Ocular Responses to Head Rotations During Mirror Viewing

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INTRODUCTION

During viewing of targets located at optical infinity, eye rotations compensate for head rotations if they are equal and opposite in direction. During viewing of a near target, the situation is more complicated because the eyes do not lie at the center of head rotation and are separated by several centimeters (Blakemore and Donaghy 1980; Crane and Demer 1998; Huebner et al. 1992, 1995; Paige et al. 1998; Viire and colleagues 1986). Thus the eyes translate during head rotations, and one eye may be closer than the other to the object of interest. In general, the gain of compensatory eye movements is increased during near viewing and the gain is greater in the eye that is closer to the object of interest.

During close viewing of one’s own image in a mirror, the visual demands during head rotation differ from when viewing a real, near target. This is mainly because translations of the subject’s head in a plane parallel to that of a mirror are matched by translations of the image. In this study, we compared compensatory eye movements as subjects viewed either stationary near stimuli or the bridge of their own nose in a mirror during horizontal head rotation. The geometry of these two viewing conditions is summarized in Fig. 1.

Viire and colleagues (1986) have pointed out how the radius of head rotation ($R$), the distance of the target from the center of head rotation ($R + D$), the interocular distance ($I$), and the target eccentricity ($\gamma$) determined the eye rotation angle (e.g., right eye, $\theta_R$) required to main target fixation during head rotation ($\phi$; see Fig. 1A)

$$\theta_R = \tan^{-1} \frac{(D + R) \sin (\gamma - \phi) - I/2}{(D + R) \cos (\gamma - \phi) - R} \tag{1}$$

If the subject views a near, earth-fixed target in a central position, $\gamma$ is equal to zero, and the gain for this near-viewing condition ($G_{RN}$) can be derived from $d\theta_{RN}/d\phi$, where $\theta_{RN}$ is the rotation angle of the right eye during this condition.

An important difference arises if subjects fixate the image of the bridge of their nose in an earth-fixed mirror during head rotation. This is because the position of the virtual image of the bridge of subject nose ($\gamma$) moves continuously as a function of head rotation angle ($\phi$; Fig. 1B)

$$\gamma = \tan^{-1} \frac{R \sin \phi}{D + 2R - R \cos \phi} \tag{2}$$

As the subject’s nose rotates to the right or left of a central position, the translation of the image of the bridge of subject’s nose in the plane of the mirror is also a function of head rotation angle ($\phi$). During mirror viewing, the total distance from the center of head rotation to the virtual image of the bridge of the nose, $d$, has the same physical meaning as $(D + R)$, which is the distance of the target from the center of head rotation in the near viewing condition. The value of $d$ during mirror viewing can be calculated from

$$d = (D \sin \phi)^2 + (D + 2R - R \cos \phi)^2 \tag{3}$$

Thus in the case of mirror viewing, the eye rotation angle (for right eye, $\theta_{RM}$) can be expressed as a function of head rotation angle ($\phi$) by putting variable $d$ (Eq. 3) and variable $\gamma$ (Eq. 2) into Eq. 1.

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The mirror-viewing gain $G_{RM}$ can then be derived from $d\theta_{RM}/d\phi$. The relationships between gain and the head rotation angle ($\phi$) under the two conditions are plotted in Fig. 1C; note that the gain while viewing a stationary near target is greater than while viewing the bridge of the nose through a mirror. By using Eqs. 1 and 4 to calculate the rotations of each eye, it is possible to plot the relationship between gain and vergence angle under each of the two conditions (Fig. 1D); note that gain remains greater during viewing a stationary near target than during viewing the bridge of the nose through a mirror, even as vergence angle varies. Also note that for each viewing condition, two different gain...
Several lines of evidence indicate that changes in the gain of eye movements to compensate for head rotations cannot be simply attributed to visually mediated responses such as smooth pursuit. Thus the gain of compensatory eye movements is modulated during transient or high-frequency head rotations and in darkness, during which smooth pursuit would not be expected to contribute (Viire et al. 1986). Indeed, Crane and Demer (1998) have presented evidence that during high-acceleration head rotations applied shortly after switching to darkness, the gain of the vestibuloocular reflex (VOR) is determined by target distance within ~10 ms of the onset of the response. Thus the proximity of the visual target and vergence angle (Paige et al. 1998), or the neural command that controls it (Snyder et al. 1992), appear to parametrically adjust VOR gain so that eye rotations will compensate for head rotations. The geometric considerations summarized in the preceding text suggest that VOR gain would be smaller during viewing the image of one’s nose in a near mirror than during fixation of a real, near target that required a similar amount of convergence. We experimentally confirmed this prediction and investigated the contribution that vision and visually mediated eye movements make to the response. Preliminary results will appear as an abstract (Han et al. 2001).

METHODS

Subjects

We studied a total of six healthy human subjects (4 male, 2 female, ages 22–53 yr); four were naive as to the purpose of the study. No subjects had any ocular motor abnormalities or were taking drugs with effects on the nervous system. Three subjects were myopes and were tested without their spectacle correction. All subjects gave informed consent in accordance with our Institutional Review Board and the tenets of the Declaration of Helsinki.

Stimuli and recording

The subjects sat in a 30-ft-lb vestibular chair (Templin Engineering, Laytonville, CA) and firmly braced their heads against the headrest of the chair. The headrest was positioned so that the axis of chair rotation corresponded approximately to the natural center of rotation of the subject’s head, and this remained unchanged throughout experimental sessions. Horizontal and vertical rotations of each eye and the head were measured using the magnetic search coil technique, with 6-foot field coils (CNC Engineering, Seattle, WA). The coil was precalibrated on a protractor device. The system was 98.5% linear over an operational range of ±20° in both planes, crosstalk between horizontal and vertical channels was <1.5% and system noise was <0.02°.

Three visual stimuli were used: a bright laser spot projected onto a wall at a viewing distance of 7.3 m (“far target”); a black cross drawn on a circular piece of white paper, 16 cm diam, aligned at the subject’s eye level at a viewing distance close to the near point of accommodation for each subject (“near target”); and a circular mirror 16 cm diam, mounted at the subject’s eye level at a viewing distance of about half the distance of the near target (“mirror”); subjects viewed a small dark ink-spot made on the bridge of their nose. The near stimulus and mirror stimuli were positioned at the near point of accommodation for each subject, and vergence angle was monitored so that it was similar during these two experimental conditions. Both the near stimulus and the mirror were illuminated by a surrounding array of bright light-emitting diodes (LEDs). In the otherwise darkened experimental room, the LED array made the near target and the subject’s own face in the mirror easily visible. The following test paradigms were used, each lasting 40 s; each trial was performed twice: 1) fixation of the far target during sinusoidal chair oscillations at 0.2 Hz with a peak velocity of 3°/s (peak-to-peak amplitude of 4.8°); 2) fixation of the far target during sinusoidal chair oscillations at 2.0 Hz with a peak velocity of 30°/s (peak-to-peak amplitude of 4.8°); 3) fixation of the near target during sinusoidal chair oscillations at 0.2 Hz with a peak velocity of 3°/s; 4) fixation of the near target during sinusoidal chair oscillations at 2.0 Hz with a peak velocity of 30°/s; 5) fixation of the bridge of the subject’s own nose in the mirror during sinusoidal chair oscillations at 2.0 Hz with a peak velocity of 3°/s; and 6) fixation of the bridge of the subject’s own nose in the mirror during sinusoidal chair oscillations at 2.0 Hz with a peak velocity of 30°/s.

During viewing of the near target and the mirror, we monitored each subject’s vergence angle to ensure that this was similar under the two conditions. During each experimental run, the far, near, and mirror targets were aligned so that the head oscillations were approximately symmetrical about the position of the target.

Control experiments

To determine the contribution to the response of visual tracking eye movements, such as smooth pursuit, which depend on retinal image motion, we carried out two sets of control experiments. PSEUDORANDOM HEAD ROTATION. To minimize the contribution of predictive mechanisms, three subjects were asked to view the far, near, and mirror stimuli while they were rotated with a sum-of-sines stimulus. The component sine waves had frequencies of 0.38, 1.23, 2.08, and 2.63 Hz, with peak velocities of 3.3, 5.5, 6.0, and 15.3°/s, respectively. Thus the velocity ratio between the highest and lowest frequency components was >4.0, which Barnes (1993) has established as a reliable strategy for causing breakdown in gain of smooth-pursuit tracking.

SECOND CONTROL EXPERIMENT. Five subjects attempted to smoothly pursue a laser spot (viewing distance of 1.2 m) moving sinusoidally at 0.2 Hz with a peak velocity of 3°/s or at 2.0 Hz with a peak velocity of 30°/s (corresponding to head rotations used in the main experiments). Three subjects attempted to pursue the laser spot as it moved with the sum-of-sines stimulus used in the pseudorandom head rotation.

Data collection and analysis

Horizontal and vertical head and gaze (eye-in-space) signals were low-pass filtered using Krohn-Hite Butterworth filters with a bandwidth of 0.02°.

<table>
<thead>
<tr>
<th>Subject</th>
<th>Condition</th>
<th>Vergence Angle</th>
<th>Gain (RE/LE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>S1</td>
<td>Near</td>
<td>21.956 ± 0.191</td>
<td>1.52/1.66</td>
</tr>
<tr>
<td>S1</td>
<td>Mirror</td>
<td>21.115 ± 0.218</td>
<td>0.91/0.87</td>
</tr>
<tr>
<td>S1</td>
<td>Far</td>
<td>—</td>
<td>0.87/0.91</td>
</tr>
<tr>
<td>S2</td>
<td>Near</td>
<td>19.38 ± 0.128</td>
<td>1.08/1.10</td>
</tr>
<tr>
<td>S2</td>
<td>Mirror</td>
<td>19.59 ± 0.273</td>
<td>0.85/0.92</td>
</tr>
<tr>
<td>S2</td>
<td>Far</td>
<td>—</td>
<td>1.02/1.03</td>
</tr>
<tr>
<td>S3</td>
<td>Near</td>
<td>15.77 ± 0.120</td>
<td>1.15/1.13</td>
</tr>
<tr>
<td>S3</td>
<td>Mirror</td>
<td>17.284 ± 0.165</td>
<td>0.79/0.89</td>
</tr>
<tr>
<td>S3</td>
<td>Far</td>
<td>—</td>
<td>1.05/1.08</td>
</tr>
<tr>
<td>S4</td>
<td>Near</td>
<td>30.768 ± 0.275</td>
<td>1.68/1.60</td>
</tr>
<tr>
<td>S4</td>
<td>Mirror</td>
<td>30.769 ± 0.234</td>
<td>0.60/0.66</td>
</tr>
<tr>
<td>S4</td>
<td>Far</td>
<td>—</td>
<td>1.04/1.05</td>
</tr>
<tr>
<td>S5</td>
<td>Near</td>
<td>17.36 ± 0.18</td>
<td>1.40/1.39</td>
</tr>
<tr>
<td>S5</td>
<td>Mirror</td>
<td>18.02 ± 0.21</td>
<td>0.79/0.87</td>
</tr>
<tr>
<td>S5</td>
<td>Far</td>
<td>—</td>
<td>0.92/0.98</td>
</tr>
<tr>
<td>S6</td>
<td>Near</td>
<td>18.08 ± 0.26</td>
<td>1.37/1.38</td>
</tr>
<tr>
<td>S6</td>
<td>Mirror</td>
<td>20.52 ± 0.18</td>
<td>0.85/0.88</td>
</tr>
</tbody>
</table>

Gain values are means during 0.2-Hz rotation, during which subjects could continuously foveate the target. Vergence angles are means ± SD during 2.0-Hz rotations. LE, left eye; RE, right eye.
FIG. 2. Representative records from 1 subject showing responses to 2.0-Hz sinusoidal rotations during viewing of the far target (A), near target (B), and the subject’s own nose in a mirror (C). The head and eye-in-orbit (but not vergence) traces have been offset to aid clarity of display. Note how the vergence angle is similar during near and mirror viewing but that eye-in-orbit amplitude is greater during near viewing (greater gain).
of 0–90 Hz, prior to digitization with 16-bit precision at 200 Hz. Eye-in-head rotations were calculated by subtracting head position from gaze. Convergence angle was obtained by subtracting right gaze from left gaze. We differentiated coil inputs to head and eye-in-head velocity and filtered these signals with a Remez FIR filter (bandwidth, 0–16 Hz). All analysis was interactive. For sinusoidal stimuli, we calculated gain and phase for each corresponding peak head and eye-in-head velocity values; over 50 estimates were made for each test condition. Cycles with saccades close to peak velocity were rejected. Because some data sets were not normal in distribution, we used the Kruskal-Wallis ANOVA on ranks to determine whether gain and phase values were different during far and near conditions versus the mirror condition. We performed this test separately for each subject to take into account the effects of refractive correction on VOR gain of each individual.

To analyze responses to sum-of-sines stimuli, prior to filtering, saccades were removed from the eye and gaze movement records via an interactive routine described elsewhere (Das et al. 1995). We determined the gain of compensatory eye movements during head rotation for each trial by calculating the ratio of the power spectral density of eye and head velocity at the frequencies of interest. The phase response was determined by measuring phase differences between these signals in the frequency domain and recording the phase shift at the frequency of interest. Similarly, smooth-pursuit gain was measured by calculating the ratio of power spectral density of gaze and target velocities.

![Comparison of gain of responses (right eye data) during rotations at 2.0 Hz for each of the test conditions for each eye for each subject. Data are displayed as Tukey box plots (indicating median, 5th, 25th, 75th, and 95th percentiles) for each subject. Each set of 3 columns corresponds, respectively, to viewing the far, near, and mirror conditions. Significant differences between either far- or near-viewing conditions vs. mirror viewing are indicated by asterisks (*, P < 0.05). Data from subjects left eyes (not shown) were similar.](image)

**FIG. 3.** Comparison of gain of responses (right eye data) during rotations at 2.0 Hz for each of the test conditions for each eye for each subject. Data are displayed as Tukey box plots (indicating median, 5th, 25th, 75th, and 95th percentiles) for each subject. Each set of 3 columns corresponds, respectively, to viewing the far, near, and mirror conditions. Significant differences between either far- or near-viewing conditions vs. mirror viewing are indicated by asterisks (*, P < 0.05). Data from subjects left eyes (not shown) were similar.

![Comparison of individual gain values from 1 near viewing and 1 mirror viewing of subject 1 during sinusoidal stimuli. Median vergence angles differed by 0.8°, but median gain was 65% greater during near viewing.](image)

**FIG. 4.** Comparison of individual gain values from 1 near viewing and 1 mirror viewing of subject 1 during sinusoidal stimuli. Median vergence angles differed by 0.8°, but median gain was 65% greater during near viewing.
Results of testing with sinusoidal stimuli

During 0.2-Hz rotations, when subjects were able to hold their gaze on the target, gain values were greatest during near viewing (group median, 1.39), intermediate during far viewing (group median, 1.02), and lowest during mirror viewing (group median, 0.86). These data are summarized in Table 1.

During 2.0-Hz rotations, all subjects showed substantially smaller gain values, for each eye, during mirror viewing compared with the near target condition; representative records from one subject during the three viewing conditions are shown in Fig. 2. All subjects showed smaller gain values during mirror viewing compared with the far target condition; data for subjects’ right eyes are summarized in Fig. 3. Vergence angles during the near and mirror paradigms were similar for each subject, being almost identical to the values during 0.2-Hz rotation and are summarized in Table 1. An example of individual gain values for one subject during one mirror-viewing and one near-viewing trial is shown in Fig. 4; median vergence angles differed by 0.8°, but median gain was 65% greater during near viewing. Phase shifts between head and eye-in-orbit were generally similar during viewing of the mirror (group median, 182°), the far target (group median, 182°), or near target (group median, 185°).

Results of testing with sum-of-sines stimuli

The gain values for each of the component sine waves for the three visual stimuli are compared in Fig. 5. Gain values at each frequency were consistently greater during viewing of the near stimulus than during mirror viewing. Gain values were also significantly greater ($P < 0.05$, paired $t$-test) during viewing of the far target than during mirror viewing. Median phase shift was 182° (range: 175–190°). Thus the overall results during sum-of-sines head rotations were similar to those during testing with a predictable 2-Hz sine wave (Fig. 3).

Comparison of geometric factors and measured responses

All subjects showed greater gains during near viewing compared with the mirror-viewing condition, a result that is consistent with geometrical considerations (Fig. 1C). Of the four geometric factors that are determinants of VOR gain (Viaire et al. 1986), the radius of rotation, $R$, and the interocular distance, $I$, are the same for each person under mirror- and near-viewing experiments. Furthermore, our geometric calculations indicate that during head rotation of ±10°, the distance ($d$) of the image of the nose from the center of head rotation, during mirror-viewing varies little. Thus in our simulation in Fig. 1, $d$ changed from 22 to 22.15 cm during mirror viewing; for near
viewing, $D + R$ was fixed at 22 cm. With regard to the last determinant of gain, in our simulation of the mirror experiment (Fig. 1), target eccentricity, $\gamma$, changed linearly from $-3$ to $3^\circ$ as the head rotated from $-10$ to $10^\circ$. During near viewing, $\gamma$ is equal to zero. During both conditions, geometry predicted minor changes of vergence angle during each cycle of head rotation ($<1^\circ$ for the example calculated in Fig. 1D). Such changes in vergence angle during head rotation were observed (Fig. 2) but were too small to account for the large differences in gain observed under mirror- and near-viewing conditions. Therefore the main geometric factor determining gain differences between mirror- and near-viewing experiments was target eccentricity, $\gamma$. For the mirror experiment, the image of the bridge of subjects’ nose was a moving visual target; for the near experiment, an earth-fixed black cross at the center position constituted a near stationary visual target.

The mirror paradigm might be regarded as a combined VOR-smooth-pursuit task in which the pursuit stimulus (the virtual image of bridge of the subject’s nose in our experiment) is moving as a linear function of head rotation. The question then arises: are the dynamic characteristics of the response during mirror viewing consistent with the known properties of smooth-pursuit eye movements?

**Comparison of dynamic properties of eye movements during viewing of mirror or near target**

We tested our subjects with sinusoidal stimuli at 2 Hz because smooth pursuit performs poorly at this frequency; median pursuit gain in our subjects was 0.05. Nonetheless, the gain of compensatory eye movements was significantly different (as required by visual demands) under the three test conditions in 83% of trials (Fig. 3). This initial evidence suggested that difference in the gain of compensatory eye movements during the three test conditions mainly reflected parametric changes in VOR gain rather than the effects of smooth pursuit. By measuring the gain of compensatory eye movements during pseudorandom, sum-of-sines stimuli, which minimize the effects of prediction in visual tracking, we found that gain differences were still apparent during the three test conditions in the three subjects tested, even though smooth pursuit gain of such stimuli was $<0.025$. Thus our present conclusion is that it is the unique context of the visual motion during each of our test conditions that serves as the stimulus to set the VOR gain to an appropriate value.

**General implications of present findings for concepts of governance of VOR**

Prior studies of vestibular responses during viewing of near objects have focused on the possible roles of factors such as target proximity, accommodation and vergence angle as “determinants” of VOR gain (Crane and Demer 1998; Demer et al. 1999; Paige et al. 1998; Snyder and King 1992; Snyder et al. 1992). Each of our subjects viewed targets at similar distances during mirror and near stimulus experiments, and sustained similar vergence angles under the two conditions. The findings of gain differences under the two conditions suggests that it was not target proximity, accommodation or vergence angle per se that caused modulation of VOR gain but rather the context of the moving visual stimulus. In each of our experiments, the visual motion stimulus differed. During viewing of the far stimulus, the target was viewed on a wall at the other end of a cluttered laboratory. During viewing of the near stimulus, little else was visible but the black cross drawn on the 16-cm diam piece of white paper. During the mirror experiment, there was relative motion between the reflection and the stationary edge of the mirror. Thus it seems possible that each test condition, the unique motion stimulus, along with the percept that it induced, was the crucial signal to set VOR gain to an appropriate value. If visually mediated eye movements did contribute to the gain differences that we observed between different paradigms, then possible candidates might be the short-latency, preattentive responses that have been characterized by Miles and colleagues (1998).

In conclusion, we have shown that viewing one’s own nose image in a mirror during head rotation induces responses quite different from those during visual fixation of a stationary near target and provides a new method to investigate the way that visual stimuli may influence the performance of the VOR.

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