BEHAVIOR OF CELLS WITHOUT EYE MOVEMENT SENSITIVITY IN THE VESTIBULAR NUCLEI DURING COMBINED ROTATIONAL AND TRANSLATIONAL STIMULI

R. D. Tomlinson, * † K. M. V. McConville, † and E.-Q. Na*

Departments of *Otolaryngology and †Physiology, University of Toronto, Toronto, Canada

Reprint address: Dr. R. D. Tomlinson, Dept. of Otolaryngology, Rm 7310, Med. Sci. Bldg., 1 King’s College Circle, Toronto, Canada M5S 1 A8; Tel: (416) 978-7160; Fax: (416) 978-8765; E-mail: R.D. Tomlinson <alan.blakeman@utoronto.ca>

Abstract — A total of 74 neurons that lacked eye movement sensitivity were recorded within the confines of the rostral medial and medial lateral vestibular nuclei. Of these, 36 had response characteristics that were consistent with combined canal and otolith inputs (CAOT neurons), 18 received canal inputs only (CA neurons), and 20 had otolith inputs only (OT neurons). Responses were measured during both rotational and combined rotational and translational stimuli at 0.5 and 3.0 Hz. The otolith signal was found to lag acceleration markedly at both frequencies. Indeed, one subset of CAOT neurons had otolith responses that led translational velocity by only 12° at 0.5 Hz. All translation-responsive neurons decreased their phase lag with respect to acceleration when the stimulus frequency was increased and exhibited a large increase in sensitivity. As these cells have response dynamics that lie between those seen in otolith afferents and those required to drive the motoneurons during the translational VOR, they may represent an intermediate stage in the signal processing.

Keywords — vestibular, translation, primate, VOR

Introduction

Many laboratories have studied the behavior of neurons in the rostral medial vestibular nuclei during eye movements and rotational stimuli (1–5). There has, however, been no systematic description of the responses of these neurons to translational or combined rotational–translational stimuli in the awake primate. Recent experiments have demonstrated that translational stimuli generate a robust translational VOR (tVOR) (6–8). Nonetheless, little is known about the neural basis of this reflex. A description of the responses in the rostral medial vestibular nucleus to translational stimuli is central to furthering our understanding of the system.

The signals that emanate from the vestibular labyrinth are not, by themselves, appropriate for providing the input to the motoneurons during the VOR. Since the canals provide a signal that is approximately in phase with head velocity, and the motoneurons require both velocity and position signals, a velocity-to-position integrator is required (9) to generate the position component. The tVOR compounds this problem. Otolith afferents provide a signal that is approximately in phase with linear acceleration (10,11) rather than with velocity. For the otoliths to provide the required velocity component, the afferent output requires a further stage of integration.

Integration by itself, however, is not sufficient. Tilt of the head in the roll plane should result in the same otolith afferent firing as does translational acceleration along the interaural line. The required compensatory eye movements, however, are quite different in the
two cases. Head tilt requires a compensatory eye movement that is torsional while interaural acceleration requires a compensatory eye movement that is horizontal. It has been suggested that the brain deals with this problem by filtering the otolith afferent signal. The low frequency components, presumably caused by head tilt, would generate torsional eye movements while the high frequency components, resulting from translational accelerations, would generate horizontal (or vertical) eye movements (12-14). There is little hard evidence, however, to support this scenario. More data are required, concerning both the dynamics of the tVOR and the behavior of the neurons themselves. The experiments described here were an attempt to address some of these lacks.

**Methods**

Animals were prepared for recordings as described elsewhere (15). Briefly, binocular search coils were implanted according to the technique of Judge and colleagues (16) along with a ‘T’ shaped piece of aluminum that served to stabilize the animal’s head. In a second surgical procedure, a recording chamber was stereotaxically implanted, its centre aimed at the midpoint between the two abducens nuclei. In this way, the vestibular nuclei on both sides could be sampled. All surgery was performed in a sterile operating suite under the supervision of a veterinarian. After the animal had recovered from the surgical procedures for 2 weeks, it was trained to fixate laser and LED targets to obtain a juice reward. In order to force the animal to converge on near targets, the animal was required to fixate the target with both eyes in order to obtain the reward.

Two different rotational conditions were used. First, animals were rotated with an axis of rotation that intersected the interaural line so as to result in a pure rotational stimulation (on-axis stimulus). Second, the axis of rotation was moved 18 cm in front of the animal’s eyes (23 cm in front of the interaural line), resulting in a combined angular and translational stimulus (off-axis stimulus). Unfortunately, we had no means for changing the orientation of the head relative to the rotation axis, so only nose-in data could be collected. Both the angular VOR (aVOR) and the tVOR have gains that are a function of viewing distance (6). Accordingly, neuronal responses were recorded with a near target (14 cm from the eyes) and a far target (100 cm from the eyes) in order to determine if viewing distance influenced the observed firing rates.

It was noted that following rapid steps in table position, the rate table underwent a brief period of oscillation at 3.0 Hz. We decided to exploit this natural oscillatory behavior in order to obtain at least one high-frequency data point since our rate table was unable to generate controlled sinusoidal stimuli above 1 Hz. When a neuron was isolated, it was tested using both a 0.5 Hz sinusoid and position steps to induce the 3.0 Hz oscillation. The oscillatory behavior had the form of a damped sinusoid, so both the table and the neuron firing rate were fitted, using a modified least-squares technique, with an equation of the form:

$$Y = A + B(e^{-Cr}[D \sin(E \omega t) + F \cos(E \omega t)])$$

as this is the equation of a dumped sinusoidal oscillation. Figure 1 illustrates the table velocity that resulted from these oscillations along with the results of fitting the velocity with the above equation.

Table velocity, acceleration, and jerk were calculated by using a central difference differentiator and then smoothed with a zero phase shift low-pass digital filter with a corner frequency of 10 Hz. The frequency of the oscillation ($E$ in the above equation), was calculated from the velocity curve. This value was then used to fit the firing rate, acceleration, and jerk data. This was probably unnecessary, as the best fit frequency was always found to lie between 2.9 and 3.1 Hz. The 0.5 Hz data were treated in precisely the same fashion.

The sensitivity and phase shift of the cell’s responses to velocity, acceleration, and jerk were calculated from the parameters of the best-fit equation. Cells that exhibited clipped firing rate behavior during the inhibitory half-
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Figure 1. (A) Table angular velocity following a position step. (B) Expanded view of the oscillations that followed the position step illustrated in panel A. Both the table velocity and the best fit damped sinusoid are illustrated. Clearly the chosen equation yields a very good fit to the data. In this and all subsequent figures, positive angular or tangential head movements are directed towards the right.

cycle, had the amplitude of the fitted curve adjusted by eye to produce the best fit of the available data.

The otolith signal was derived by subtracting the on-axis response (canal stimulus only) from the off-axis response (canal + otolith stimulation). This correction proved to be negligible for the 3.0 Hz stimulus, as peak table velocity rarely exceeded 3°/s and so canal contributions to the overall response were very small.

Both horizontal and vertical binocular gaze position were measured using the search coil technique (CNC Engineering), while head position was measured with a linear potentiometer that was attached to the motor shaft. During a preliminary experiment, eye movements were measured monocularly so that the second phase detector could be used to measure head position. These coil measurements of head position were compared with the potentiometer measurements, and the two were identical. During the remaining experiments, eye movements were monitored binocularly to be certain that the animal was converging on the near targets. Both gaze and head position were digitized at 1 KHz and stored on disk for further off-line analysis. Spikes were detected with a window discriminator (BAK), and the time of occurrence of each action potential was measured with an accuracy of ± 10 μs.

Firing rates were calculated from spike density curves obtained by replacing each action potential with a Gaussian curve with a width of 19 ms (17). The Gaussian curves were then summed to yield spike density.

Average firing rate response curves were generated by aligning the head position traces from several trials and then averaging the resulting neuronal responses. The standard error of each data point in the average curve was calculated and displayed. The results from two different series of trials were considered to be different if the standard errors of the two averages did not overlap. The head position records were also averaged to minimize noise. This was found to be necessary because the calculation of jerk required that the rate table signal be differentiated 3 times, and so small amounts of noise resulted in large errors.

Results

A total of 233 cells were recorded within the confines of the rostral medial and medial lateral vestibular nuclei. Eye position and velocity sensitivities were measured during fixation and smooth pursuit trials prior to the onset of rotation. As we were particularly interested in the behavior of position-vestibular-pause (PVP) and eye-head-velocity (EHV) neurons,
recordings were concentrated in those portions of the medial and lateral vestibular nuclei that contain large numbers of these cells. Only 112 neurons could be recorded throughout both conditions because of the inherent difficulties in obtaining stable recordings during both on- and off-axis rotations. Thirty-eight were classified as being PVP, EHV, or burst-tonic (BT) in their behavior and have been reported elsewhere (15). The remaining 74 neurons were classified as being otolith inputs (CA neurons), 8 had canal input only (CA neurons), and 20 had only otolith input (OT neurons). All of the neurons described were tested with both near and far targets, to determine whether changes in modulation depth were associated with changes in VOR gain. Such changes were rarely seen. If any change was noted, the change in modulation was either insignificant or was associated with poor cell isolation.

**Canal and Otolith (CAOT) Neurons**

The Canal and Otolith (CAOT) cells demonstrated a significant difference in their on- and off-axis responses, but responded with a non-zero modulation in all cases. These cells were judged to have both canal and otolith inputs. Thirty-six of these cells were analyzed, of which 4 exhibited a very small amount of eye position sensitivity (less than 0.2 spikes/s\(^\circ/s\)) and 2 slowed their firing during ipsilateral saccades. As these 6 cells otherwise behaved in the same fashion as those without eye movement sensitivity and did not exhibit the characteristics of PVP or EHV neurons, they were included in the sample reported here. The CAOT cells were divided into subcategories as follows:

- **Otolith and canal responses with opposite on-directions**: 11 (CAOT-)
- **Otolith and canal responses with the same on-direction**: 25 (CAOT+)

The animal was oriented nose-in towards the axis of rotation during off-axis trials, thus CAOT+ cells that were excited by ipsilaterally directed rotations were also excited by contralateral tangential accelerations. Obviously, this classification is somewhat arbitrary, and the designations of “+” or “−” simply indicate that with the nose-in orientation, the addition of the otolith signal during off-axis rotation either increased (+ cells) or decreased (− cells) the modulation depth.

The cells were subdivided into Type I cells (firing rate increases for ipsilateral head rotation) and Type II cells (firing rate increases for contralateral head rotation) behavior. Fourteen CAOT cells were Type I, 20 were Type II, and 2 changed from Type II to Type I between the on- and off-axis conditions. These cells represent the largest single group of Type II vestibular neurons present in our sample. There were no apparent differences between the response characteristics of the Type I and the Type II cells.

As example of typical CAOT+ cell behavior during 0.5 Hz rotation is shown in Figure 2. Note that although the off-axis modulation is quite robust (sensitivity = 1.82 spikes/s\(^\circ/s\); phase lead = 43\(^\circ\)), the on-axis response is substantially reduced (sensitivity = 0.44 spikes/s\(^\circ/s\); phase lead = 23\(^\circ\)). The behavior of this cell can be explained if it has both otolith and semicircular canal input and both inputs are activated during clockwise (contralateral) rotation. The mean angular velocity sensitivity for CAOT+ cells, calculated from the on-axis trials, was determined to be 0.47 spikes/s\(^\circ/s\) (range 0.13 to 0.90) and the phase lead was 24\(^\circ\) (range 45\(^\circ\) lead to 9\(^\circ\) lag).

When off-axis rotations were used, the CAOT+ neurons exhibited a mean sensitivity of 1.24 spikes/s\(^\circ/s\) (range 0.61 to 3.05) and a phase lead with respect to velocity of 41\(^\circ\) (range 18\(^\circ\) to 63\(^\circ\) lead). Thus, the addition of an otolith signal increased the mean sensitivity of these cells by 0.77 spikes/s\(^\circ/s\) and increased the mean phase lead by 17\(^\circ\).

The otolith modulation was calculated by subtracting the on-axis spike density curve from the off-axis one. The resulting curve was fitted with a sinewave, and the sensitivity and phase were measured. The results of these calculations indicated that the CAOT+ cells had a mean sensitivity with respect to acceleration
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Figure 2. Responses of a CAOT+ neuron during off-axis (A) and on-axis (B) rotations. Note that although the neuron exhibits a modest response (sensitivity = 0.44 spikes/s/°/s; phase lead = 23°) during on-axis rotation, the response is substantially increased during off-axis rotation (sensitivity = 1.82 spikes/s/°/s; phase lead = 43°). (In this and subsequent illustrations, the heavy trace is the neuron firing rate and the thin trace is the table rotatory stimulus.)

On- and off-axis responses of a CAOT+ neuron are illustrated in Figure 3. In contrast to the CAOT+ neurons, the off-axis response (sensitivity = 1.1 spikes/s/°/s; phase lead = 10°) is clearly smaller than that seen with on-axis stimulation (sensitivity = 2.1 spikes/s/°/s; phase lead = 10°). Note that in this cell, the phase lead during on-axis stimulation is re-

Figure 3. Responses of a CAOT− neuron during off-axis (A) and on-axis (B) rotations. Note that although the neuron exhibits a substantial response during on-axis rotation (sensitivity = 2.1 spikes/s/°/s; phase lead = 10°), the response is decreased during off-axis rotation (sensitivity = 1.1 spikes/s/°/s; phase lead = 21°). Since the addition of an otolith signal during off-axis rotation leads to a decrease in the phase lead, the otolith signal must be nearly in phase with tangential velocity at this frequency. Flattening of the response during the inhibitory half-cycle was caused by the neuron being silenced during several of the 10 cycles that make up this average response.

of 0.61 spikes/s/cm/s² (range 0.27 to 1.17), and a phase lag with respect to acceleration of 43° (range 31 to 77).

This technique, unfortunately, requires that the two firing rate curves obtained in the on- and off-axis rotations be subtracted, and this has the effect of magnifying the noise present in each curve. The phase lead and sensitivity of the otolith signal can also be calculated by comparing the on-axis response (sensitivity = 0.47 spikes/s/°/s; phase lead = 24°) with the off-axis response (sensitivity = 1.24 spikes/s/°/s; phase lead = 41°). This vectorial addition approach was used as a check on the accuracy of the subtraction method. Using the vectorial approach, the mean sensitivity of these neurons to linear acceleration was found to be 0.63 spike/s/cm/s², very similar to the result obtained by the subtraction method. Simi-
duced relative to that seen during off-axis rotation. Since the otolith and canal signals on this cell results in comparable modulation amplitudes, the otolith signal must be approximately in phase with tangential velocity and thus must lag acceleration by nearly 90°.

The CAOT− cells exhibited markedly greater sensitivity during on-axis rotation (mean 1.25 spikes/s/s; range 0.18 to 3.01) and less phase lead (mean phase lead 7°; range 18° lead to 4° lag) than did the CAOT+ cells. The off-axis response of CAOT− neurons was 0.35 spikes/s/s (range -1.18 to 1.30), and the mean phase lead was 10° (range 0° to 44°). The effect of the otolith signal in these cells was to reduce the modulation by 0.89 spikes/s/s and to increase the phase lead by 4°. This change in phase lead is less than the measurement error from the least-squares fitting technique, which was estimated to be approximately 5°. The otolith signal calculated from the above results had a mean sensitivity of 0.71 spikes/s/cm/s² and a phase lag of 78° with respect to tangential acceleration (12° lead with respect to velocity). Direct subtraction of the on- and off-axis responses yielded a sensitivity of 0.75 spikes/s/cm/s² and a phase lag of 78°, essentially identical to the calculated values.

The phase lead with respect to velocity of the canal signal and the phase lag with respect to acceleration of the otolith signal varied over a considerable range. We attempted to determine if the phase behavior of the two signals was related in any fashion. Accordingly, we plotted the phase shifts of the two signals as a function of one another. Due to the potential error involved in estimating the phase of small or noisy responses, only the cells that exhibited the largest modulation amplitudes were considered. The results of this analysis are shown in Figure 4. Although there is considerable cell to cell variation, the phase behaviors of the two signals are related (p < 0.001). Cells that exhibited a large phase lead with respect to velocity in the canal component of their modulation also tended to exhibit a reduced phase lag with respect to acceleration in their otolith component.

The response of CAOT+ neurons during the 3 Hz oscillation that followed table position steps was markedly different from that seen during 0.5 Hz oscillations. The response of a typical CAOT+ neuron during these high frequency oscillations is illustrated in Figure 5. The response, which had led angular velocity by 45° at 0.5 Hz in this cell, is now nearly in phase with head tangential acceleration. The cell underwent a phase advance of some 45° when the frequency was increased. This phase advance was seen in all CAOT+ cells, although the magnitude of the increase varied from cell to cell (the mean increase in phase lead was 32°, range 7 to 65). In addition the calculated sensitivity with respect to tangential acceleration also increased by a factor of 3.6.

It has been suggested (18) that central otolith neurons may encode jerk rather than acceleration. Accordingly, the sensitivity of the otolith component of CAOT neurons was calculated as a function of the tangential velocity, acceleration, and jerk for both the 0.5 Hz
and the 3.0 Hz data. The results of this analysis are given in Table 1. The same basic pattern was observed in all of our CAOT+ cells. When the frequency was increased from 0.5 Hz to 3.0 Hz, the phase lag with respect to acceleration decreased (see Table 1). The sensitivity at 3.0 Hz with respect to velocity was increased by a factor of 22 and that with respect to acceleration by factor of 3.6, whereas the sensitivity with respect to jerk was reduced to one-third of its 0.5 Hz value.

Just as they did during 0.5 Hz rotation, the CAOT− neurons behaved differently from the CAOT+ neurons during 3.0 Hz oscillation. While the CAOT+ neurons exhibited a mean increase in phase lead of approximately 32°, the CAOT− neurons exhibited slightly less change in their phase angles when the frequency was increased (see Figure 6). Thus, at 3.0 Hz, their firing rate modulation lagged tangential velocity by 40° (range 3° to 60°). The sensitivity of these cells with respect to tangential velocity and acceleration increased markedly at 3.0 Hz, but the sensitivity with respect to jerk was somewhat reduced relative to the 0.5 Hz value.

The effect of target distance, and thus of vergence angle, on cell modulation was also determined, because both the aVOR and the tVOR are known to change the gain in these circumstances. As eye position was measured binocularly, trials were analyzed only when the animal was within ±2° of the vergence angle that was appropriate for the target distance. Although occasional neurons exhibited small differences, these differences were mi-

Table 1. Sensitivity and Phase of Cells Receiving Otolith Input to Translational Stimuli

<table>
<thead>
<tr>
<th>Cell Type</th>
<th>0.5 Hz Vel.</th>
<th>0.5 Hz Accel.</th>
<th>0.5 Hz Jerk</th>
<th>3.0 Hz Vel.</th>
<th>3.0 Hz Accel.</th>
<th>3.0 Hz Jerk</th>
</tr>
</thead>
<tbody>
<tr>
<td>CAOT−</td>
<td>12 ± 2.35</td>
<td>0.75</td>
<td>0.24</td>
<td>40 ± 25.9</td>
<td>−53 ± 1.36</td>
<td>43 ± 0.08</td>
</tr>
<tr>
<td>CAOT+</td>
<td>47 ± 1.91</td>
<td>−43 ± 0.61</td>
<td>47 ± 0.19</td>
<td>79 ± 41.1</td>
<td>−9 ± 2.22</td>
<td>82 ± 0.12</td>
</tr>
<tr>
<td>OT</td>
<td>36 ± 3.13</td>
<td>−54 ± 1.00</td>
<td>36 ± 0.32</td>
<td>81 ± 54.1</td>
<td>−12 ± 2.82</td>
<td>82 ± 0.15</td>
</tr>
</tbody>
</table>

CAOT+ and CAOT− cells receive both otolith and canal inputs, whereas OT cells receive otolith input only. The sensitivities and phases listed are for the otolith signal only. The sensitivity units are spikes/cm/s/(1.3. or 9). Positive phase values indicate lead, negative values indicate lag. Velocity, acceleration, and jerk should be 90° out of phase with one another at 3.0 Hz as they are at 0.5 Hz. The small differences were caused by fitting each of the curves separately, and noise became a larger factor for the higher derivatives.
Figure 6. Responses of a CAOT− neuron during damped 3 Hz oscillation. In contrast to the CAOT+ neuron illustrated in Figure 5, the responses of this cell were approximately in phase with tangential velocity (and, thus, with jerk). The best-fit damped sinusoid yielded a value of 25° phase lead with respect to tangential velocity for this response. During 0.5 Hz stimulation, this cell was found to lead tangential velocity by 20°. Thus, this cell exhibited very similar phase behavior at both 0.5 and 3 Hz. As in Figure 5, the on-axis response was subtracted.

nor, and there was no effect of target distance on the population as a whole.

Otolith Only (OT) Neurons

These cells were identified as those that did not modulate during the on-axis trials but did during off-axis trials. Twenty such cells were identified. None of the OT cells demonstrated any eye position or movement sensitivity. These cells had a low resting rate, averaging 26 spikes/s (range 0 to 60), and as a result often exhibited saturating responses.

All 20 OT cells had Type 1 responses in that they were excited during rotations towards the ipsilateral side. The peak firing rate for all OT cells occurred between peak ipsilateral head velocity and peak ipsilateral head acceleration. The responses of a typical OT cell to on- and off-axis rotations are illustrated in Figure 7. As can be seen, the cell modulates strongly during off-axis rotations, but there is no evidence of modulation during on-axis stimula-
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Figure 7. Responses of an OT neuron to off-axis (A) and on-axis (B) rotation. The neuron modulates vigorously during off-axis rotation (B), but there is no discernible response during on-axis rotation (A). Off-axis rotation yielded a sensitivity of 1.53 spikes/s/°, and a phase lead of 34° in this cell. In both cases, the thin trace is head position and the thick trace is firing rate.

When the 3.0 Hz oscillations were used, again the responses observed were similar to those seen in the CAOT neurons. The response of a typical OT neuron during these low amplitude oscillations is illustrated in Figure 8. The spike density curves is very nearly in phase with tangential acceleration at 3.0 Hz, even though this cell lagged acceleration by 47° at 0.5 Hz. The average OT neuron was found to lag acceleration by 12° at 3.0 Hz (range 5° lead to 35° lag), a phase shift of some 42° relative to the 0.5 Hz data. The sensitivity of the neurons with respect to velocity, acceleration, and jerk was measured, and the average values for the OT neurons are given in Table 1. Not only is there a change in the phase of the response when the frequency is increased, but the sensitivity with respect to acceleration increases by a factor of 2.8 times. The sensitivity with respect to jerk was found to decrease modestly, by a factor of about 2, which was very similar to the results found for the CAOT neurons.

The enormous sensitivity of these neurons to high frequency translational movements was striking. This sensitivity is perhaps best illustrated in Figure 9. Following each step in table position, the table was reset to its rest position prior to the next step. This reset resulted in an exponentially decaying velocity curve upon which was superimposed some ripple caused by “cog-wheeling” of the servo motor. This “cog-wheeling” resulted in a very large modulation of the firing of the OT neurons (see Figure 9). This observation provides further support for the idea that these neurons must be much more sensitive to high frequencies than they are to low frequencies, since the relative amplitude of the decaying exponential.

Canal Only (CA) Neurons

These cells were identified as those with no significant difference in the firing rate between on- and off-axis conditions. Eighteen such cells were identified, of which one had a small eye position sensitivity with a slope of 0.19
spikes/s/°, and 10 paused during saccades. Of the 18, 9 were Type I, and 9 were Type II. All of the CA cell responses to both on- and off-axis rotations were clipped sinusoids. Seven CA cells showed a slight increase that was not statistically significant in response to on-axis trials. The phase of the responses was very consistent for each cell between trials as well as across all CA cells. The Type I responses had a phase lead relative to ipsilateral head velocity of 9° to 27°; the Type II responses had a phase lead of 0° to 27°. As with the CAOT and OT neurons, viewing distance was not found to effect the observed responses.

**Discussion**

Certainly one of the most striking findings of this study was that our recordings in the rostral medial vestibular nuclei identified large numbers of neurons that carried pure otolith signals. Indeed, when one uses a purely rotational stimulus to search in this area, cells are
Figure 9. Response of an OT neuron during the oscillation that occurred when the rotating table reset to its rest position (as in earlier tables, the thin trace is the table movement and the thick trace is the firing rate in each case). As can be seen, this very low amplitude oscillation of approximately 4 Hz resulted in a very vigorous modulation of the cell firing rate. Note that although the table velocity, and thus acceleration, are decaying in an approximately exponential fashion and the oscillation is simply superimposed on this decay, the cell appears to respond predominantly to the oscillation and is relatively insensitive to the slow decay.

frequently encountered that do not respond to any stimulus. When a combined rotational-translational search stimulus is used, as was done here, few unresponsive neurons are encountered. It seems likely that many of the normally encountered unresponsive neurons are otolith cells.

One of the requirements for both the aVOR and the tVOR is that the reflex gain must be a function of viewing distance (6). We were particularly interested in the effects of viewing distance on neuronal modulation during both rotation and combined rotations and translations. We have demonstrated that both PVP and EHV neurons changed their modulation when the viewing distance changed (15). It might be expected that these viewing-distance-related effects would also be seen in
other cell types in the same area, since both the PVP and EHV cells exhibit changes. This was not the case; instead, none of the CAOT, OT, or CA cells showed any effects of viewing distance. PVP cells do not receive floccular inputs (19), and so it seems likely that they receive their otolith signal from some source in the vestibular nuclei. We were unable to identify any potential source with the appropriate viewing-distance-related behavior.

**CAOT and OT Neurons**

The presence of neurons with convergent canal and otolith inputs has been known for some time (20–22). The function of these neurons, however, remains a mystery. Neurons have traditionally been classified as Type I or Type II, depending on whether they were excited by ipsilateral or contralateral head rotations (23). The results of such a classification have consistently found that approximately 30% to 50% of the sample had Type II response characteristics (1,2,24–27). In this study, the majority of CAOT cells, 56%, exhibited Type II responses, while the CA neurons were equally divided between Type I and Type II behavior. This preponderance of Type II responses in CAOT neurons should not be surprising, as recent experiments have demonstrated in the rat that 79% of Type II horizontal canal neurons receive otolith input (28).

The response of the CAOT and OT neurons to translational stimuli was quite unexpected. Fernandez and Goldberg (10) precisely characterized the firing patterns of otolith afferents in primates. Their results demonstrated that at 0.5 Hz, the regular and irregular afferents exhibited sensitivities of approximately 48 and 170 spikes/s/g, respectively. The regular afferents were found to be in phase with tangential acceleration, while the irregular afferents had a phase lead of approximately 26°. When they increased the stimulus frequency to 2.0 Hz, there was a minimal change in the behavior of the regular afferents, while the irregular afferents increased their sensitivity by about 65%. More recently, Goldberg and colleagues (11) have demonstrated that the irregular afferents from the utricle in the chinchilla exhibit a mean sensitivity of 255 spikes/s/g and a phase lead with respect to acceleration of 35° at 2.0 Hz. The most irregular afferents exhibited phase leads as great as 80°, and some of these units had sensitivities of up to 800 spikes/s/g with the same stimulus.

Our OT and CAOT neurons exhibited comparable sensitivities, but their phase behavior is incompatible with their receiving an essentially unmodified afferent input, as they were found to lag tangential acceleration slightly at 3.0 Hz. In addition, utricular afferents should exhibit very modest changes in sensitivity and phase behavior between 0.5 and 3.0 Hz, whereas all of our neurons had large changes. By comparison, our CAOT+ neurons exhibited a sensitivity of nearly 600 spikes/s/g at 0.5 Hz and a phase lag with respect to acceleration of 43°. The differences become even more pronounced during 3.0 Hz stimulation, as the sensitivity was found to increase to approximately 2200 spikes/s/g and the phase lag decreased to 9°. Obviously, considerable processing of the peripheral signal has occurred.

Involvement of these neurons in the tVOR may provide an explanation for their high sensitivity. During head rotations of the type used here, the axis of rotation is 23 cm in front of the otolith organs. When the target viewed is located at the axis of rotation, the aVOR and tVOR will act in opposite directions and with nearly equal gain (6,15). Since the PVP neurons responsible for the aVOR have a mean sensitivity of approximately 1 spike/s°/s, their peak modulation during an 0.5 Hz rotation with a peak velocity of 31°/s will be about 31 spikes/s. Thus, if the tVOR is to cancel the aVOR under these circumstances, the neurons responsible for the tVOR must also modulate at 31 spikes/s. Since the peak tangential acceleration is approximately 0.040 g, the required sensitivity of the neurons in question would be about 0.79 spikes/s/cm², a value very close to the one reported here. We do not mean to suggest that these cells might contact ocular motoneurons, but simply that the neurons that do supply the necessary signal to the motoneu-
rons should have a very high sensitivity. These neurons may represent an intermediate stage in the processing.

The potential difficulty arises from the fact that the tVOR neurons should encode head tangential velocity rather than tangential acceleration. Unfortunately, from our data, it is not immediately apparent whether the neurons are encoding acceleration or jerk, although it is certainly not tangential velocity. To be certain, it would be necessary to obtain gain and phase values at several different frequencies and head orientations. We lacked the appropriate equipment to do this. Certainly, there seem to be only small changes in sensitivity with respect to jerk between the 0.5 Hz and 3.0 Hz data, an observation that would be in keeping with the idea that these cells might encode jerk.

As alternative explanation for the frequency response characteristics of these neurons is that they might be simply carrying a high-pass filtered version of the signal supplied by the peripheral afferents. In this view, the responses at 3.0 Hz would represent the neuronal response in the filter pass band, whereas the response at 0.5 Hz would be the result of high-pass filtering. If this is the case, the otolith afferents supplying the input to these cells would likely be members of the regularly discharging group, as these afferents exhibit minimal phase leads at high frequencies (11). Certainly the phase and sensitivities of the cells, as well as their response during the cogwheeling that occurred during table resets, would argue in favor of the filter hypothesis.

The neurons underlying the tVOR must send a signal to the motoneurons that exhibits very similar dynamics to that seen in PVP neurons during rotational stimuli, since the plant is the same for both reflexes. PVP cells lead angular velocity by 10° to 15° (3,15). Therefore, one would predict that the otolith signal driving the tVOR should lead translational head velocity by 10° to 15°. Most of the CAOT and OT neurons reported here exhibit phase leads that are intermediate between the values reported for otolith afferents (10,11) and the angular signals seen on PVP cells. Given this observation, these neurons may represent an intermediate step between the otolith afferents and the integrated signal necessary for the motoneurons.

This suggestion is particularly attractive for the CAOT- neurons. These cells exhibited reduced modulation during off-axis rotations, as do PVP neurons (15). In addition, their otolith signals exhibited the largest phase lag with respect to acceleration of all the cell types we found. Our results demonstrate that the phase behavior of the otolith signal is very similar to the canal signal at 0.5 Hz (12° lead), and even at 3.0 Hz the responses led velocity by only 40°. These values are close to what would be required by neurons involved in the tVOR.

This suggestion can find additional support in another of our observations. The neurons reported here clearly respond far more vigorously to high frequency stimuli than to low. The compensatory eye movement that must be generated in response to a tilt is different from that required by a translation. It has been suggested that the otolith signals are filtered so that the low frequency components could be used to generate torsional compensation for tilts, whereas the high frequency components would be used to generate the horizontal (or vertical) compensatory eye movements for translation (29). Thus, one would predict that otolith signals destined for horizontal PVP and EHV neurons should exhibit reduced gain at low frequencies, as the horizontal PVP and EHV neurons are not involved in torsional eye movements. This is, of course, precisely what was found.

Another characteristic of the tVOR is that its gain is increased when fixating a target located close to the head. Thus, the otolith sensitivity of the premotor neurons needs to be a function of target distance. We have demonstrated that PVP and EHV neurons exhibit this property (15), however, the OT and CAOT neurons do not. Additional processing is required if they are to supply the otolith signal to the PVP and EHV neurons. In addition, neither the OT nor the CAOT neurons exhibit behavior that is a function of vergence angle. The source of this vergence-related signal remains a mystery.
REFERENCES


