it was computed for every trial, all trials were aligned using it.

The selection of a quadratic instead of higher-order models was based on the associated Bayesian information criterion (BIC) (Galiana et al. 1995). The BIC model selection criterion takes into account the quality of the fit and the complexity of the model in terms of the number of its parameters and allows one to weigh the level of performance in terms of its computational cost. Thus if the increase in the order of the model increases the quality of the fit more than would be expected statistically by the larger number of degrees of freedom, the BIC value decreases. We found that increasing the order of the

Fig. A1. Comparison of head onset determined using the 3SD technique and fitting technique. ‘+’ sign: head movement onset as determined using the fitting technique. ‘×’ sign: head movement onset determined using the 3SD technique.
model used for fitting the data did not reduce the corresponding BIC value; thus no improvement was achieved with cubic and quartic models. The quality of the fit itself was instead assessed using the variance accounted for (VAF), a number providing, for nonlinear models, information similar to that obtained with the squared regression coefficient in linear regressions.

The selected model therefore had the following structure

\[
\begin{align*}
    y^2 &= \frac{-b^2 + 4ac}{4a} \quad t < -\frac{b}{2a} \\
    y(t) &= \frac{a}{t^2} + bt + c \quad t \geq -\frac{b}{2a}
\end{align*}
\]

where \(a, b, c\) are the free parameters and \(t = -(b/2a)\) (i.e., the vertex of the parabola) represents the chosen head movement onset.

An example of the results obtained using such a technique in comparison with the 3SD technique is shown in Fig. A1. In the example shown the 3SD technique indicates a head movement onset that exceeds by 8 ms that determined by the fitting technique.

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DISCLOSURES

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