Effects of Viewing Distance on the Responses of Vestibular Neurons to Combined Angular and Linear Vestibular Stimulation

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Chen-Huang, Chiju and Robert A. McCrea. Effects of viewing distance on the responses of vestibular neurons to combined angular and linear vestibular stimulation. J. Neurophysiol. 81: 2538–2557, 1999. The firing behavior of 59 horizontal canal–related secondary vestibular neurons was studied in alert squirrel monkeys during the combined angular and linear vestibulocochlear reflex (CVOR). The CVOR was evoked by positioning the animal’s head 20 cm in front of, or behind, the axis of rotation during whole body rotation (0.7, 1.9, and 4.0 Hz). The effect of viewing distance was studied by having the monkeys fixate small targets that were either near (10 cm) or far (1.3–1.7 m) from the eyes. Most units (50/59) were sensitive to eye movements and were monosynaptically activated after electrical stimulation of the vestibular nerve (51/56 tested). The responses of eye movement–related units were significantly affected by viewing distance. The viewing distance–related change in response gain of many eye-head-velocity and burst-position units was comparable with the change in eye movement gain. On the other hand, position-vestibular-pause units were approximately half as sensitive to changes in viewing distance as were eye movements. The sensitivity of units to the linear vestibulocochlear reflex (LVOR) was estimated by subtraction of angular vestibulocochlear reflex (AVOR)–related responses recorded with the head in the center of the axis of rotation from CVOR responses. During far target viewing, unit sensitivity to linear translation was small, but during near target viewing the firing rate of many units was strongly modulated. The LVOR responses and viewing distance–related LVOR responses of most units were nearly in phase with linear head velocity. The signals generated by secondary vestibular units during voluntary cancellation of the AVOR and CVOR were comparable. However, unit sensitivity to linear translation and angular rotation were not well correlated either during far or near target viewing. Unit LVOR responses were also not well correlated with their sensitivity to smooth pursuit eye movements or their sensitivity to viewing distance during the AVOR. On the other hand there was a significant correlation between static eye position sensitivity and sensitivity to viewing distance. We conclude that secondary horizontal canal–related vestibulocochlear pathways are an important part of the premotor neural substrate that produces the LVOR. The otolith sensory signals that appear on these pathways have been spatially and temporally transformed to match the angular eye movement commands required to stabilize images at different distances. We suggest that this transformation may be performed by the circuits related to temporal integration of the LVOR.

INTRODUCTION

During most natural behaviors, the movements of the head in space are a complex combination of angular rotation and linear translation. The vestibulocochlear reflex (VOR) functions to stabilize images on the retina during both types of head movement. Angular head acceleration stimulates the labyrinthine semicircular canals and evokes an angular vestibulocochlear reflex (AVOR). Linear, or translational head acceleration stimulates vestibular otolith receptors and evokes the linear vestibulocochlear reflex (LVOR). The relationship between translational head velocity and the rotational eye velocity required to stabilize a visual target on the retina during the LVOR is inversely related to the distance of the target from the eyes (Bronstein and Gresty 1988; Paige and Tomko 1991; Schwarz and Miles 1991; Telford et al. 1998; Viirre et al. 1986). When the distance of a visual target from the eyes is large, the eye movement required to stabilize the image is negligible. But as the distance of the image from eyes decreases, the eye rotational velocity required to maintain image stability for even small head translations can be considerable. For example, in a squirrel monkey, a relatively small interaural linear head translation of 1 cm/s evokes an oppositely directed rotational eye velocity of 5°/s when a visual target is 10 cm away from the eyes.

In the accompanying paper, we presented evidence that semicircular canal afferent signals related to angular head velocity are multiplied by an AVOR central network and added onto secondary VOR pathways when the gain of the AVOR is modified as a function of viewing distance. The question of whether secondary AVOR pathways are appropriate for generating the LVOR is unsettled. First of all, the sensory signals related to the LVOR arise from separate endorgans (Fig. 1A), and there is evidence for the existence of separate otolith-ocular pathways in mammals (Uchino et al. 1994, 1996). Second, the dynamic characteristics of semicircular canal afferents and otolith afferents are significantly different. During mid- to high-frequency head movements, canal afferents tend to lead angular head velocity by a few degrees, whereas otolith afferents lead linear head acceleration (Fernandez and Goldberg 1976; Goldberg and Fernandez 1971). The sensory otolith signals are presumably integrated and transformed into angular eye velocity commands as a function of viewing distance before being sent to extracochlear motoneurones (Paige and Tomko 1991; Raphan et al. 1996). Finally, the amplitude and direction of eye movements generated by the LVOR are dependent on the orientation of head position with respect to the direction of gaze (Paige and Tomko 1991). These considerations suggest that the brain stem mechanisms and circuits related to the LVOR, particularly viewing distance–related adjustments in the LVOR, are separate from the circuits related to the AVOR.

On the other hand, there is some reason to believe that the central processing of signals related to the AVOR and LVOR may not be entirely separate. McConville et al. (1996) reported...
that some classes of eye movement–related vestibular neurons in the rhesus monkey, in particular so-called eye-head-velocity (EHV) neurons, were sensitive to head and eye movements related to the combined angular and linear VOR (CVOR) evoked by off-axis rotation. They also reported that the amplitude of these CVOR signals was sensitive to viewing distance. This observation suggested that the AVOR and LVOR share at least some central neural pathways and raises the possibility that horizontal canal–related VOR pathways form a significant part of the central neural premotor substrate for generating compensatory eye movements in the horizontal plane, regardless of the sensory origin of signals.

If AVOR pathways participate in the generation of the LVOR, otolith linear head acceleration signals must be transformed into appropriate angular eye velocity commands. The head movement signals generated by some eye movement–related secondary vestibular units lag head velocity, whereas other units lead head velocity. On average, the signals carried by premotor central AVOR pathways during angular rotation are in phase with angular head velocity in the mid- to high-frequency range of head movements (King et al. 1976; Pola and Robinson 1978). To produce comparable eye velocity commands during linear head movements, the linear acceleration otolith signals would be integrated and multiplied by a factor inversely related to viewing distance. The question addressed in the present study is whether...
AVOR pathways also carry signals related to the translational LVOR. We recorded the responses of horizontal canal–related vestibular neurons in the rostral vestibular nuclei during different combinations of angular and linear translation produced by changing the position of the axis of head rotation at several different frequencies. Secondary vestibular neurons were identified and classified by their responses following electrical stimulation of the ipsilateral vestibular nerve, and by their firing behavior during saccades, steady fixation, smooth pursuit eye movements, and VOR cancellation. The effects of viewing distance on AVOR and LVOR responses were assessed by comparing responses recorded during fixation of earth-stationary visual targets that were near (10 cm) and far (1.3–1.7 m) from the monkey’s eyes. The results show that LVOR signals carried by AVOR pathways phase lag otolith afferent signals and are multiplied by a factor inversely related to viewing distance. Although some AVOR pathways are more strongly linked with the LVOR than others, we conclude that the direct AVOR pathways are likely to be an important part of the central neural substrate that produces the LVOR. Some of the results (related to vestibular units that project into the ascending tract of Deiters) have been previously reported (Chen-Huang and McCrea 1999).

Methods
General description of experimental methods

The results reported in this study were obtained from two squirrel monkeys that had been prepared for chronic single-unit and eye movement recordings. Each monkey was trained to fixate small visual targets at different distances from the head, to pursue moving visual targets, and to cancel its VOR by fixating a head-stationary target in return for liquid rewards. During experiments, the head-restrained monkeys were seated on a vestibular turntable that was surrounded by a cylindrical screen 90 cm from the monkey’s eyes. Smooth pursuit eye movements and VOR cancellation were evoked by projecting a turntable-mounted laser beam onto the screen. The effects of viewing distance on the VOR were studied by rewarding the monkeys for fixating earth stationary light-emitting diode (LED) targets located at different distances (10 and 150 cm) from the eyes on the midline at eye level during turntable rotation (Fig. 1B). Single-unit recordings were obtained from neurons in the vestibular nuclei with metal microelectrodes. The location and synaptic relationship of units to the vestibular nerve were determined by using stereotaxic methods in combination with recordings of field potentials and unit responses to brief (0.1 ms) cathodal pulses of current (50–300 μA) through chronically implanted labyrinthine electrodes.

The methods for surgical preparation, eye movement recording, behavioral training, electrical stimulation of the vestibular nerve and ascending tract of Deiters, and the methods for obtaining single-unit recordings from horizontal canal–related central vestibular neurons are described in detail in the accompanying paper (Chen-Huang and McCrea 1999). Briefly, the position of both eyes and vergence angle were monitored with an angular velocity sensor (Watson) mounted on the apparatus that was used to restrain the monkey’s head. Angular head velocity was monitored with an angular velocity sensor (Watson) mounted on the primate chair, the magnetic field coils and the cross bracing for the micromanipulator that advanced the microelectrode on a pair of rails (Schneeburger) bolted to the top of the turntable (Fig. 1B). The eye movement and rotational responses of most units were recorded with the monkey’s interaural plane centered on the axis of turntable rotation (see accompanying paper, Chen-Huang and McCrea 1999 for details). The monkey was then moved so that its interaural plane was 20 cm in front of the axis of rotation, the nose out (NO) position. If the unit was still isolated after recording its rotational responses to several frequencies of turntable rotation during far and near viewing in the NO position, the monkey was moved to a nose in (NI) position, 20 cm behind the axis of rotation so that its responses could be recorded in that position. In many cases, unit isolation was lost when the experimenter entered the recording room and moved the monkey from one position to another. The tendency to lose units while moving the monkey from one position to another, together with the fact that successful execution of all of the protocols in the head center and NO positions required at least 40 min, were the primary reasons why the responses of relatively few units were tested in the NI position.

Although sinusoidal rotations were commanded, the movement of the turntable was not perfectly sinusoidal; particularly when the superstructure was moved into an off-axis position, and high-frequency stimuli were used. The turntable rotations used in this study produced average peak interaural linear accelerations of ~0.031 g at 0.7 Hz, 0.043 g at 1.9 Hz, and 0.054 g at 4.0 Hz, when the monkey was seated in the off-axis positions.

In all experiments the distance of the near target was 10 cm. An earth-stationary near target was mounted on a remotely controlled retracted antenna that was positioned with the aid of a motorized gantry attached to the ceiling of the recording room (Fig. 1B). During trials in which the near target was presented, the antenna was advanced to position a small LED 10 cm directly in front of the monkey. The far LED target was also mounted on a retractable antenna that was fixed to the ceiling 1.5 m from the eyes. Both targets were retracted when they were not in use. The approximate gain of the CVOR required to maintain image stability on the retina was estimated from the following formula

\[ CVOR \text{ gain} = 1 + \frac{R}{D} \]

where \( R \) is the distance between the eyes and the axis of rotation and \( D \) is the distance of the target from the eye (Fig. 1C). The CVOR eye movements evoked concomitantly during the single-unit recordings in this study were usually slightly smaller than predicted during both far and near target viewing. The average peak velocity of the CVOR during far target viewing (CVORf ) recorded concomitantly with single-unit recordings was ~23°/s (0.7 Hz), 11°/s (1.9 Hz), and 6°/s (4.0 Hz) in the NO position, and was 17°/s (0.7 Hz), 8°/s (1.9 Hz), and 4°/s (4.0 Hz) in the NI position. The average peak velocity of the CVOR during near target viewing (CVORn ) recorded in the NO and NI positions was 55 and ~8°/s at 0.7 Hz, 28 and ~3°/s at 1.9 Hz, and 13 and ~1°/s at 4.0 Hz (negative values indicate phase reversal).

The most important difference between the NI and NO positions...
was that the peak angular head velocity and peak linear head velocity were in phase in the NO position and 180° out of phase in the NI position. When the monkey fixated a near-earth-stationary target, the sum of angular and linear head movement in the NO position produced peak VOR eye velocities that were more than twice the amplitude of those recorded in the head center position and produced a phase reversal in the VOR in the NI position (Fig. 1C). A second difference between the NI and NO positions was the distance of the far target, which was 1.7 m distant in the NI position (0.59 meter angle), and 1.3 m distant in the NO position (0.8 meter angle). A third difference was that rotating (head-stationary) parts of the turntable and rails were in the visual field of the monkey in the NI position, which may have been responsible for the slightly smaller CVOR responses evoked in this position. Finally, as noted above, there were small differences in linear acceleration in the NI and NO positions.

Single-unit recording protocols

The recording protocols used for identifying vestibular units and categorizing them are described in the accompanying paper (Chen-Huang and McCrea 1999). Units were identified by synaptic activation following electrical stimulation of the vestibular nerve (Fig. 1D) and by their responses during fixation, smooth pursuit, AVOR, and VOR cancellation while the monkey was seated in the head center position. Only units that were judged to be located in the vestibular nuclei that were sensitive to rotation in the plane of the horizontal semicircular canals are included in this study. A few units were antidromically activated following electrical stimulation of the ipsilateral vestibular nerve. Six units were antidiromically activated following electrical stimulation of the ipsilateral ascending tract of Deiters (Chen-Huang et al. 1998). The eye position and smooth pursuit eye velocity sensitivity of each unit was determined by recording its firing behavior during spontaneous eye movements and during sinusoidal smooth pursuit of 0.7 Hz (20°/s peak velocity) moving visual targets. Each unit’s response during VOR cancellation was recorded during fixation of a head-stationary laser target projected onto the cylindrical screen. The responses of each unit during sinusoidal rotation were then studied while the monkey fixated an earth-stationary LED target. Usually the responses at three rotational frequencies (0.7 Hz, 20°/s; 1.9 Hz, 10°/s and 4.0 Hz, 6°/s) were recorded. Sinusoidal functions whose frequency was the same as the stimulus frequency were fit to the averaged, desaccaded records of horizontal eye velocity, head velocity, and unit firing rate to determine the gain and phase of the unit’s response with respect to target or table velocity.

Data analysis

The techniques used for analyzing single-unit data were the same as those described in the accompanying paper (Chen-Huang and McCrea 1999). In that study it was useful to describe the effects of viewing distance on unit and eye movement responses as scalar differences (AVOR $\Delta VD$) in the gain of the AVOR responses evoked during near (AVOR$_n$) and far (AVOR$_f$) viewing, and as near/target/far target response gain ratios (N/F ratio). These scalar descriptions of response changes were reasonable to use when near viewing produced only small phase changes in unit and eye movement responses. In this study changes in viewing distance sometimes produced significant changes in both the gain and phase of eye movements and unit responses. Consequently it proved to be useful to define several phasor dependent variables derived from the eye and unit responses recorded in different experimental conditions. The change ($\Delta$) in unit (u) response related to viewing distance (VD) is a phasor ($\Delta VD_u$) determined from the difference in CVOR response recorded during near and far target viewing (CVOR$_n$ and CVOR$_f$). The viewing distance-related change in the LVOR responses was also calculated, based on the assumption of linear interaction between the AVOR and LVOR during off-axis rotation (Telford et al. 1998). The phasors related to far viewing LVOR (LVOR$_f$) and near viewing LVOR (LVOR$_n$) were computed from the differences between AVOR$_n$ and CVOR$_n$ and from AVOR$_f$ and CVOR$_f$. Finally the phasors related to viewing distance-related changes in LVOR unit responses, LVOR $\Delta VD_u$, were calculated from the vector difference between LVOR$_n$ and LVOR$_f$ responses.

RESULTS

The effects of viewing distance on the responses of 59 vestibular units during the VOR evoked by combined angular and linear vestibular stimuli (CVOR) were examined. The majority (51 of 56 units tested) of these units were activated at monosynaptic latencies ($\leq 1.3$ ms) following electrical stimulation of the ipsilateral vestibular nerve. Six units were antidiromically activated following electrical stimulation of the ipsilateral ascending tract of Deiters.

Units from each of the major classes of vestibular units described in the accompanying paper (Chen-Huang and McCrea 1999) are included in this sample. The firing behavior of the majority (50/59) of the units was related to eye movements. Most of the eye movement–related vestibular units studied were position-vestibular-pause (PVP) units (n = 30) or eye-head-velocity (EHV) units (n = 12). EHV units were subdivided into those that were sensitive to ipsilateral (EHVI, n = 4) and contralateral (EHVII, n = 8) head velocity during VOR cancellation. The remaining eight eye movement–related units included five burst-position (BP) units (one of which was monosynaptically activated following stimulation of the vestibular nerve) and three position-vestibular (PV) units. The CVOR responses of seven vestibular only (VI) units and two type II vestibular (VII) units were also studied.

Responses of vestibular nucleus units during combined angular and linear vestibular stimulation

The CVOR responses of most eye movement–related vestibular units were affected by a change in the axis of rotation, particularly during near target viewing. Figure 2 illustrates the firing behavior of a horizontal canal–related PVP unit in the left vestibular nucleus during rotation in the NO and NI off-axis positions at 1.9 Hz. It was monosynaptically activated following electrical stimulation of the left vestibular nerve. The unit’s firing rate was related to ipsilateral angular head velocity during the VOR and during VOR cancellation. Its firing rate was related to contralateral eye position during fixation and to contralateral eye velocity during horizontal smooth pursuit eye movements. It paused during saccades. An example of the firing behavior of this class of vestibular unit is shown in Fig. 6 of the accompanying paper (Chen-Huang and McCrea 1999). Unit and eye movement responses recorded during far (CVOR$_f$) and near target fixation (CVOR$_n$) in the NO position are illustrated in Fig. 2, A and B. Figure 2C shows superimposed averaged, desaccaded records obtained from this unit during $\sim 1$ min of near and far target viewing. The PVP unit modulation evoked during CVOR$_n$ (orange filled histogram) was more than twice as large as those evoked during CVOR$_f$ (superimposed green striped histogram), although the phase of the response was not significantly affected. The responses of the unit in the NI position are shown in Fig. 2, D–F. Unit responses during CVOR$_f$ were slightly smaller in the NI position than in the NO position (compare green striped histograms in Fig. 2, C and F). During near target viewing, the direction of the unit responses in the NI position was opposite to that recorded in the NO position.
The spontaneous firing rate of the unit was reduced when the eyes converged during near target viewing. This amplitude of the change in background firing rate was correlated with this unit’s rightward eye position sensitivity. When the two eyes were tonically converged (dotted, blue trace in Fig. 2, B and E), the right eye was deviated leftward and the left
The tonic decrease in firing rate observed during convergence suggests that this unit, like most PVP units, received eye position inputs related primarily to the contralateral eye (Chen-Huang and McCrea 1999).

The CVOR responses of an EHVII unit that was monosynaptically activated following electrical stimulation of the left vestibular nerve are illustrated in Fig. 3. The unit’s firing rate was related to leftward angular head velocity during the VOR, rightward eye position and rightward eye velocity during horizontal smooth pursuit eye movements, and rightward head velocity during VOR cancellation. Sample records during near and far target fixation in the NO position are illustrated in Fig. 3, A and B, whereas Fig. 3, D and E, illustrates the unit’s responses in the NI position. The averaged, desaccaded responses of the unit are illustrated in Fig. 3, C and F. The CVOR responses of this EHV cell, like the PVP unit illustrated in Fig. 2, showed a significant increase in gain during near viewing in the NO position and reversed in direction during near viewing in the NI position.

Effects of viewing distance on vestibular unit CVOR responses

The CVOR responses of most eye movement–related vestibular units were significantly enhanced during near target viewing. The gain and phase of the CVOR_n and CVOR_f responses of all of the units recorded in the NO position are plotted in polar coordinates (Fig. 4, A and B). Only the unit
FIG. 4. Polar plots of unit 1.9-Hz NO-CVORf and CVORn responses. Phase angle is expressed with respect to ipsilateral angular table velocity (ipsi H', right dashed line). The length of each phasor represents the unit’s CVOR gain (spikes/s/deg/s). A: the CVORf and CVORn responses of PVP, position-vestibular (PV), and type II vestibular (VII) units. B: the CVORf and CVORn responses of EHVI, EH VII, burst-position (BP), and vestibular only (VI) units. C: population CVORf and CVORn responses of EH VII and PVP units. See legend in C for symbols associated with each type of unit.
Mean unit gains (G) and phases (P) of the six classes of vestibular neurons recorded in the 20-cm nose-out off-axis position. Responses recorded during 0.7-Hz 20°/s, 1.9-Hz 10°/s, and 4.0-Hz 6°/s turntable rotations, and in the nose out, far target paradigm (NO-CVOR_f), nose out, near target paradigm (NO-CVOR_n) are included. Two sets of coefficients are reported for each of the six conditions. The coefficients are sinewave fits to averaged, desaccaded records; the coefficients (in parentheses) were obtained from records in which static eye position signals were subtracted out (K_c corrected). Phase values are expressed relative to ipsilateral turntable velocity. N is the number of neurons in each class included in the table.

Table 1. CVOR responses of central vestibular neurons

<table>
<thead>
<tr>
<th></th>
<th>PVP</th>
<th>EHVII</th>
<th>EHV1</th>
<th>PV</th>
<th>BP</th>
<th>VI</th>
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<tr>
<td>N</td>
<td>30</td>
<td>8</td>
<td>4</td>
<td>3</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>0.7 Hz</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NOF</td>
<td>G 2.1</td>
<td>2.5</td>
<td>1.0</td>
<td>5.1</td>
<td>0.9</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>P −17</td>
<td>25</td>
<td>136</td>
<td>160</td>
<td>−27</td>
<td></td>
</tr>
<tr>
<td>NON</td>
<td>G 3.7</td>
<td>6.2</td>
<td>3.2</td>
<td>8.0</td>
<td>0.9</td>
<td>−36</td>
</tr>
<tr>
<td></td>
<td>P −31</td>
<td>−11</td>
<td>168</td>
<td>154</td>
<td>203</td>
<td></td>
</tr>
<tr>
<td>1.9 Hz</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NOF</td>
<td>G 1.9</td>
<td>3.1</td>
<td>1.2</td>
<td>1.7</td>
<td>3.8</td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td>P 4</td>
<td>23</td>
<td>138</td>
<td>15</td>
<td>186</td>
<td>−31</td>
</tr>
<tr>
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<td>G 3.4</td>
<td>7.0</td>
<td>3.1</td>
<td>1.7</td>
<td>7.9</td>
<td>1.3</td>
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<td>156</td>
<td>180</td>
<td>200</td>
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<tr>
<td>4.0 Hz</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>NOF</td>
<td>G 2.3</td>
<td>3.7</td>
<td>0.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>P 14</td>
<td>24</td>
<td>146</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NON</td>
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<td>6.2</td>
<td>0.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>P −6</td>
<td>27</td>
<td>205</td>
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</table>

Responses recorded during 1.9-Hz turntable rotations are included. The right-hand axis corresponds to ipsilateral turntable velocity (H'), and the top axis to ipsilateral turntable acceleration. Some classes of vestibular units were more sensitive to the CVOR than others. In general, EHV and BP units exhibited larger responses (note scale) during the CVOR than other classes of eye movement–related units, and most eye movement–related units were more strongly modulated during the CVOR than non-eye movement–related units. The mean population responses of PVP and EHVII units evoked during CVOR in the nose out position during far target viewing (NO-CVOR_f) and near target viewing (NO-CVOR_n) are shown in Fig. 4C. On average, the responses of EHVII units were approximately twice as large as those of the responses of PVP units, both during far and near target viewing. The mean responses of each class of vestibular unit evoked at three frequencies of rotation for each class of vestibular unit are summarized in Table 1. On average, unit CVOR response gain was not significantly affected by subtraction of static eye position signals (K_c corrected coefficients, Table 1).

The off-axis responses of many vestibular units were similar to the responses recorded when the head was centered on the axis of turntable rotation when the monkeys fixated a far target. The NO-CVOR response of most eye movement–related units had a slightly increased gain and roughly the same phase as the AVOR response recorded in the head center position (Fig. 5A); even though the off-axis rotation produced a significant interaural translational head acceleration (∼0.43 g at 1.9 Hz) that phase led angular head velocity by 90°. In the NI position, units exhibited a slight decrease in rotational gain (Table 1). These changes in unit response gain were in the same direction as the changes in VOR gain recorded concomitantly in the off-axis positions. The response phase of vestibular nucleus units, which changed only slightly as a function of frequency (Table 1), tended to be clustered around ipsi- or contralateral velocity (Fig. 4) and was similar to their response phase during AVOR (Fig. 5B).

The NO-CVOR response of most eye movement–related vestibular units had a significantly larger gain and tended to phase lag their NO-CVOR response. In Fig. 5, C and D, unit CVOR response gain and phase during near target viewing are plotted versus responses recorded during far target viewing. The dashed line in Fig. 5C indicates a unit response increase of 134% and is proportional to the effects of viewing distance on eye velocity. The solid line corresponds to the response expected if viewing distance had no effect on unit responses. The viewing distance–related changes in the response gain of many PVP, EHV, and BP units were comparable with the concomitant change in CVOR gain, but many other PVP and EHV units were less sensitive to viewing distance than the CVOR. Some units, particularly VI, PV, and a few PVP units, were remarkably unaffected by viewing distance.

An estimate of the signal added to vestibular neurons during near target viewing, CVOR ∆VD_u, was made by vector subtraction of a unit’s CVOR response from its CVOR response. The NO-CVOR ∆VD_u of different types of vestibular neurons during 1.9-Hz rotation is illustrated in the polar plots in Fig. 6. EHV units, particularly EHVII units, tended to be more sensitive to changes in viewing distance than PVP units (note that the difference in amplitude calibration in the plots in Fig. 6, A and B). At 1.9 Hz, the average EHVII NO-CVOR ∆VD_u was nearly in phase with ipsilateral turntable velocity, whereas the average PVP NO-CVOR ∆VD_u lagged table velocity by an average of 35° (Fig. 6C). In most units the viewing distance–related CVOR responses during 0.7- and 4.0-Hz rotations were qualitatively similar to the responses recorded during 1.9-Hz rotation (Tables 1 and 2). The NO-CVOR ∆VD_u tended to have a slightly higher gain when estimated at 0.7 Hz, and a lower gain when estimated at 4.0 Hz, whereas the NO-CVOR ∆VD_u phase tended to advance slightly as stimulus increased (Table 2).

In sum, many vestibular units, particularly eye movement–related vestibular neurons, exhibited robust changes in response gain when gain of the CVOR changed as a function of viewing distance. The viewing distance–related changes in response to rotation of some units, in particular EHV and BP units, were comparable with the change in eye movements recorded. However, in most units, including most PVP and PV units, the viewing distance–related changes in response gain were not as large as the changes in eye movements recorded concomitantly. The phase of CVOR eye movements was essentially unaffected by viewing distance at the stimulus frequencies tested in this study, but the viewing distance–related signals exhibited by most eye movement–related units phase lagged head velocity at each of the frequencies tested. In the next section, an attempt will be made to estimate the translatonal, or otolith sensitivity of individual secondary vestibular units.
Effects of viewing distance on the calculated responses of vestibular units to linear translation

The off-axis rotations used in this study produced sinusoidal linear acceleration of the head in the interaural axis at the rotational frequency (0.031–0.054 g), and a small second harmonic centrifugal acceleration (0.0002–0.002 g) in the nasal-occipital axis. The fraction of the unit response related to the translational VOR (LVOR) produced by interaural linear acceleration was estimated by subtraction of the unit’s head center response from the response recorded in the off-axis position (Fig. 7, A and B). The validity of the estimate depends primarily on the assumption that the LVOR and AVOR summed linearly to produce the CVOR, and that the second harmonic unit responses to centrifugal force were negligible.

Both linear (spikes/s/cm/s) and angular (spikes/s/deg/s) units are used for describing LVOR gains rather than the angular unit used for describing AVOR and CVOR responses. For purposes of comparison, the linear velocities recorded with an offset radius of 20 cm correspond to angular turntable velocities according to the following formula.
The angular velocity is defined as

$$\omega = \frac{\text{linear velocity}}{20 \text{ cm}}$$

or

$$\omega = 2.86 \times \text{linear velocity}$$

The estimates of LVOR sensitivity determined by using NI-CVOR responses usually differed from the estimates determined by NO-CVOR data. Because the responses of every unit included in this study were recorded in the nose out off-axis position, the LVOR results described below were determined from subtraction of head center responses from NO-CVOR responses. The CVOR and LVOR responses of the fraction of units recorded in the NI off-axis position are described subsequently.

### PVP units

The calculated near and far LVOR responses of PVP units are illustrated in Fig. 7, C and D. The desaccaded, averaged CVOR and AVOR responses of a typical PVP unit during near and far target viewing recorded at NO and NI positions are illustrated in Fig. 7, A and B. The LVOR–related signal generated by this cell was estimated by subtracting its averaged response during the AVOR from the CVOR average responses. The difference signal was fit with a sinusoidal function using an algorithm that minimized the effects of nonlinearity related to inhibitory saturation (see Chen-Huang and McCrea 1999 for details). This unit was weakly modulated by linear translation during far target viewing, but was strongly modulated, roughly in phase with linear head velocity, during near target viewing. The NO-LVOR responses of all the PVP units and one PV unit recorded at 1.9 Hz are summarized in the polar plot in Fig. 7C. The NO and NI population responses of PVPs recorded during near and far viewing are plotted in Fig. 7D.

PVP units were only weakly sensitive to linear translation during far target viewing (Fig. 7, C and D, filled circles), and the phase of these small PVP LVOR signals varied considerably (Fig. 7D). PVP units also varied considerably in their viewing distance–related sensitivity to the LVOR. Some PVPs were nearly insensitive to the LVOR during near target viewing, because their AVORn and CVORn responses were nearly identical, whereas others, like the unit illustrated in Fig. 7, A and B, were nearly as sensitive to the LVORn as they were to the AVORn. The average modulation in PVP firing rate related to linear translation in the NO-LVORn condition was $5.07 \pm 1.62$.

### Table 2. Viewing distance changes in CVOR responses (CVOR \(\Delta V_D_u\)) of central vestibular neurons

<table>
<thead>
<tr>
<th></th>
<th>PVP</th>
<th>EHVII</th>
<th>EHVII</th>
<th>BP</th>
<th>VI</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.7 Hz</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NO</td>
<td>30</td>
<td>8</td>
<td>4</td>
<td>5</td>
<td>7</td>
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<tr>
<td>G</td>
<td>1.6</td>
<td>4.2</td>
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<tr>
<td>P</td>
<td>-35</td>
<td>-166</td>
<td>-35</td>
<td>1.0</td>
<td>1.0</td>
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<tr>
<td>NI</td>
<td>12</td>
<td>6</td>
<td>2</td>
<td>4</td>
<td>9</td>
</tr>
<tr>
<td>G</td>
<td>1.5</td>
<td>3.7</td>
<td>3.7</td>
<td>2.1</td>
<td>3.7</td>
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<tr>
<td>P</td>
<td>-182</td>
<td>-152</td>
<td>-152</td>
<td>9.9</td>
<td>-195</td>
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<tr>
<td>1.9 Hz</td>
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<tr>
<td>4 Hz</td>
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<tr>
<td>NO</td>
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<td>P</td>
<td>-182</td>
<td>-152</td>
<td>-152</td>
<td>9.9</td>
<td>-195</td>
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The mean \(\Delta V_D_u\) gains (G) and phases (P) (reciprocals of ipsilateral table velocity) of six classes of vestibular neurons. \(n\) is number of units tested in each condition. Responses recorded during 0.7-Hz 20°/s, 1.9-Hz 10°/s, and 4.0-Hz 6°/s turntable rotations in the nose out (NO), and nose in (NI) off-axis positions are shown. For abbreviations, see Table 1.
0.57 (SE) spikes/s/cm/s at 1.9 Hz. The peak eye velocity attributable to the LVOR in NO position was 15.5°/s, and the unit response re NO-LVOR eye velocity was 1.14 spikes/s/deg/s. This compares with an average PVP unit sensitivity re AVOR eye velocity of 1.91 spikes/s/deg/s. Thus, on average, PVP units were more sensitive to the AVOR than to the LVOR during near target viewing.

The LVOR responses of most PVP units phase lagged ipsilateral linear head velocity (Fig. 7, C and D). The average PVP NO-LVOR response phase lag calculated at 1.9 Hz was 24.2 ± 8.5°. For comparison, the response phase of utricular afferents at 1.9 Hz ranges from 5 to 25° phase lead re head acceleration (Fernandez and Goldberg 1976). Thus the LVOR response of PVP units phase lagged utricular nerve afferents by ~120°.

**EHV units**

EHV units were more sensitive to the LVOR than other secondary vestibular units. The NO-LVOR responses of 12 EHV units are illustrated in the polar plot in Fig. 7E. The population summed LVOR-related signals of EHVII units during 1.9 Hz LVOR are shown in Fig. 7F. EHVII units were nearly three times as sensitive to linear translation in the NO position during far target viewing as PVP units. During near target viewing at 1.9 Hz, their LVOR signals were nearly twice as large as the signals carried by PVP units. These LVOR responses typically phase lead ipsilateral linear head velocity during both near and far target viewing in both the NO and NI positions (Fig. 7, E and F). EHVII units tended to be slightly more sensitive to the LVOR than they were to the AVOR during near target viewing. Their gain re NO-LVOR, eye velocity was 2.62 spikes/s/deg/s, compared with an average sensitivity of 2.44 spikes/s/deg/s re AVOR, eye velocity.

The LVOR responses of four EHVI units (Fig. 7E, inverted triangles) were studied in the NO off-axis position. The LVOR sensitivity of EHVI units varied considerably. One unit was comparable with EHVII units in its sensitivity to the LVOR (gain, 2.26 and 15.7 spikes/s/cm/s during LVOR, and LVOR, respectively). The other three EHVI units were relatively insensitive to linear head movements during both the far and near target viewing. It is noteworthy that the static eye position sensitivity, x, of the sensitive EHVI unit was 3.91 spikes/s/deg ipsilateral eye position, whereas the mean x coefficients of the other three units were smaller: 1.21, 0.82, and −0.54 spikes/deg/s re ipsilateral eye position. The correspondence between eye position sensitivity and sensitivity to viewing distance will be discussed in more detail below.

**LVOR responses of other vestibular units**

The LVOR-related responses of 17 other vestibular nucleus units were calculated. In general, the LVOR sensitivity of these cells varied inversely with their sensitivity to eye movements. The LVOR responses of the five burst position units are illustrated in the polar plot in Fig. 7E (upward triangles). BP units were comparable with EHVII units in their sensitivity to the LVOR (mean gain re ipsilateral linear head velocity, 11.17 ± 3.26 spikes/s/cm/s at 1.9 Hz). The response of the single position vestibular unit included in this study was comparable with PVP units (Fig. 7C).

The linear velocity signals generated by the nine non-eye movement–related VI and VII units were idiosyncratic and were usually not significantly affected by viewing distance. The phase of the calculated linear translation signals was often significantly different from angular rotation signals and sometimes varied as a function of stimulus frequency. The calculated LVOR signals of some (4/7) VI units were closely related to contralateral linear head acceleration and ipsilateral angular head velocity during 1.9-Hz rotation, a combination of signals that was never observed in eye movement–related units. Similar observations from non-eye movement–related neurons were recently reported by Tomlinson et al. (1996). Because relatively few units of this type were included in the present study, their complex responses will not be described in detail here.

**Viewing distance changes in unit responses related to the LVOR**

The viewing distance changes in vestibular unit responses related to linear translation are summarized in the polar plots in Fig. 8. Decreases in viewing distance increased the sensitivity of central vestibular units to linear head velocity. This increase was related to ipsilateral head translation in most of the units that were sensitive to ipsilateral angular head velocity (e.g., PVP, EHVII, and PV units) during the VOR. The phase of unit LVOR, varied over a wide range but was related more closely to linear head velocity than linear head acceleration, which suggests that the otolith inputs to most of these cells had been temporally integrated.

**Directional gain asymmetry in vestibular unit LVOR responses**

The LVOR responses of 25 vestibular units were recorded in both the NO and NI off-axis positions (summarized in Table 3). Many units were more sensitive to linear translation in one of the two off-axis positions. In Fig. 9 the gain of the LVOR related signals recorded in the NI position are plotted against the signals recorded in the NO position. Differences in responses were evident in individual units during both far (Fig. 9A) and near (Fig. 9B) target viewing, although the NI or NO positional preference observed during near target viewing was not always the same as that observed during far target viewing. The individual preferences for one position or the other were roughly equally distributed across the population of units recorded. Because the main difference in the NO and NI off-axis rotations was only that the direction of the interaural translation was reversed, individual unit response differences in the two positions presumably reflect inputs related to centrifugal force, or other nonlinearities in otolith or oculomotor inputs.

**FIG. 7.** Calculated responses of all units to linear translation. The method used to estimate linear vestibuloocular reflex (LVOR)–related responses is illustrated for 1 unit in A and B. The LVOR-related responses for a PVP was computed by vector subtraction of the AVOR response from either the NO-CVOR (A) or NI-CVOR (B) response. C: the calculated NO-LVOR, and NO-LVOR responses of PVP and PV units are plotted in polar coordinates. D: LVOR, and LVOR population responses of PVP units recorded in the nose out and nose in positions. E: the calculated NO-LVOR, and NO-LVOR, responses of EHV, BP, and VI units, plotted in polar coordinates. F: LVOR, and LVOR, population responses of EHVII units recorded in the NO and NI positions. Rightward vectors in C–F are in phase with ipsilateral linear head velocity (H) and contralateral eye velocity. The key in C also applies to E. The turntable stimulus was 1.9-Hz, 10°/s peak velocity.
Relationship of vestibular unit LVOR and AVOR sensitivity

The unit signals related to linear and angular head movement were usually similar in direction, but there was no consistent relationship between the gain of unit responses related to linear translation and angular rotation. In Fig. 10A, unit LVOR response gain is plotted as a function of AVOR response gain. Figure 10B plots LVOR viewing distance sensitivity (LVOR \( \Delta VD_u \)) versus AVOR viewing distance sensitivity (AVOR \( \Delta VD_u \)). The gain values related to linear translation on the abscissa of each graph have been transform into angular values for purposes of comparison. The corresponding linear velocity sensitivity is indicated in parentheses. There was no consistent relationship between AVOR and LVOR responses (Fig. 10A), or AVOR \( \Delta VD_u \) and LVOR \( \Delta VD_u \) responses (Fig. 10B). Unit sensitivity to linear translation and angular rotation were not correlated \((r = 0.048)\), and the viewing distance–related changes in the responses of units during the AVOR and LVOR were poorly correlated \((r = 0.20 \text{ for EHVII}, 0.37 \text{ for PVP}; \text{Fig. 10B})\). These observations suggest that the inputs to units that produce their responses during the AVOR and LVOR, as well as the inputs involved in producing viewing distance–related signals, are relatively independent.

Frequency sensitivity of vestibular unit LVOR responses

The LVOR responses of most cells were recorded at more than one frequency of turntable rotation. In Fig. 11, A and C, LVOR gain is plotted as a function of frequency for PVP and EHVII units, respectively. Only those units that were fully tested in all three frequencies are included in the plots. Far and near target LVOR gains and the LVOR \( \Delta VD_u \) gain increased slightly for both classes of units as frequency increased. The increases in gain with frequency were not proportional to the sixfold increase in head acceleration and were not statistically significant for either class of cell. As noted above, the LVOR responses of PVP units tended to phase lag linear head velocity, whereas EHVII units usually led velocity. The LVOR response phase of both classes of cells advanced re linear velocity as the frequency of turntable rotation increased (Fig. 10, B and D). In sum, the LVOR signals generated by putative secondary VOR neurons were, on average, in phase with linear head velocity in the mid- to high-frequency bandwidth explored in this study. The gain of this velocity signal tended to increase slightly as a function of frequency. These signals phase lagged squirrel monkey utricular primary vestibular afferents by \(-90^\circ\), which suggests that otolith afferent inputs were integrated before they could affect the firing rate of secondary VOR neurons.

Relationship between eye movement sensitivity and LVOR \( \Delta VD_u \)

Most of the vestibular units in this study were sensitive to eye position and/or eye velocity. It may not be possible to

Table 3. Comparison of PVP and EHVII unit LVOR \( f \) and LVOR \( n \) responses in the NO and NI off-axis positions

<table>
<thead>
<tr>
<th></th>
<th>PVP</th>
<th>EHVII</th>
</tr>
</thead>
<tbody>
<tr>
<td>NO-LVOR ( f ) G</td>
<td>1.4</td>
<td>2.7</td>
</tr>
<tr>
<td>P</td>
<td>-1.0</td>
<td>26</td>
</tr>
<tr>
<td>NI-LVOR ( f ) G</td>
<td>1.5</td>
<td>2.0</td>
</tr>
<tr>
<td>P</td>
<td>50</td>
<td>-142</td>
</tr>
<tr>
<td>NO-LVOR ( n ) G</td>
<td>6.6</td>
<td>11.6</td>
</tr>
<tr>
<td>P</td>
<td>-13</td>
<td>25</td>
</tr>
<tr>
<td>NI-LVOR ( n ) G</td>
<td>5.6</td>
<td>12.5</td>
</tr>
<tr>
<td>P</td>
<td>-220</td>
<td>-162</td>
</tr>
<tr>
<td>NO-( \Delta VD_u ) G</td>
<td>6.1</td>
<td>9.2</td>
</tr>
<tr>
<td>P</td>
<td>-15</td>
<td>24</td>
</tr>
<tr>
<td>NI-( \Delta VD_u ) G</td>
<td>5.6</td>
<td>11.0</td>
</tr>
<tr>
<td>P</td>
<td>-220</td>
<td>-166</td>
</tr>
</tbody>
</table>

Values are mean unit gain (G) and phase (P) re linear head velocity recorded at 1.9 Hz. The estimated gain and phase of linear vestibuloocular reflex (LVOR) \( \Delta VD_u \) for each unit class is also included. For abbreviations, see Tables 1 and 2.
distinguish between “sensory” and “motor” signals in second-
ary, premotor VOR pathways. However, it is reasonable to ask
whether the viewing distance–related signals generated by
central vestibular neurons were better related to central eye
movement commands, or to a centrally generated efference
copy signal related to eye movements, than to parametric
changes in sensory vestibular afferent inputs. Two methods
were used to examine this question. The first method involved
examination of the correlation between eye movement sensi-
tivity and LVOR $\Delta VD_u$. A second, more abstruse, method
involved examination of the responses of units during cancel-
lation of the CVOR.

The correlation between the smooth pursuit eye velocity
sensitivity of vestibular units and their 1.9-Hz LVOR $\Delta VD_u$
gain was rather poor ($R^2 = 0.15, n = 23$ for PVP units; $R^2 =
0.36, n = 12$ for EHV units). The unit dynamic eye position
sensitivity estimated during smooth pursuit was also unrelated
to LVOR $\Delta VD_u$ in PVP ($R^2 = 0.06, n = 24$) or EHV ($R^2 =
0.08, n = 12$) units. In BP units, the relationship between
smooth pursuit eye velocity sensitivity and LVOR $\Delta VD_u$ gain
was slightly higher ($R^2 = 0.48, n = 5$).

The static eye position signals generated by secondary ves-
tibular neurons were much too weak to produce the LVOR

![Fig. 9. LVOR-related responses obtained at nose in position (NI-LVOR) are plotted as a function of the LVOR-related responses recorded at nose out position. A: LVOR$_r$ gains for the population of neurons in this study recorded at NI position are plotted vs. the responses from NO position. B: LVOR$_r$-related unit gains recorded at NI position are plotted vs. the gains from NO position. C: unit gains related to LVOR $\Delta VD_u$, recorded at NI position are plotted against the gains recorded in the NO position. Thin line in all 3 graphs is the line of unity.](http://jn.physiology.org/)

![Fig. 10. Relationship between AVOR and LVOR unit responses. Unit gains related to LVOR represented on the ordinates in A and B are with respect to linear head velocity (spikes/cm/s; in parentheses) and are also expressed in angular coordinates. A: gain of unit responses related to LVOR, is plotted as a function of their AVOR$_r$ gain. Symbols related to different classes of vestibular unit are shown in the legend. B: unit LVOR $\Delta VD_u$ gain plotted as a function of unit AVOR $\Delta GVD$ gain. Negative values in LVOR $\Delta VD_u$ and AVOR $\Delta GVD$ indicate a near viewing–related reduction in gains.](http://jn.physiology.org/)
ΔVDu signals observed, but static eye position sensitivity, \( K_s \), and LVOR ΔVDu gain were correlated (Fig. 12). Static eye position sensitivity and LVOR ΔVDu gain were strongly correlated in EHVII units (\( R^2 = 0.72, n = 8 \); Fig. 12A). The two variables were more weakly correlated in PVP units (\( R^2 = 0.18; n = 24 \); Fig. 12B).

In sum, viewing distance–related changes in unit responses to linear translation were not readily attributable to the eye movement–related signals they generate. However, the correlation between the strength of static eye position signals and LVOR ΔVDu gain suggests that the central pathways that integrate otolith signals to produce the LVOR ΔVDu signals in vestibular units may share a common neural substrate with the circuits related to generating static eye position signals.

Effect of viewing distance on the responses of vestibular units during VOR cancellation

The responses of most (31) units were recorded during VOR cancellation (VORC) both in the head center position and when the monkey was seated in the NO off-axis position. VORC was evoked by having the monkey fixate a head-stationary laser target that was projected onto the cylindrical screen that was 70 cm (NO position) or 90 cm (head center position) from the center of the monkey’s head. In many (21/31) of those units, the responses during VORC evoked by fixation of a near, head-stationary LED target that was 10 cm from the eyes were also recorded. In all cases, vestibular stimulation was produced by 0.7-Hz 20°/s turntable rotation. The results of these experiments are presented in Fig. 13. Changing the axis of rotation did not significantly change the signals generated by central vestibular neurons during VORC. In Fig. 13A the gain of the unit responses during VORC in the NO position is plotted as a function of the gain recorded in the head center position. The superimposed line indicates a unitary slope (no change in response).

The squirrel monkeys readily canceled the CVOR evoked in the off-axis position by fixating head-stationary targets that were either near or far from the eyes. The residual eye movement gain during near target fixation (mean gain, 0.08 ± 0.01°/s) tended to be slightly smaller than during far target fixation (mean gain = 0.13 ± 0.02°/s). The responses of most units during near target CVOR cancellation were comparable with the responses during far target CVOR cancellation, although some EHV units, which reverse the direction of their response to turntable rotation during VORC, tended to be less sensitive to near target VORC than to far target VORC.

It is noteworthy that cancellation of VOR significantly affected the CVOR and AVOR responses of virtually all of the eye movement–related vestibular units. However viewing distance had little effect on the monkey’s ability to cancel the VOR or on the responses of most vestibular units recorded during VORC. Even the few EHV units whose VOR responses were affected by viewing distance still exhibited the...
characteristic reversal in response direction compared with their response during fixation of earth-stationary targets. Thus the mechanisms involved in VORC appear to have similar effects on the firing behavior of vestibular units, regardless of the distance of the head-stationary target that evokes the cancellation.

**DISCUSSION**

Most, but not all, horizontal canal–related vestibular neurons in the squirrel monkey receive significant inputs related to linear head translation during combined angular and linear head movements produced by passive, off-axis, whole body rotation. A quantitative assessment of these head translation signals leads us to conclude that central horizontal canal vestibular pathways are an important part of the neural substrate that mediates the LVOR and the changes in the LVOR related to viewing distance during off-axis head rotation.

The classes of vestibular units that were most sensitive to head translation were those that have been shown to project to medial or lateral rectus motoneurons in previous studies (Chen-Huang and McCrea 1998; McCrea et al. 1987; Scudder and Fuchs 1992). The units that were most sensitive to the LVOR, particularly when the gain of the reflex was enhanced during near target viewing, were EHV units and BP vestibular units. PVP units were also sensitive to the LVOR, but their signals were only approximately half as large as the signals carried by BP and EHV units. All of these units were also sensitive to horizontal smooth pursuit eye movements, but their sensitivity to linear translation was not well correlated with their smooth pursuit eye movement sensitivity. This and other observations suggest that the signals involved in generating the unit and eye movement responses to linear head translation were primarily related to central processing of sensory utricular afferent information (Snyder and King 1992; Takeda et al. 1990) and not eye movements per se. Even so, both the LVOR component of head translation were those that have been shown to project to medial or lateral rectus motoneurons in previous studies (Chen-Huang and McCrea 1998; McCrea et al. 1987; Scudder and Fuchs 1992). The units that were most sensitive to the LVOR, particularly when the gain of the reflex was enhanced during near target viewing, were EHV units and BP vestibular units. PVP units were also sensitive to the LVOR, but their signals were only approximately half as large as the signals carried by BP and EHV units. All of these units were also sensitive to horizontal smooth pursuit eye movements, but their sensitivity to linear translation was not well correlated with their smooth pursuit eye movement sensitivity. This and other observations suggest that the signals involved in generating the unit and eye movement responses to linear head translation were primarily related to central processing of sensory utricular afferent information (Snyder and King 1992; Takeda et al. 1990) and not eye movements per se. Even so, both the LVOR component of
the latency of the AVOR (Snyder and King 1992). Distance–related changes in the LVOR is slightly longer than the observation that the latency of the LVOR and viewing neurons are significantly different from otolith afferents and by pathways. The idea is supported by the observation that the signals pass through several stages of central processing before circular canal vestibular afferents, whereas otolith afferent inputs to horizontal canal–related neurons arise from semi–saccular units putatively related to the VOR could be voluntarily suppressed by fixation of a head-stationary target.

To produce a compensatory eye movement that stabilizes an earth-stationary image on the retina during head translation, the head acceleration signals carried by otolith afferents must be integrated and transformed into angular eye velocity commands. The gain of these eye velocity commands must also be increased as viewing distance decreases (Crane et al. 1997; Paige and Tomko 1991; Telford et al. 1997). The signals carried by eye movement–related vestibular neurons reflect both of these computations. On average, PVP, EHV, and BP LVOR signals phase lagged utricular afferent signals by ~90° at each of the frequencies tested (cf. Fernandez and Goldberg 1976). The amplitude of these velocity signals increased during near target viewing, although the increase in unit gain was usually not as large as the increase in eye movement gain. The results suggest that the signal processing related to the transformation of otolith signals into oculomotor commands is carried out in some region of the brain other than the vestibular nuclei. The computed eye velocity commands are then added to other vestibular and oculomotor signals (e.g., semicircular canal, ocular pursuit, and gaze position signals) that are necessary for producing smooth eye movements that stabilize images on the retina. The neural pathways that link the semicircular canals to the extraocular motor nuclei not only produce smooth eye movements that reduce image slip on the retina in response to angular head rotation, but also produce smooth eye movements in response to image slip on the retina caused by motion of the image itself or by head translation.

**Independent processing of otolith and semicircular canal signals**

The neural pathways that mediate the AVOR are also used to generate the LVOR, but the inputs to those pathways appear to arise from different sources. The gain of $LVOR_{AVOR}$ signals and $LVOR_{AVOR}$ signals generated by eye movement–related secondary vestibular neurons were not well correlated with their AVOR signals. The independent processing of AVOR and LVOR signals is supported by other observations. When squirrel monkeys cancel their VOR by fixating an earth-stationary target, the angular rotation signals generated by PVP units are reduced in gain by ~50%, but their linear velocity signals are completely canceled. Functional ablation of irregular vestibular afferents significantly reduces the gain of the AVOR during near target viewing but has little effect on viewing distance–related changes in the LVOR (Chen-Huang et al. 1998). One explanation for these differences is that the direct monosynaptic inputs to horizontal canal–related neurons arise from semicircular canal vestibular afferents, whereas otolith afferent signals pass through several stages of central processing before being allowed to affect the firing behavior of premotor VOR pathways. The idea is supported by the observation that the linear translation signals that are present on secondary VOR neurons are significantly different from otolith afferents and by the observation that the latency of the LVOR and viewing distance–related changes in the LVOR is slightly longer than the latency of the AVOR (Snyder and King 1992).

**Contribution of AVOR pathways to the LVOR**

The LVOR signals carried by secondary vestibular units are temporally integrated and multiplied by a factor that is inversely related to viewing distance before they are added to secondary AVOR pathways. However, it seems likely that the signals carried by central semicircular canal–related pathways are not sufficient to generate the LVOR. Considered together, the signals generated by eye movement–related vestibular neurons might be sufficient to produce the small $LVOR_{AVOR}$ response, but are probably not adequate to produce the $LVOR_{AVOR}$ response. On average, eye movement–related vestibular units were only 60–70% as sensitive to the eye movements related to $LVOR_{AVOR}$, as they were to the AVOR or smooth pursuit eye movements. Moreover, unit LVOR-related responses typically exhibited a larger phase lag with respect to evoked eye movements than the unit responses recorded during the AVOR and smooth pursuit. Thus it seems likely that other premotor pathways contribute to the LVOR whose signals phase lag those observed in AVOR pathways, particularly during near viewing. One possibility is that there is a separate vestibulocular pathway to the extraocular motor nuclei that receives direct inputs from the otolith afferents (Uchino et al. 1994, 1996), although it is not known what signals these secondary otolith-ocular pathways carry in alert animals.

A second reason why separate otolith-ocular pathways may be necessary is that it is unlikely that the same neural substrate that mediates the translational LVOR also mediates the ocular counterrolling response to static tilt. The static tilt response is particularly evident at low stimulus frequencies (Baarsma and Collewijn 1975; Diamond et al. 1979; Lichtenberg et al. 1982; Telford et al. 1997), and the oculomotor response is a tonic counter-rotation of the eyes (Collewijn et al. 1985; Krejcová et al. 1971). The counter-rolling reflex clearly requires different central pathways to be recruited in response to a similar displacement of the otocoria. The oculomotor responses to static tilt and translation are separable either by central filtering of otolith signals (Paige and Tomko 1991; Telford et al. 1997) or by comparing otolith signals to semicircular canal signals. Regardless of which mechanism is involved, it is clear that the otolith signals related to the two behaviors are likely to be processed in different ways in the brain stem, and that different premotor pathways are required to execute the appropriate response.

**Contribution of visual signals to the LVOR**

We made no attempt to study signals related to LVOR signal processing in the dark. One reason for this is that in the frequency range we studied (0.7–4.0 Hz) the translational LVOR is strongly related to viewing distance, and we were unable to train our monkeys to fixate imaginary, earth-stationary targets in the dark. A second reason is that we felt the important question is not whether vision is necessary to produce viewing distance–related changes in the LVOR, but what changes occur in the signals carried by VOR pathways once the gain of the eye movements had been changed.

The question of the relative contribution of ocular pursuit to the compensatory eye movements recorded during the CVOR and LVOR was not directly addressed in this study. The viewing distance–related changes in the CVOR are clearly not entirely dependent on pursuit. The gain of the CVOR changes
before the eye movement that is made to a near target, and the
gain change persists in the dark in the absence of visual
feedback (Snyder et al. 1992). Moreover, changes in LVOR
gain are demonstrable in the dark as a function of vergence

Unit classes that were more sensitive to pursuit also tended to be more sensitive to the LVOR, but the viewing distance–
related signals of individual secondary vestibular neurons were
not well correlated with their smooth pursuit eye velocity
sensitivity. The gain of smooth pursuit eye movements in the
squirrel monkeys used in this study was \( \sim 0.5 \) at 1.9-Hz sinusoidal tracking of small targets, and close to zero during 4.0-Hz
tracking. This drop-off in gain was not observed in the CVOR
or in unit responses as stimulus frequency increased from 0.7
to 4.0 Hz, so it is unlikely that the viewing distance–related
changes in unit gain were entirely related to smooth pursuit eye
movements. On the other hand, the fact that LVOR signals on
secondary VOR neurons were dramatically reduced during
fixation of head-stationary near and far targets suggests that
these signals were strongly dependent on visual estimates of
relative target motion. In sum, ocular pursuit signals may
contribute to off-axis rotational responses, but the primary
contribution of the visual system to the LVOR is probably to
provide an estimate of target distance that is used to adjust the
gain of otolith inputs to VOR pathways appropriately.

**Viewing distance–related signal processing and eye position
signals**

Unit sensitivity to LVOR \( \Delta VD_u \) was positively correlated
with static eye position sensitivity. One explanation for this
correlation is that the neural networks that mediate central
velocity-position integration related to maintaining stable gaze
are also intimately involved in transforming otolith linear ac-
celeration signals into signals that are appropriate for main-
taining gaze stability during linear translation of the head. This
idea does not require that the same circuits are involved in both
saccade velocity-position integration and VOR integration, or
that the AVOR and LVOR share a common velocity-position
integrator. However, it is motivated by the physiological ob-
servation that neurons in the prepositus nucleus, which are
thought to be intimately involved in central integration of eye
velocity (Cullen et al. 1993; Escudero et al. 1992; Lopez-
Barneo et al. 1982; McFarland and Fuchs 1992), usually carry
combinations of static and dynamic eye position signals related
to steady fixation and to smooth eye movements. Different
prepositus neurons may be specifically concerned with integra-
tion of the eye velocity commands related to saccades, smooth
pursuit, the AVOR or the LVOR, and may have efferent
projections that are appropriate for controlling one or more of
these eye movements. But so far no unit has been observed
whose firing behavior is related to head or eye position during
the VOR but not during steady fixation. It is this observation
that suggests that the correlation between static eye position
sensitivity and LVOR \( \Delta VD_u \) might be due to the fact that the
pathways that transmit an integrated, viewing distance–multi-
plied, otolith signal to secondary horizontal canal–related neu-
rons also carry signals related to static eye position.

**Viewing distance multiplication of otolith signals**

The anatomic location and physiological characteristics of the
central mechanism used to multiply otolith signals as a
function of viewing distance are unknown. In the accompany-
ing paper (Chen-Huang and McCrea 1999), we suggested that
viewing distance–related changes in the AVOR were accom-
plished by multiplication of irregular semicircular canal affer-
ents by a signal that was proportional to vergence angle. The
low-pass filtered characteristics of the viewing distance–related
changes in the AVOR, and the phase of the viewing distance–
related signals on vestibular neurons required that the multi-
plied vestibular afferent signals be partially centrally integrated
before being input to secondary VOR pathways. We proposed
that parallel pathways carrying viewing distance–multiplied
semicircular canal irregular afferent inputs and integrated canal
irregular afferent inputs to secondary VOR pathways exist. The
observations in this study suggest that viewing distance adjust-
ments in the otolith-ocular pathways related to linear transla-
tion may be similarly organized.

Galvanic ablation of irregular vestibular nerve afferents has
little effect on the CVOR evoked by off-axis rotation both
during near and far target viewing (Chen-Huang et al. 1998), so
it appears that regularly discharging otolith afferents are suf-
cient to produce the LVOR at the stimulus frequencies we
studied. Because the linear translation signals carried by semi-
circular canal–related VOR pathways phase lag regularly dis-
charging otolith afferents by \( \sim 90^\circ \), the irregular otolith affer-
ent signals appear to have been centrally integrated. It seems
likely that the main pathways for transmitting centrally inte-
grated, viewing distance–adjusted, otolith regular afferent sig-
nals to medial and lateral rectus motoneurons are the secondary
horizontal canal-ocular pathways.

**Model of the mechanisms involved in producing the
translational LVOR during combined angular and linear
translation**

Figure 14 is a diagram that summarizes how horizontal
semicircular canal and utricular afferent signals may be com-
bined to produce the CVOR during off-axis rotation. Utricular
afferents, probably primarily of the regularly discharging va-
riety, carry signals related to linear translation that are multi-

![FIG. 14. Schematic diagram summarizing how horizontal semicircular ca-
nal and utricular afferent signals are combined to produce the CVOR during
diff-off-axis rotation. Linear head acceleration signals generated by otolith affer-
ents are multiplied by a factor inversely related to viewing distance and are
transformed into linear velocity signals by a temporal integrator (\( N_{L\text{VOR}} \)).
These linear head velocity signals are then transformed into angular eye
velocity motor commands by superimposing them on horizontal canal–related
VOR pathways that are anatomically designed to produce angular eye rotation.
Thus the signals carried by central VOR pathways code the angular eye
velocity required to produce stable vision during different combinations of
linear and angular head movement.](http://jn.physiology.org/Downloaded from http://jn.physiology.org/)
plied by a signal that is inversely related to viewing distance, such as vergence angle (Crane et al. 1997; Telford et al. 1997; Viirre et al. 1986). This internal estimate of the angular eye acceleration required to produce the LVOR is then integrated. The output of the LVOR integrator is an angular velocity signal that is appropriate for producing the viewing distance–adjusted LVOR. This LVOR velocity signal is transmitted to horizontal canal AVOR pathways, where it sums with angular head velocity signals. This combination appears to occur on most, but not all of the units that participate in generating the AVOR. A direct pathway from the LVOR integrator to motoneurons is also postulated because the signals carried by secondary AVOR pathways do not appear to be sufficient to produce the LVOR.

Conclusion

The transformation of linear acceleration signals to angular gaze velocity commands as a function of image distance is a fundamental function that is likely to have been addressed at an early stage of vertebrate evolution. It is done in large part by adding integrated, viewing distance–multiplied, otolith signals to semicircular canal–related vestibuloocular pathways. This simple, but elegant spatial-temporal transformation is probably a fundamental feature of the architecture of the brain stem and cerebellar circuits that produce the vestibuloocular reflex.

This work was supported by National Eye Institute Grants EY-08041 and EY-06483, and by the Women’s Council of the University of Chicago Brain Research Foundation.

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Received 26 June 1998; accepted in final form 31 December 1998.

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