Fastigial Nucleus Activity During Different Frequencies and Orientations of Vertical Vestibular Stimulation in the Monkey

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Siebold, C., J. F. Kleine, L. Glonti, T. Tchelidze, and U. Bütter. Fastigial nucleus activity during different frequencies and orientations of vertical vestibular stimulation in the monkey. J. Neurophysiol. 82: 34–41, 1999. Neurons in the rostral part of the fastigial nucleus (FN) respond to vestibular stimulation but are not related to eye movements. To understand the precise role of these vestibular-only neurons in the central processing of vestibular signals, unit activity in the FN of alert monkeys (Macaca mulatta) was recorded. To induce vestibular stimulation, the monkey was rotated sinusoidally around an earth-fixed horizontal axis at stimulus frequencies between 0.06 (±15°) and 1.4 Hz (±7.5°). During stimulation head orientation was changed continuously, allowing for roll, pitch, and intermediate planes of orientation. At a frequency of 0.6 Hz, 59% of the neurons had an optimal response orientation (ORO) and a null response (i.e., no modulation) 90° apart. The phase of neuronal response was constant except for a steep shift of 180° around the null response. This group I response is compatible with a semicircular canal input, canal convergence, or a single otolith input. Several other features indicated more complex responses, including spatiotemporal convergence (STC). 1) For 35% of the responses at 0.6 Hz, phase changes were gradual with different orientations. Fifteen percent of these had a null response (group II), and 20% showed only a minimal response but no null response (group III). The remaining responses (6%), classified as group IV, were characterized by a constant sensitivity at different orientations in most instances. 2) For the vast majority of neurons, the stimulus frequency determined the response group, i.e., an individual neuron could show a group I response at one frequency and a group II (III or IV) response at another frequency. 3) ORO changed with frequency by >45° for 44% of the neurons. 4) Although phase changes at different frequencies were close to head velocity (±45°) or head position (±45°) for most neurons, they exceeded 90° for 29% of the neurons between 0.1 and 1.0 Hz. In most cases, this was a phase advance. The change in sensitivity with change in frequency showed a similar pattern for all neurons; the average sensitivity increased from 1.24 imp · s⁻¹ · deg⁻¹ at 0.1 Hz to 2.97 imp · s⁻¹ · deg⁻¹ at 1.0 Hz. These data demonstrate that only an analysis based on measurements at different frequencies and orientations reveals a number of complex features. They moreover suggest that for the vast majority of neurons several sources of canal and otolith information interact at this central stage of vestibular information processing.

INTRODUCTION

The fastigial nucleus (FN), the most medial deep cerebellar nucleus, plays an important role in the processing of vestibular information. Anatomically it receives a strong direct input via mossy fiber collaterals from the vestibular nuclei (Noda et al. 1990). The axons of these mossy fibers project to the vermis, mainly to the anterior part (lobulus I–V) (Kotchabhakdi and Walberg 1978; Voogd et al. 1996). In turn the Purkinje cells (PCs) of the anterior vermis send efferents to the FN (Armstrong and Schild 1978). Finally, the efferents of the FN project back to the vestibular nuclei (Noda et al. 1990).

Functionally the FN has been divided into a rostral and a caudal part (Bütter et al. 1991; Noda et al. 1990). The caudal part has also been labeled fastigial oculomotor region (FOR) (Noda et al. 1990) because many of its neurons are modulated during either saccadic (Fuchs et al. 1993; Helmchen et al. 1994) or smooth pursuit eye movements, including the interaction of smooth pursuit and vestibular stimuli (Bütter et al. 1991). In contrast, the rostral FN contains neurons that are modulated during vestibular stimulation; they show no eye-movement- or eye-position-related sensitivity (Bütter et al. 1991; Gardner and Fuchs 1975; Siebold et al. 1997). They therefore have been called “vestibular-only” neurons and are believed to participate in the control of spinal mechanisms (neck, gait, posture).

The precise functional role of these vestibular-only neurons is not known. Previous studies have shown that vestibular-only neurons in FN respond to vestibular stimulation in both the horizontal and vertical planes (Gardner and Fuchs 1975; Siebold et al. 1997). As regards vertical stimulation, neurons reach their optimal modulation when orientated along the rotation axis (also called response vector orientation, RVO) (Goldberg and Fernandez 1984) not only for vertical canal planes, i.e., in the right anterior-left posterior (RALP) or left anterior-right posterior (LARP) plane, but also during roll and pitch stimulation, which indicates canal convergence (Siebold et al. 1997). Based on their response to static tilt and their phase relation during sinusoidal stimulation, >20% of the neurons that responded to vertical vestibular stimulation were classified as receiving an otolith input (Siebold et al. 1997). However, these responses were only determined at one frequency (0.6 Hz). The percentage of neurons receiving an otolith input might actually be higher because otolith-related neurons in the vestibular nuclei may have frequency-related phase changes of >180° (Schor et al. 1984). Thus a phase related to the stimulus velocity of the neuronal activity does not exclude an otolith-related input.

Three different groups of neurons have been distinguished in the vestibular nuclei of the decerebrate cat based on their phase and gain characteristics: vertical canal, otolith, and otolith plus canal-related neurons (Kasper et al. 1988). The convergence of canal and otolith inputs also has been found to lead to more complex response patterns (spatiotemporal convergence, STC), which occur when inputs have a different phase behav-
ior and different response orientations (Angelaki et al. 1992; Baker et al. 1984b).

To evaluate the possible functional role of vestibular-only neurons in FN, particularly in comparison with vestibular nuclei neurons (Kasper et al. 1988) and vestibular nerve afferents (Goldberg and Fernandez 1984), it is important to know their response characteristics at different stimulus frequencies and orientations. These responses were examined in the alert monkey during vertical stimulation around an earth-fixed horizontal axis. Some preliminary results have been published elsewhere (Büttner et al. 1999).

METHODS

Three monkeys (Macaca mulatta, 4–5 kg) were prepared for chronic single-unit recordings. Under general anesthesia and aseptic conditions, a chamber for single-unit recordings was implanted (coordinates: mediolateral 0 mm, posterior 6 mm) to allow a vertical approach in the stereotactic plane of FN on both sides. Bolts were attached to the skull to maintain a stable head position during the experiments (for details, see Boyle et al. 1985). Before surgery monkeys were familiarized with the experimental environment and trained to sit in a primate chair. Single-unit activity was recorded with varnished tungsten microelectrodes (impedance 2.5–4 MΩ) and horizontal, vertical, and torsional eye position with a dual search-coil system (for techniques and calibration, see Bartl et al. 1996). During the experiment, the head was immobilized by a head holder so that the monkey sat with its head erect (stereotaxic horizontal) in a primate chair. In this head position, the horizontal semicircular canals are tilted 15° upward from the optimal orientation for yaw stimulation.

Definitions and coordinates

Directions are expressed in a head-fixed, right-handed Cartesian system with positive values for leftward movements around the z axis (yaw), downward movements around the y axis (pitch), and right-ear-down movements around the x axis (roll).

Vestibular stimulation

For vertical vestibular stimulation, the monkey was rotated sinusoidally around an earth-fixed horizontal axis at amplitudes up to ±20°. The following stimulus protocol was applied. First, the optimal neuronal response (optimal response orientation, ORO) was determined at 0.6 Hz (±15°). An independent motor rotated the monkey on the turntable at a low speed (0.36–2.2°/s) to different orientations over a range of 180° including roll (β = ±90°), pitch (β = 0°), RALP (β = ±45°) and LARP (β = −45°) stimulation (Fig. 1). After this rotation, neurons were investigated at different frequencies between 0.06 (±15°) and 1.4 Hz (±7.5°), usually including 0.1, 0.2, 0.4, 0.8, 1.0, and 1.2 Hz. At each frequency, the ORO also was determined by continuously changing the head orientation at low speed. For some neurons, different frequencies were investigated only at the ORO obtained at 0.6 Hz. With this stimulus protocol, the applied velocities ranged from 5.6 to 66°/s. The maximal acceleration was 580°/s² and occurred at 1.4 Hz.

Data analysis

All data (single-unit activity, eye position, vestibular stimuli) were stored on an FM magnetic tape recorder (TEAC XR310) for further analysis. Signals were digitized with real-time occurrence for neuronal activity and at a sampling rate of 200 Hz for the other channels. When head orientation remained constant, 5–15 cycles were averaged at different stimulus frequencies. During continuously changing head orientation, one to seven cycles (0.06–1.4 Hz) corresponding to a 12–15° sector were averaged. This yielded 12–15 phase and sensitivity values for the 180° range of orientations that were assigned to the centers of the respective sectors. Averaged neuronal activity was fitted by a least-square best-sine function. Silencing of neurons (“cutoff”) during part of the stimulation was taken into account by introducing a weighting factor W (W = 1 for the episode with neuronal activity and W = 0 for the cutoff). Thus assuming that the modulation of the neuronal activity had the same frequency as the sinusoidal vestibular stimulation, the least-square best-sine function was defined by the neuronal activity above threshold. Sensitivity (imp · s⁻¹ · deg⁻¹) and phase were determined in relation to head position. A response was assumed when neuronal modulation exceeded 0.5 imp · s⁻¹ · deg⁻¹ (sensitivity criterion). Positive phase values indicate that neuronal activity leads head position. The phase behavior of an individual neuron in relation to the vertical stimulation was attributed to head velocity or head position for phase values ±45° around head velocity respectively position. Only neurons with phase changes exceeding 90° were attributed to a third class.

At selected recording sites small electrolytic lesions (30–100 μA of DC anodal current for 20–30 s) or tracer substances [i.e., Di I (Snodderly and Gur 1995), nontoxic cholera toxin subunit B] were placed to aid the reconstruction of electrode tracks. At the end of all experiments, the monkeys were deeply anesthetized with barbiturate and perfused transcardially with 10% formalin. The brain was removed and blocked in the stereotactic plane. Coronal sections, taken every 50 μm, were processed for the tract-tracing substances and counterstained with cresyl violet.

RESULTS

General characteristics

The data presented in this paper are based on a quantitative analysis of 89 neurons in three monkeys. All neurons re-
sponded to sinusoidal vertical vestibular stimulation around an earth-fixed horizontal axis and were located in the rostral FN of both sides by means of histological reconstructions. Activity in FN was generally easy to identify. In the applied approach, the electrode passed initially through layers of Purkinje cells, which could be recognized by the presence of complex spikes. Immediately dorsal to FN, the electrode passed through white matter. No neurons were isolated here, indicating that the electrodes used were unsuitable for fiber recordings. The presence of activity related to saccadic and smooth pursuit eye movements in caudal, but not in rostral FN, allowed a functional separation of both structures. Neurons were investigated at a minimum of two frequencies. The general characteristics of the neurons presented here were comparable with those in our previous study (Siebold et al. 1997). All neurons responded only to vestibular stimulation; they were not modulated during saccadic or smooth pursuit eye movements. Neurons responded in only one stimulus direction. Neurons responding in both stimulus directions (type III responses) (Duensing and Schaefer 1958) were not observed. The neurons were spontaneously active (average 62 imp/s, range 18–108 imp/s) with an irregular firing rate. The coefficient of variation of the inter-spike intervals was determined for 10 arbitrarily chosen neurons. It ranged from 0.34 to 1.50 (0.65 ± 0.39; mean ± SD). The level of alertness as judged by the eye movements did not affect the response of the neurons. Waxing and waning (periods of no response during vestibular stimulation), which were described for vestibular responses in the oculomotor vermis (Suzuki and Keller 1988), were generally not observed.

As described in our previous paper (Siebold et al. 1997), all neurons (n = 89) investigated were modulated at 0.6 Hz (±15°) vertical vestibular stimulation around an earth-fixed horizontal axis. For all neurons, the orientation of the head was varied continuously over a range of 180° from roll (β = −90°) through pitch (β = 0°) to roll (β = +90°). These changes of orientation during the vertical stimulation systematically altered the modulation of the neuronal response (Fig. 1).

The changes of modulation were fitted by a cosine function for 84 (of 89) neurons. All these neurons had either a null response or a minimal modulation at a given orientation and an optimal modulation (ORO) at an orientation 90° apart. According to their response characteristics, neurons were assigned to one of the following three response groups. Neurons with a group I response had a null response, and their phase was constant at all orientations except for a steep phase reversal of 180° around the null response (Fig. 2, A–D). Thus a clear response vector orientation (RVO) could be determined for these neurons (Baker et al. 1984a). Fifty-nine percent of the neurons in our study belonged to group I at 0.6 Hz.

Neurons with group II responses also had an optimal response and a null response (not illustrated). However, their phase changes around the null response were more gradual and extended over a range of ±70°. Often phase changes were continuous over the whole range of orientations. Group II responses were encountered in 15% of the neurons at 0.6 Hz.

Neurons with group III responses did not show a null response, i.e., they were modulated at all orientations. However, they had an optimal response (ORO) and a minimal response, which occurred 90° away from the ORO (Fig. 2F). The minimal response sensitivity was on the average 31% (range 13–56%) of the optimal response. Total phase changes were 180° for 180° changes in orientation. The phase changes of 50% of the group III responses were steeper around the minimal response, whereas they were continuous and lacked a steeper phase change for the other 50% (Fig. 2F). Group III responses were seen in 20% of the neurons at 0.6 Hz.

ORO is used here as a general term for optimal responses of groups I–III. Because the term RVO is established in the literature to signify group I responses only (Baker et al. 1984a), it is not used here.

For the few neurons remaining (5 of 89), these rules did not apply, and they accordingly were classified as group IV. The sensitivity was constant for three neurons that lacked an ORO and a minimal response; their phase changed continuously with orientation. The response could not be further classified for the other two neurons.

**ORO at different frequencies**

The responses of 41 neurons were investigated at different frequencies (0.06–1.4 Hz) and orientations. At a given frequency, orientation was altered continuously from $\beta = -90°$ to $\beta = +90°$. This continuous change of orientation was carried out in 235 instances. Twenty-three of (41) neurons were examined at six to nine frequencies, including low ($\leq 0.2$ Hz) and high frequencies ($\geq 1.0$ Hz). Neurons responded at all frequencies with the exception of seven neurons (of 30 investigated), which were not modulated at 0.06 and/or 0.1 Hz.

Group I responses were encountered at all frequencies. They amounted to 60% of the total responses (140 of 235 investigations). Group II responses were also found at all frequencies and were observed in 22% of all investigations (51 of 235). Group III responses were only rarely encountered at low frequencies (≤5% of the low-frequency investigations). Thirteen percent of the responses for all frequencies and neurons were group III responses.

Five percent of the responses (13 of 235) were classified as group IV. They were encountered in 12 of 41 neurons. Thus group IV responses rarely occurred at different frequencies for a given neuron. For the vast majority of neurons, the responses could be attributed to groups I, II, or III, which were found at all frequencies. Six (of 41) neurons consistently exhibited only group I responses and 3 (of 41) only group II and/or group III responses at all frequencies. The remaining neurons exhibited a combination of responses depending on the stimulus frequency. Because a clear optimum and minimum could be determined for all responses except the small number of group IV responses, the ORO was taken as the indicator for neuronal behavior at different frequencies.

For the majority of neurons (23 of 41), frequency had little effect on ORO, i.e., the ORO varied by <45° (Table 1, Figs. 3A and 4A). The remaining neurons had larger ORO changes, often exceeding 90° (Table 1, Figs. 3B and 4B). For instance, the neuron in Fig. 4B had an ORO with RALP at 0.2 Hz and an ORO with LARP stimulation at 1.2 Hz.

**Effect of stimulus frequency on phase and sensitivity at the response orientation (ORO)**

For most of the 23 neurons with stable OROs, the phase was close to head velocity (Table 1, Fig. 4A). For these neurons, phase advanced on the average from 75° at 0.1 Hz to 106° at
1 Hz. Neurons with head position-related phase changes were generally rare. Phase changes exceeding 90° were more common for neurons with ORO changes >45° (Table 1, Fig. 4B). If all neurons (n = 41) were considered, there was a weak tendency for neurons with larger ORO changes to also have larger phase changes (correlation coefficient $r = 0.48$, $P = 0.0014$). Phase changes exceeding 90° between 0.1 and 1.0 Hz meant that a head position and a head velocity-related phase could easily occur for individual neurons depending on the stimulus frequency. Group I responses also tended to be more common among neurons with stable OROs than among those with ORO changes >45° (Table 1).

The sensitivity of the ORO was remarkably uniform for the different subgroups (Table 1). It increased, on average, for all neurons (n = 41) from 1.24 imp·s$^{-1}$·deg$^{-1}$ at 0.1 Hz to 2.97 imp·s$^{-1}$·deg$^{-1}$ at 1.0 Hz. There were only four neurons with an 8- to 9-fold increase of sensitivity, which is still less than the 10-fold increase expected for a relationship encoding velocity. A 10-fold increase in sensitivity to position (imp·s$^{-1}$·deg$^{-1}$) manifests itself as a stable sensitivity to velocity (imp·s$^{-1}$/deg·s$^{-1}$).

**Responses at different frequencies and the ORO at 0.6 Hz**

For 89 neurons the ORO was initially determined at 0.6 Hz. Then the neurons were examined at this orientation at different frequencies (0.06–1.4 Hz). This protocol included the 41 neurons described above. Of the 89 neurons, 70 were tested at three or more frequencies, including ≤0.2 and ≥1 Hz and used for further analysis. Sixty-four neurons were tested at ≤5 frequencies. Neurons were divided into three groups according to their dominant phase behavior: neurons with a head velocity-related response over the whole frequency range, neurons with a head position-related response, and neurons with phase changes >90°.

**Head velocity-related neurons**

The largest group of neurons (32 of 70, 46%) encoded head velocity over the whole frequency range (Figs. 5A and 6). On the average they showed a slight phase advance with increasing frequency. Whereas neurons generally lagged behind head velocity by 20–30° at frequencies <0.4 Hz, there was a phase advance of 10–20° at frequencies >0.4 Hz (Fig. 6). Sensitivity
was low at 0.1 Hz (average 1.11 imp \( \cdot \) s\(^{-1} \cdot \) deg\(^{-1} \)) and increased to 3.45 imp \( \cdot \) s\(^{-1} \cdot \) deg\(^{-1} \) (average) at 1.0 Hz (Fig. 6).

**Head position-related neurons**

The smallest group of neurons (11 of 70, 16%) had a phase close to head position over the whole frequency range (Fig. 6). Phase lagged slightly on the average with increasing frequency; it exhibited a small lead at 0.06 Hz and a lag of 20–30° at frequencies 0.1 Hz (Fig. 6). Sensitivity on average did not differ from that of the velocity-related neurons (Fig. 6), with a value of 0.87 imp \( \cdot \) s\(^{-1} \cdot \) deg\(^{-1} \) at 0.1 Hz and 3.75 imp \( \cdot \) s\(^{-1} \cdot \) deg\(^{-1} \) at 1.0 Hz.

**Neurons with larger phase changes**

Twenty-seven neurons (of 70, 39%) had phase changes of more than 90° between 0.1 and 1.0 Hz (Figs. 5B and 6). This was in most instances \( (n = 21) \) an increasing phase lead, which exceeded 150° for 11 (of 21) neurons and on the average was >120° (Fig. 6). The sensitivity increased with frequency from 1.29 imp \( \cdot \) s\(^{-1} \cdot \) deg\(^{-1} \) at 0.1 Hz to 2.82 imp \( \cdot \) s\(^{-1} \cdot \) deg\(^{-1} \) at 1.0 Hz.

**DISCUSSION**

**General considerations**

This analysis of orientation and frequency of a large sample of vestibular neurons in the FN of an alert animal has shown that spatiotemporal convergence (STC) is quite common among vestibular-only neurons. Despite the irregular firing rate of FN neurons, it was possible to clearly attribute the responses to one of four different groups. Although group I responses were clearly the most common type of response at all frequencies, neurons with group I responses at all frequencies accounted for only 15% of the total neurons. All other neurons were

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**TABLE 1. Effect of stimulus frequency**

<table>
<thead>
<tr>
<th>ORO changes with frequency</th>
<th>&lt;45°</th>
<th>45–90°</th>
<th>&gt;90°</th>
</tr>
</thead>
<tbody>
<tr>
<td>( n )</td>
<td>23</td>
<td>11</td>
<td>7</td>
</tr>
<tr>
<td>Sensitivity (imp ( \cdot ) s(^{-1} \cdot ) deg(^{-1} )) 0.1 Hz</td>
<td>1.51</td>
<td>0.96</td>
<td>1.32</td>
</tr>
<tr>
<td>Average</td>
<td>0.67–2.51</td>
<td>&lt;0.5–2.10</td>
<td>0.98–1.76</td>
</tr>
<tr>
<td>Range</td>
<td>3.29</td>
<td>2.24</td>
<td>3.15</td>
</tr>
<tr>
<td>Head velocity</td>
<td>1.34–7.99</td>
<td>1.01–4.91</td>
<td>1.49–4.86</td>
</tr>
<tr>
<td>Phase changes with frequency</td>
<td>( n )</td>
<td>19</td>
<td>5</td>
</tr>
<tr>
<td>Head position</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>&gt;90 deg ( n )</td>
<td>2</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Group I responses, %</td>
<td>63</td>
<td>56</td>
<td>45</td>
</tr>
<tr>
<td>Group II/III responses, %</td>
<td>37</td>
<td>44</td>
<td>55</td>
</tr>
</tbody>
</table>

The effect of stimulus frequency on changes of response orientation (ORO), sensitivity, phase, and the prevalence of group I and II/III responses. Group I: response with null response and constant phase at different orientations; group II: null response and continuous phase changes; group III: continuous modulation (null response absent) and continuous phase changes. The distribution of 41 neurons is shown. \( n \), number of neurons.
exhibited a combination of group I, II, III, or IV responses, depending on the stimulus frequency, which indicates STC. A single otolith or canal/canal input predicts that the ORO will be stable at different frequencies. Although this was found in nearly 60% of the neurons, the remaining neurons had ORO changes that increased with stimulus frequency. In many instances they exceeded 90°, again indicating STC. When tested at a single frequency, the responses of most neurons could be attributed to a canal or otolith input. However, when investigated at various frequencies, the factors discussed above [group II–IV responses; different groups (I–IV) at different frequencies for a given neuron; and changes of ORO with stimulus frequency] show quite clearly, that there are probably only a few, if any, neurons that reflect only an otolith or a canal input.

In view of the large variation of phases and OROs with regard to stimulus frequency, it is remarkable that sensitivity was rather uniform in relation to stimulus frequency. The sensitivity of nearly all neurons increased with stimulus frequency by 2.5-fold on the average. Thus the sensitivity for 2 neurons (A and B) at different stimulus frequencies. For the neuron in A, the ORO is at all frequencies close to roll and the phase changes are moderate. In B, the ORO changes exceed 120°, and the phase changes are pronounced. For both neurons, there is a moderate sensitivity increase with increasing stimulus frequency.

Comparison with vestibular nuclei neurons and neurons in cerebellar structures

In their investigation of nuclei neurons in the alert cat Baker et al. (1984a,b) showed that about one-third of the neurons had response characteristics indicating STC. Thus the signs of STC found for vestibular neurons in FN already are present in the vestibular nuclei. This has also been shown recently for the monkey (Yakushin et al. 1999).

STC seems to be less common in the decerebrate cat (<10% of the neurons examined) (Kasper et al. 1988; Wilson et al. 1996). Another study found similar results with little evidence of STC in the decerebrate and the alert cat (Iwamoto et al. 1996). However, only one stimulus frequency (0.5 Hz) was applied in the study. As our present results demonstrate, this is insufficient to exclude STC.

Neurons were examined in the decerebrate cat at different frequencies and attributed to a canal, otolith, and canal plus otolith group based on their phase and sensitivity behavior (Kasper et al. 1988; Wilson et al. 1996). Our data do not permit such a distinction for vestibular-only neurons in the FN. Neurons with a phase related to head velocity (presumably receiving a canal input) should have a sensitivity quite distinct from those neurons with a phase related to position (assumed to receive an otolith input); however, this was generally not found for FN neurons. As mentioned in the preceding text, the sensitivity increase was independent of the phase behavior.

STC of Purkinje cells in the anterior vermis recently has been investigated in the decerebrate cat (Pompeiano et al. 1997). As in our study of the FN, neurons in the anterior vermis had a broad distribution of response vector orientations in response to vertical vestibular stimulation. Although only one stimulus frequency was applied, >70% of the neurons had signs of STC (broadly tuned bidirectional and unidirectional neurons). Purkinje cells in the cerebellar cortex and the deep cerebellar nuclei are known to have an irregular firing rate, which also is seen for the vestibular neurons described here. Also with regard to vestibular functions it is not well understood which information is reflected in the irregularity of the activity pattern.

Functional considerations

Spatiotemporal convergence can be achieved by combining two inputs with a different phase and different spatial orientation. Generally this is assumed for canal-otolith convergence, but it certainly also can occur for otolith-otolith interaction. At a given frequency, the behavior of many of our neurons can be modeled by assuming linear summation of signals from two cosine tuned neurons (Kleine, unpublished results). However, it often seems impossible to simply assume a canal-otolith interaction. With such an approach neuronal responses would be dominated in the low frequency range by an otolith-related and in the high-frequency range by a canal-related input. Evidence for this has been found in the vestibular nuclei (Baker et al. 1984b). Group I responses and a phase related to
head position should dominate at low frequencies, whereas signals should be related to head velocity at high frequencies. Group II–IV responses should occur mainly in the mid-frequency range. We generally did not find such a clear separation.

We also hardly encountered any neurons for which the phase and sensitivity relationships allowed the classification of a simple canal- or otolith-related neuron. In a previous study, we showed (Siebold et al. 1997) that some FN neurons respond to static tilt and thus prove otolith-related input. For most of these neurons, dynamic sensitivity was higher than static sensitivity. Thus, given our limited stimulus range, an absence of static sensitivity does not rule out an otolith input (Siebold et al. 1997).

The interaction of two signals allows for the shift of the ORO over a certain range of orientations. However, we encountered a number of neurons in which the ORO changes clearly exceeded 90°. These neurons also tended to have phase changes of >90°. Further investigations are needed to determine whether these large changes still can be achieved by a linear combination of only two inputs if realistic assumptions are made as to the frequency dependence of the converging signals.

All evidence supports the view that neurons in the rostral FN are involved in vestibulospinal mechanisms. Unilateral lesions produce a tendency to fall to the ipsilateral side (Kurzan et al. 1993; Pélisson et al. 1998). FN neurons project to the vestibular nuclei (Homma et al. 1995; Noda et al. 1990) and in addition back to the cerebellar cortex (Batini et al. 1989). It could be demonstrated that muscimol microinjections into the anterior vermis alter the gain and spatiotemporal properties of vestibulospinal reflexes (Manzoni et al. 1997). It is quite possible that FN neurons interfere with vestibulospinal reflexes in the skeletomotor system in a similar way. In this context, it is of interest that the anterior cerebellar vermis sends efferents both directly and indirectly via the FN to the vestibular nuclei (Corvaja and Pompeiano 1979; Voogd 1989; Voogd et al. 1991). It will be a challenge for further investigations to determine how these direct and indirect pathways from the anterior vermis to the vestibular nuclei differ functionally.

With regard to the transformation of sensory inputs to motor performance in three-dimensional space, it becomes increasingly clear that these relations appear to be far more complex in the skeletomotor system (Georgopoulos et al. 1988) than in the oculomotor system (Graf et al. 1993). Our results moreover suggest that the temporal sequence of events also might be an important factor for determining the neuronal response patterns. They also clearly demonstrate that such a complex response as STC often can be revealed only by a detailed investigation using different frequencies and orientations, whereas the use of a single stimulus frequency would suggest a simple canal- or otolith-related input for a large majority of neurons. The responses of many neurons cannot be attributed to a certain response orientation (ORO) because it varies with stimulus frequency. Similarly, phases can change over a narrow frequency range by >90°. This indicates central process-
FASTIGIAL ACTIVITY DURING VESTIBULAR STIMULATION


