Spatiotemporal Processing of Linear Acceleration: Primary Afferent and Central Vestibular Neuron Responses

DORA E. ANGELAKI AND J. DAVID DICKMAN
Department of Neurobiology, Washington University School of Medicine; and Department of Research, Central Institute for the Deaf, St. Louis, Missouri 63110

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Angelaki, Dora E. and J. David Dickman. Spatiotemporal processing of linear acceleration: primary afferent and central vestibular neuron responses. J Neurophysiol 84: 2113–2132, 2000. Spatiotemporal convergence and two-dimensional (2-D) neural tuning have been proposed as a major neural mechanism in the signal processing of linear acceleration. To examine this hypothesis, we studied the firing properties of primary otolith afferents and central otolitheurons that respond exclusively to horizontal linear accelerations of the head (0.16–10 Hz) in alert rhesus monkeys. Unlike primary afferents, the majority of central otolitheurons exhibited 2-D spatial tuning to linear acceleration. As a result, central otolithe dynamics vary as a function of movement direction. During movement along the maximum sensitivity direction, the dynamics of all central otolitheurons differed significantly from those observed for the primary afferent population. Specifically at low frequencies (∼0.5 Hz), the firing rate of the majority of central otolitheurons peaked in phase with linear velocity, in contrast to primary afferents that peaked in phase with linear acceleration. At least three different groups of central response dynamics were described according to the properties observed for motion along the maximum sensitivity direction. “High-pass” neurons exhibited increasing gains and phase values as a function of frequency. “Flat” neurons were characterized by relatively flat gains and constant phase lags (∼20–55°). A few neurons (“low-pass”) were characterized by decreasing gain and phase as a function of frequency. The response dynamics of central otolitheurons suggest that the ∼90° phase lags observed at low frequencies are not the result of a neural integration but rather the effect of nonminimum phase behavior, which could arise at least partly through spatiotemporal convergence. Neither afferent nor central otolitheurons discriminated between gravitational and inertial components of linear acceleration. Thus response sensitivity was indistinguishable during 0.5-Hz pitch oscillations and fore-aft movements. The fact that otolithe-only central neurons with “high-pass” filter properties exhibit semicircular canal-like dynamics during head tilts might have important consequences for the conclusions of previous studies of sensory convergence and sensorimotor transformations in central vestibular neurons.

INTRODUCTION

As we move our head in the world, we experience both gravitational and translational accelerations. Both acceleration components are sensed by primary otolithe afferents that innervate the utricular and saccular maculae. These linear acceleration signals are transmitted to the CNS, primarily to the vestibular nuclei and vestibulo-cerebellum. Otolithe signals related to changes of the head relative to gravity or translatory head movements have been shown to be critical for the control of the eyes, head, body, and limb movements (Ikegami et al. 1994; Lacour et al. 1987; Lacquaniti et al. 1984; Pozzo et al. 1990; Watt 1976; Wilson and Schor 1999) as well as for perceptual orientation responses (Clark and Graybiel 1964, 1966; Glasauer 1995; Schone and Lechner-Steinleitner 1978; Seidman et al. 1998; Stockwell and Guedry 1970). More recently, head tilt signals have also been shown to be important for the autonomic control of the respiratory and cardiovascular systems (Uchino et al. 1970; Yates 1992; Yates and Miller 1994; Yates et al. 1999).

One of the most challenging aspects in understanding the function of the otolithe system is determining the nature of central processing of gravitational and translational accelerations. Even though this has never been directly investigated, it is generally thought that primary otolithe afferents respond similarly to both head tilts relative to gravity and to translational movements (Dickman et al. 1991; Fernandez and Goldberg 1972, 1976a; Loe et al. 1973; Si et al. 1997). Despite indiscriminate primary otolithe afferent information, eye movement responses to head tilts and translations have been shown to be different (Angelaki et al. 1999a). How and where the discrimination between gravitational and translational components of acceleration takes place remains illusive (Angelaki et al. 1999a; Glasauer and Merfeld 1997; Guedry 1974; Mayne 1974; Merfeld 1995; Merfeld et al. 1999a; Paige and Tomko 1991; Telford et al. 1997; Young 1974).

Despite the diverse functional demands of the otolithe system, primary otolithe afferents exhibit relatively stereotypic responses, demonstrating dynamic properties consistent with encoding of linear accelerations over a broad frequency range (Dickman et al. 1991; Fernandez and Goldberg 1976a–c; Fernandez et al. 1972; Goldberg et al. 1990; Loe et al. 1973; Si et al. 1997; Tomko et al. 1981). Afferent response dynamics have been shown to vary across a continuum from purely tonic to phasic-tonic (regularly and irregularly discharging afferents, respectively) with a phase distribution in squirrel monkeys that reflects small phase lags or leads relative to linear acceleration (Fernandez and Goldberg 1976c). The functional correlate of the characteristic distribution of response dynamics has been a matter of speculation in recent years. For example, the diversity in vestibular afferent dynamics

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has been suggested to be related to different roles in vestibulo-ocular versus vestibulo-spinal systems (Boyle et al. 1992; Highstein et al. 1987; Minor and Goldberg 1991), constant velocity rotations (Angelaki and Perachio 1993; Angelaki et al. 1992b, 2000a) and viewing distance-dependence changes of the rotational VOR (Chen-Huang and McCrea 1998). Different roles of tonic and phasic-af-ferent afferents have also been proposed for VOR adaptation and recovery after lesions (Lasker et al. 1999; Lisperger and Pavelko 1988; Minor et al. 1999). An involvement of irregularly firing otolith afferents in producing the viewing distance dependence and dynamics of the translational VOR has been suggested from reversible ablation studies (Angelaki et al. 2000a).

The diversity in response dynamics of the otolith afferent population, in particular, has also been proposed to facilitate spatiotemporal processing of sensory information. Spatiotemporal convergence (STC) between primary otolith afferents that differ in both their spatial and temporal response properties represents a means of spatiotemporal filtering. Thus STC may be an alternative to distinct spatial and temporal channels of information in the central otolith system (Angelaki 1993a). Even the simplest form of a linear, spatiotemporal summation of otolith afferents could result in central neurons with different dynamic properties that might be dependent on movement direction (Angelaki 1992, 1993a,b). Since primary otolith af- ferents differ in their polarization vector direction, as well as response dynamics (Fernandez and Goldberg 1976a–c; Fernan-dez et al. 1972; Loe et al. 1973; Si et al. 1997), spatiotem- poral convergence might be the rule rather than the exception in the central otolith system. In fact, evidence of spatiotem- poral processing of otolith signals in the majority (78%) of vestibular nuclei neurons of decerebrate rats has been previ- ously reported (Angelaki et al. 1993; Bush et al. 1993).

The implications of spatiotemporal processing of linear ac- celeration have remained unexplored, largely due to the lack of direct evidence regarding the presence of two-dimensional (2-D) spatial tuning in the otolith system of alert animals. Furthermore because of the diverse motor correlates of the otolith system, it is possible that distinct populations of re- sponse dynamics should exist centrally, with neurons exhibiting high-, low-, or band-pass filter properties. The present study was undertaken to directly investigate the spatiotemporal properties of central otolith neurons in the vestibular nuclei of alert rhesus monkeys. Specifically, we investigated the follow- ing questions: first, do central otolith neurons exhibit 2-D tuning to linear acceleration? Second, are the dynamics of central otolith neurons different from those of the afferent population and are they suggestive of a central integration of linear acceleration? Finally, the ability of afferent and central neurons to discriminate between different sources of linear acceleration was also directly investigated here by comparing neural responses during sinusoidal pitch oscillations and fore- aft displacements. The data confirm the commonly used as- sumption that neither primary otolith afferents nor central-o tolith-only neurons can discriminate tilt from translation.

**Methods**

**Animals**

Four juvenile rhesus monkeys were chronically implanted with a circular molded, lightweight dental acrylic ring that was anchored by stainless steel inverted T-bolts secured under the skull. For single unit recordings from the vestibular nerve (3 of the animals) and the vestibular nuclei (3 of the animals), a platform (3 × 3 × 0.5 cm) constructed of plastic delrin was stereotaxically secured to the skull and fitted inside the head ring. The platform had staggered rows of holes (spaced 0.8 mm apart) that extended from the midline to the area overlying the vestibular nerves bilaterally. In separate surgeries, all animals were also implanted with dual eye coils on both eyes (cf. Angelaki 1998; Angelaki et al. 2000a,b). Eye coils were calibrated both prior to implantation and daily during experiments, as explained in detail elsewhere (Angelaki 1998; Angelaki et al. 2000b). Subse- quent to the eye coil surgeries, animals were sufficiently trained to fixate visual targets. Next labyrinthe stimulating electrodes were implanted in both ears of one of the animals to be used for vestibular nuclei neuron recordings (c.f., Angelaki et al. 2000a). All surgical procedures were performed under sterile conditions in accordance to institutional and National Institutes of Health guidelines.

**Experimental set-up and protocols**

During experiments, the monkeys were seated in a primate chair with their heads statically positioned 18° nose-down, which aligned the major plane of the utricle and horizontal canals with an earth-horizontal plane. The animal’s body was secured with shoulder and lap belts, while the extremities were loosely tied to the chair. The primate chair was then secured inside the inner frame of a vestibular turntable consisting of a three-dimensional (3-D) rotator on top of a 2-m linear sled (Acutronics). For each recording session, the eight voltage signals of the two eye-coil assemblies, the three output signals of a 3-D linear acceler- ometer (mounted on fiberglass members that firmly attached the animal’s head ring to the inner gimbal of the rotator), as well as velocity and position feedback signals from the linear sled and/or rotator were low-pass filtered (200 Hz, 6-pole Bessel), digitized at a rate of 833.33 Hz (Cambridge Electronics Design, model 1401, 16-bit resolution), and stored on a PC for off-line analysis.

Extracellular recordings from single primary otolith afferents or vestibular nuclei neurons were obtained with epoxy-coated, etched tungsten microelectrodes that were inserted into the brain through a 26-gauge stainless steel guide tube (457 µm OD). Electrodes were inserted into guide tubes, then advanced through a predrilled hole in the recording platform and manipulated vertically with a remote- control mechanical microdrive. After neural activity was amplified and filtered (300 Hz to 6 kHz), it was directed to an audiomonitor as well as passed through a BAK Instruments dual time-amplitude window discriminator whose output was displayed on an oscilloscope. For each recorded cell, acceptance pulses from the BAK window discriminator were used to trigger the event channel of a Cambridge Electronics Design (model 1401) data-acquisition system, which stored the time of the spike at a 10-µs resolution. Both stimulus presentation and recording protocols were computer-controlled with the CED using scripts written for the Spike2 software environment.

**Vestibular nuclei neuron recordings**

Initial experiments in each animal were performed to identify the abducens nuclei based on the characteristic burst-tonic activity of motoneurons (Fuchs and Luschei 1970). Subsequent penetrations explored an area that extended 0.8–4 mm lateral and 0.0–3 mm posterior to the abducens nucleus. Recordings were concentrated in rostral areas of the vestibular nuclei, mainly in the rostral portions of the medial subdivision and around the ventral lateral vestibular nucleus. All neurons reported here were recorded either in the same penetrations as eye-movement-related cells or within an area extend- ing no more than 1.6 mm lateral or posterior from penetrations where eye-movement-sensitive cells were recorded. No electrode tracks were identified in the caudal medial or descending vestibular nuclei.
In the animal that was implanted with bilateral labyrinthine stimulating electrodes, the location of the vestibular nuclei was also guided by vestibular field potentials evoked with electrical stimulation of the ipsilateral vestibular nerve (0.1-ms monophasic pulses, 50–400 μA).

A few cells in this animal were also tested for mono- or polysynaptic inputs from the ipsilateral labyrinth based on orthodromic activation with monosynaptic single pulses (0.1-ms duration, 50– to 400-μA amplitude) delivered at a frequency of 2 or 5 Hz. Two of the three cells that were positively identified as receiving monosynaptic input from the ipsilateral labyrinth (latency less than 1.2 ms) belonged to the “flat” dynamics category (the 3rd cell was not tested at sufficient frequencies to allow identification of its dynamics). The three cells that were not activated at monosynaptic latencies belonged to the high-pass category.

Once a vestibular nuclei neuron was isolated, the responsiveness of each cell was characterized by examining its sensitivity to eye movement as well as rotational and translational motion. The responses during horizontal and vertical smooth pursuit (0.5 Hz, ±10°), as well as fixation and visually guided saccades, were first obtained. Only cells that did not exhibit any eye-velocity or -position sensitivity [termed vestibular-only (VO) neurons] (e.g., Scudder and Fuchs 1992) were included in the present study. Isolated VO cells were tested during lateral and fore-aft motion at 0.5, 2, or 5 Hz. Cells that did not respond during translation were excluded. Neurons that responded to linear acceleration were further tested during (0.5 Hz, ±10°) rotations about different head axes. The axis of rotation always remained earth-vertical during the classification protocol to avoid simultaneous dynamic otolith activation and to investigate if the cell exhibited any rotational sensitivity due to activation of the semicircular canals. Earth-vertical axis rotations were first delivered with the animal upright as well as pitched 30° nose-up and 30° nose-down (eliciting horizontal or combinations of horizontal and torsional VOR). If neural isolation was maintained, the cell was further tested during earth-vertical axis rotations in additional planes (by re-orienting the animal relative to the rotation axis). Only translation-sensitive VO neurons that did not modulate during any earth-vertical axis rotation and whose firing rate was unrelated to eye movements were further investigated in the present study.

The main experimental protocols consisted of an array of translational stimulus profiles (using a linear sled that moved in an earth-horizontal plane). At two different frequencies (0.5 and 5 Hz), the animal was re-oriented relative to the linear sled so that translations in different directions in the horizontal plane were provided. The orientations used varied through 180° in steps of 30°. Next, for a minimum of two different translational directions (usually during lateral and fore-aft motion), the frequency of the translational acceleration was varied between 0.16 and 5 Hz (0.16 and 0.2 at 0.1 G, all other at 0.2 G). An attempt was made to complete these experimental protocols in as many cells as possible. However, adequate isolation was maintained in only a subpopulation of the total number of cells tested. To determine if central otolith neurons discriminated between tilt and translational motion, pitch oscillations (0.5 Hz, ±10°) with the animal upright were also delivered to a few cells. During these pitch oscillations, a component of gravity modulated sinusoidally along the animal’s naso-occipital axis. Since the neurons tested were known not to receive any semicircular canal inputs, comparison of the neural activity during pitch oscillations and fore-aft translation could be used as a direct test of whether or not cells distinguished between the gravitational and translational components of linear acceleration.

**Otolith afferent recordings**

Neural recordings from otolith afferents were obtained using similar techniques as those described in the preceding text for central neurons. Recordings were made as the fibers entered the brain stem proximal to Scarpa’s ganglion. Electrode penetrations were made 8–10 mm from the midline at the level of A-P 0. Most tracks were made outside the boundary of the medulla, with several being histologically identified in cross-sections (e.g., Fig. 1). To identify primary vestibular afferents on-line, the fiber selectivity was carefully characterized through a combination of yaw/pitch/roll rotations and linear sled movements (e.g., Dickman 1996; Estes et al. 1975). Specifically, each afferent was tested with the following rotational stimuli (0.5 Hz, ±10°): yaw and pitch rotations, as well as rotations in the plane of the anterior and posterior semicircular canals (i.e., 45° away from the pitch and roll axes). Afferents were also tested during 0.5 Hz (0.2 G peak) translation along the lateral and fore-aft axes. All fibers were shown to receive input from only one sensory organ with spatial and dynamic properties consistent with those characterizing the vestibular nerve in squirrel monkeys (Fernandez and Goldberg 1971, 1976a–c). Once a recorded fiber was characterized as a primary otolith afferent (i.e., it responded during translation), units were tested at different frequencies (0.16–10 Hz) and different orientations. The peak amplitude and stimulus characteristics were identical to those described in the preceding text for central otolith neurons. This allowed a direct comparison between the properties of afferent and central neuron responses to translation.

**Histology**

At the completion of all recording experiments, the animals were deeply anesthetized (pentobarbital sodium) and perfused transcardially with a 2% paraformaldehyde/2% glutaraldehyde solution. The brain was removed, sectioned (80 μm), and counterstained (alternate sections with cresyl violet and Weil). An approximate recording location map was reconstructed for each animal, using the penetration records and known cell type location (e.g., abducens neurons) as well as identification of electrode tracks. The exact recording sites could not be verified based on histological examination (extensive marking lesions were not employed).
Data analyses

All data analyses were performed off-line using custom-written scripts in Matlab (Mathworks). Since none of the neurons examined exhibited any oculomotor sensitivity, the eye-movement signals (which were recorded and stored in each experimental run) were not used for quantitative analyses. For each neuron, the instantaneous firing rate (IFR) was computed as the inverse of interspike interval and assigned to the middle of the interval. For each experimental run, data were folded into a single cycle by overlaying neural IFR from each response cycle. A linear accelerometer mounted near the animal’s head provided the stimulus measure during translation. The neural sensitivity (gain) and phase during translation were determined by fitting a sine function (1st and 2nd harmonics and a DC offset) to both response and stimulus using a nonlinear least-squares minimization algorithm (Levenberg-Marquardt). Silent portions of the neural activity, when present, were excluded from the least-square optimization. Neural sensitivity was then expressed as spikes s⁻¹ (with G = 9.81 m/s²). Phase was expressed as the difference (in degrees) between peak neural activity and peak linear acceleration. Responses were considered significant if the second harmonic was less than 50% of the fundamental. As the animal was repositioned relative to the sled displacement, each stimulus direction was characterized by a polar angle α, defined relative to the lateral (interaural) axis. During lateral motion (0° orientation), peak linear acceleration was to the right. During fore-aft motion (90° orientation), peak linear acceleration was backward.

A cell was considered to respond to either translation or rotation, if the following criteria were met: 1) the harmonic distortion was less than 20% during rotation/translation in at least one stimulus direction; 2) response gain was larger than a minimum (0.10 spikes/s per °/s for rotation and 15 spikes s⁻¹ 1 G⁻¹ for translation) along the directions of minimum harmonic distortion. For the cells that fulfilled these two criteria, a clear modulation in firing rate was also heard through the audiomonitor.

The spatial tuning at each tested frequency was characterized by applying the previously described 2-D spatiotemporal model to both the gain and phase data from each cell during fore-aft and lateral translation (Angelaki 1991; Angelaki et al. 1992; Schor and Angelaki 1992). If data were available at more than these two orientations, all tested directions contributed equally to the tuning estimate by fitting the following equations simultaneously to the gain and phase values as a function of stimulus direction, α (e.g., Fig. 4).

\[
G(\alpha) = (G_0 \cos^2(\alpha) + G_{\alpha} \sin^2(\alpha) + G_{\alpha} \sin(2\alpha) \cos(\phi_{G} - \phi_{a}))^{1/2} \tag{1}
\]
\[
\cos(\phi(\alpha)) = \frac{G_{\alpha} \cos \alpha \cos \phi_{a} + G_{\alpha} \sin \alpha \cos \phi_{a} - G(\alpha)}{G(\alpha)} \tag{2}
\]
\[
\sin(\phi(\alpha)) = \frac{G_{\alpha} \cos \alpha \sin \phi_{a} + G_{\alpha} \sin \alpha \sin \phi_{a} - G(\alpha)}{G(\alpha)}
\]

where \(G_0/G_0^a\) and \(\phi_0/\phi_{G0}\) are the now computed (rather than directly measured) neural response gain and phase during lateral and fore-aft motions, respectively. In these equations, α is the heading direction (α = 0° and α = 90° for lateral and fore-aft motions, respectively). It was then these \(G_0/G_0^a\) and \(\phi_0/\phi_{G0}\) estimates that were used to compute the maximum and minimum sensitivity directions (Angelaki 1991; Angelaki et al. 1992; Schor and Angelaki 1992).

In addition to the 2-D model, cells that were tested along at least five different directions were also fitted with the one-dimensional (1-D) cosine-tuning model. For both models, the goodness of fit was evaluated through two measures (see following text), the variance accounted for (VAF) and the mean square error (MSE) divided by the maximum gain (for a direct comparison of cells with a wide distribution of response sensitivities). Such a comparison was made to extend the results of Bush et al. (1993) that a 2-D model provides a more accurate description of the cell’s spatial tuning.

Afferent cells were classified into “regular” and “irregular” according to the normalized coefficient of variation [CV* was computed as in Goldberg et al. (1984); regular afferents: CV* ≤ 0.1; irregular afferents: CV* > 0.1]. The coefficient of variation was also estimated for central neurons. It was found to be at least 0.9 with no systematic correlation with any aspect of response properties.

Transfer functions

Several functions were fitted to the mean dynamics (gain and phase simultaneously) of the afferent and central otolith neurons. For this and before the gain and phase averages were estimated, all neurons’ response sensitivities were normalized by dividing with the respective response gain at 0.5 Hz (thus all cells had unity sensitivity at 0.5 Hz). To compare each model’s ability to describe the gain and phase data for each group of neurons, two measures were used. First, VAF coefficients were computed as VAF = \(1 - [\text{var (model – data)}/\text{var (data)}]\}. Separate VAF values were calculated for neuronal gain and phase (although the functions were fitted to both gain and phase simultaneously). The VAF provided a normalized measure of the goodness of fit. For example, a VAF of 0.50 indicates that 50% of the gain or phase dependence on frequency is described by the model. Second, the mean square error (MSE) was also computed as MSE = \(\sum_{i=1}^{N} [\text{model}(f) - \text{data}(f)]^2/(N - P)\), where data(f) represents the gain or phase values experimentally measured at each frequency f, model(f), the corresponding values estimated from the fit, N, the number of different frequencies tested, and P, the number of model parameters fitted. Whereas the VAF measure provides a goodness of fit criterion that is independent of the number of model parameters fitted, the MSE measure takes into account the number of parameters fitted. Thus MSE also serves to provide an index as to whether increasing the complexity of the model was warranted. VAF and MSE were also used for a quantitative description of the goodness of fit for the spatial tuning functions.

It should be stated that the goal behind these transfer function fits was not to reveal the underlying temporal processing, but merely to provide a quantitative description of the response dynamics of the neurons. This is particularly the case for 2-D central neurons whose properties might be shaped by spatiotemporal rather than purely temporal interactions (see DISCUSSION). In this case, the terms used to describe the neuron’s dynamics need not necessarily correspond to actual temporal processing.

Simulations of spatiotemporal convergence

To simulate spatiotemporal convergence, a simple model was constructed based on the following assumptions: 1) a central otolith cell (whose dynamics were simulated) was assumed to receive inputs from two otolith afferents whose dynamics were described by the mean sensitivity and phase of the regular and irregular afferent populations; 2) summation was linear, with \(k_{RE}\) and \(k_{IRR}\) being the relative strengths of the two inputs; 3) there were no dynamics in the interaction of the two inputs (i.e., \(k_{RE}\) and \(k_{IRR}\) were frequency-independent); and 4) the vector of the “regular” afferent was oriented along the lateral axis (x axis), whereas the vector orientation of the “irregular” afferent formed an angle of \(\theta^o\) (counterclockwise is positive).

A detailed description of the equations describing this interaction has been presented before (Angelaki 1993a,b). Briefly, if \(G_{RE} \cos (\omega t + \phi_{RE})\) and \(G_{IRR} \cos (\omega t + \phi_{IRR})\) describe the responses of the “regular” and “irregular” afferents at a frequency \(\omega\), the response of the target neuron along the lateral (x axis) and fore-aft (y axis) orientations can be calculated as

\[
S_x = k_{RE}G_{RE} \cos (\omega t + \phi_{RE}) + k_{IRR}G_{IRR} \cos \omega t \cos (\omega t + \phi_{IRR})
\]
\[
= G_x \cos (\omega t + \phi_{d})
\]
\[
S_y = k_{IRR}G_{IRR} \sin \omega t \cos (\omega t + \phi_{IRR}) = G_y \cos (\omega t + \phi_{d})
\]
where

\[
G_{\alpha} = \sqrt{\left( k_{RE}G_{RE}\cos\phi_{RE} + k_{IRR}G_{IRR}\cos\phi_{IRR}\cos\theta\right)^2 + \left( k_{RE}G_{RE}\sin\phi_{RE} + k_{IRR}G_{IRR}\sin\phi_{IRR}\cos\theta\right)^2}
\]

\[
\phi_{\alpha} = \tan^{-1}\frac{k_{RE}G_{RE}\sin\phi_{RE} + k_{IRR}G_{IRR}\sin\phi_{IRR}\cos\theta}{k_{RE}G_{RE}\cos\phi_{RE} + k_{IRR}G_{IRR}\cos\phi_{IRR}\cos\theta}
\]

\[G_{\alpha} = k_{IRR}G_{IRR}\sin\theta \quad \text{and} \quad \phi_{\alpha} = \phi_{IRR}\]

The gain and phase of the simulated target neuron along the lateral and fore-aft axes were computed at each frequency based on these equations. The maximum and minimum responses, as well as the tuning ratio were subsequently computed from \(G_{\alpha}/G_{\alpha}\) and \(\phi_{\alpha}/\phi_{\alpha}\), as previously described (Angelaki 1991; Angelaki et al. 1992).

**RESULTS**

Of 288 neurons in the rostral vestibular nuclei that were isolated long enough to be characterized, 129 exhibited eye-movement-related activity. 95 responded to activation of the semicircular canals (48% of which also responded to translation), whereas 64 were only activated during linear acceleration. The responses from these 64 vestibular nuclei neurons that responded exclusively during translational motion and 30 primary otolith afferents were used for the present analyses. None of the 64 central neurons responded during yaw rotation. None of the neurons had response components related to either fast or slow eye movements during fixations, visually guided saccades, or smooth-pursuit eye movements. The majority of the cells (47/64) were also tested during earth-vertical axis rotations in multiple head planes (see METHODS). None of the 47 cells received either horizontal or vertical canal input. The remaining 17 central otolith cells were lost before an extensive rotational protocol could be delivered, thus the possibility of vertical canal input could not be excluded. All quantitative data and frequency response properties were, therefore, confined to the 47 central cells that were positively characterized as receiving only otolith inputs.

**Spatiotemporal properties and tuning**

The spatial tuning of primary otolith afferents and central otolith cells was characterized using the neural responses ob-

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**FIG. 2.** Instantaneous firing rate (IFR) of primary otolith afferent h18t during 0.5-Hz translation along different directions in the horizontal plane. Stimulus orientations of 0 and 180° correspond to lateral motion, whereas 90° corresponds to fore-aft motion. Stimulus directions of 30, 60, 120, and 150° correspond to in-between orientations. The superimposed solid line in each subplot is the best-fit sine function consisting of 1st and 2nd harmonics. The bottom traces represent the linear acceleration stimulus (in units of G; \(G = 9.81 \text{ m/s}^2\)).
ained during 0.5- and 5-Hz translation along six different directions in the horizontal plane. The responses to different directions of translation from one primary otolith afferent and a central otolith neuron are shown in Figs. 2 and 3, respectively. Stimulus orientations of 0° (and 180°) corresponded to lateral motion, whereas 90° corresponded to fore-aft motion. Stimulus directions of 30, 60, 120, and 150° corresponded to orientations in between lateral and fore-aft motion. All of the afferents tested were cosine-tuned. That is, the afferent’s maximum modulation in firing rate occurred at a certain orientation (∼60° for the afferent of Fig. 2) and the minimum modulation occurred at an orientation of approximately 90° away from the maximum. Translation along the minimum response direction typically elicited no response (null response direction). The afferent’s response phase was the same for all stimulus directions, except for a 180° reversal that occurred at the minimum response direction.

In contrast, the central otolith neurons were generally not cosine-tuned. For example, the neuron shown in Fig. 3 had no clear response null with some modulation occurring at all orientations. The neural response phase exhibited a more gradual dependence on stimulus direction, as observed in the responses to 90, 60, and 30° orientations. This noncosine behavior has previously been described as 2-D tuning (Angelaki 1991; Angelaki et al. 1992, 1993). To characterize the spatial tuning of these neurons, the gain and phase values of afferent and central otolith neurons were simultaneously fitted with a 2-D spatial tuning model (Angelaki 1991; Angelaki et al. 1992). Examples of 2-D fits for these central otolith neurons are illustrated in Fig. 4. These neurons were chosen to demonstrate the differences between 1-D (cosine-tuned) and 2-D neurons. Cell p90f (▲) was cosine-tuned with a sensitivity that varied as a rectified cosine function and a response phase that abruptly shifted 180° at the zero sensitivity direction (33°). Cell p96f (●) also exhibited sensitivities that were dependent on stimulus orientation; however, the sensitivity was a complex sinusoidal function characterized by a broader peak and a narrower trough (see Eq. 1) and not a rectified cosine. An important characteristic of neurons exhibiting 2-D tuning was that the minimum response sensitivity was not zero. For cell p96f, the minimum gain was 26% of the maximum, corresponding to a tuning ratio (i.e., computed minimum response

**Fig. 3.** IFR of vestibular nuclei neuron p96f during 0.5-Hz translation along different directions in the horizontal plane. Stimulus orientations of 0 and 180° correspond to lateral motion, whereas 90° corresponds to fore-aft motion. Stimulus directions of 30, 60, 120, and 150° correspond to in-between orientations. The superimposed solid line in each subplot is the best-fit sine function consisting of 1st and 2nd harmonics. The bottom traces represent the linear acceleration stimulus (in units of G; G = 9.81 m/s²).
divided by the computed maximum response sensitivity) of 0.26. The response phase of cell p96f was not constant but decreased as the stimulus angle increased. The changing phase relationship was well described by Eq. 2. Cell p83d (f) is another example of a 2-D neuron where the minimum sensitivity was 66% of the maximum (tuning ratio of 0.66), and the response phase exhibited a strong dependence on stimulus direction. In general, the larger the tuning ratio, the greater the dependence of phase on stimulus orientation (Angelaki 1991; Angelaki et al. 1992).

To provide a quantitative comparison of the 2-D model with the more traditionally used 1-D (cosine-tuned) model, we also fitted 1-D, cosine-tuning functions to data from a subset of 17 neurons, which were tested along at least five different directions and were characterized by tuning ratios larger than 0.10. The VAF values for the 2-D fits have been plotted versus the corresponding values for the 1-D fits in Fig. 5A. For the majority of the cells, data points plotted above the unity-slope line (zzz), suggesting a substantial improvement in the ability of the 2-D model to describe the dependence of sensitivity and phase on stimulus direction. As we have also reported in the past, this improvement was larger for the phase than for the gain dependence on stimulus direction (Angelaki et al. 1992).

The distributions of tuning ratios for all afferent and central neurons tested at multiple orientations at 0.5 and 5 Hz have been plotted in Fig. 6. All afferents were cosine (1-D)-tuned with tuning ratios that were less than 0.15. Even though the dependence of response phase on stimulus direction was significant even at smaller tuning ratios (Fig. 5) (see also Bush et al. 1993), we have chosen this value as a qualitative divider between what we have classified as 1- and 2-D central otolith neurons. Accordingly, the majority of central otolith neurons (22/37, 59% at 0.5 Hz and 16/23, 70% at 5 Hz) exhibited 2-D spatial tuning (tuning ratios more than 0.15). In contrast to what was reported in decerebrate rats (Bush et al. 1993), we found no linear correlation between the amplitude of the minimum and maximum sensitivities at 0.5 Hz in primate central otolith cells (R² = 0.04). At higher frequencies, the correlation improved but remained insignificant (R² = 0.39 at 5 Hz). Thus, no derivative relationship between the maximum and minimum sensitivity vectors exists in primate rostral vestibular nuclei neurons.

**Phase distribution**

The phase distributions of afferent and central otolith neurons at 0.5 and 5 Hz have been illustrated in Fig. 7. Because of...
the dependence of response phase on stimulus direction in many of the central otolith neurons, only the phase computed along the maximum sensitivity direction was used to compare distributions across neurons. Similar to previous reports in other species, primary otolith afferents were characterized by response phases that slightly led head acceleration (Fig. 7). In contrast, central otolith neurons exhibited a broad phase distribution at 0.5 Hz (Fig. 7, top). Thirty-two percent of the neurons had phases that were similar to those of the afferents, i.e., closely in phase or slightly leading head linear acceleration. However, the majority of the central neurons (68%) lagged acceleration and were phase shifted 30°–110° relative to the afferents (and to linear acceleration) at 0.5 Hz. It should be pointed out that phase values around 90° do not necessarily suggest that neuronal firing encodes the linear velocity of the head, as will be shown in the following text, data at multiple frequencies are not consistent with a temporal integration of linear acceleration in most central neurons.

When tested at 5 Hz, the phase distribution of central cells was narrower and the majority of central neurons exhibited phases that only slightly lagged linear acceleration at 5 Hz (Fig. 7, bottom). No systematic correlation between response phase and tuning ratio was found.

Response dynamics

The dependence of response gain and phase on frequency was very different for afferent and central otolith neurons. This was the case not only for 2-D but also for 1-D central neurons. It is also important to point out that characterization of the response dynamics for the otolith neurons that exhibited 2-D spatial properties is complicated by the fact that these cells typically should exhibit different dynamic properties depending on stimulus direction (Angelaki 1991, 1993a,b). The fact that this was indeed the case is illustrated in Fig. 8, which plots the neural sensitivity and phase across different frequencies for two directions of stimulation, i.e., lateral and fore- aft motion (●, ▲, ▼, ■, ● and ○, △, ▽, □, ○ respectively). Two main results were further examined. First, central and afferent dynamics to linear acceleration were very different from each other. Second, 2-D neurons were found to differ in their response dynamics for different directions of linear acceleration.

As the simplest example, Fig. 8A illustrates the responses from two otolith afferents (● and ○ and ▼ and ▽) that were characterized by 1-D, cosine-tuned spatial properties. Afferent dynamics were the same during both lateral and fore- aft motion. Afferent response gains increased and phase leads were small, during both directions of motion. The dynamics of two cosine-tuned central neurons have been plotted in Fig. 8B (left). One of these central cells exhibited sensitivities and phase lags that increased with frequency, whereas the other exhibited sensitivities that decreased with frequency and phase leads that increased with frequency during both stimulus directions. Even though the dependence on frequency was very different from the afferent population, these two central 1-D neurons were characterized by relatively similar response dynamics during lateral and fore- aft motion (Fig. 8B, left; ■, □ and ● and ○).

An example of two other central otolith neurons that exhibited 2-D tuning is shown in Fig. 8B, right (●, ○ and ▼ and ▽). These neurons both exhibited dynamics that differed during lateral and fore- aft motion. The phase difference between lateral and fore- aft motion responses in one of these two cells was ~90° (and not 180° as in Fig. 8A) at low frequencies and progressively decreased as frequency increased (Fig. 8B, right. ●, ○). This dynamic behavior is very different from that of

FIG. 6. Distribution of tuning ratios (minimum/maximum response sensitivity) for primary otolith afferents (hatched) and central otolith neurons (gray) during translation at 0.5 and 5 Hz.

FIG. 7. Distribution of the neuronal phase of the maximum sensitivity vector for primary otolith afferents (●) and central otolith neurons (□) during translation at 0.5 and 5 Hz. A phase of 0° corresponds to a response in phase with linear acceleration. A phase of 90° corresponds to a response in phase with linear velocity. Positive values represent phase leads.
1-D, cosine-tuned neurons that always exhibit similar phases (or shifted 180°) during lateral and fore-aft motion across all frequencies (e.g., Fig. 8, A and B, left). In the other cell (Fig. 8B, ▲, △), response dynamics were also different during lateral and fore-aft motion. Phase leads increased versus frequency during fore-aft motion and decreased with frequency during lateral motion.

The lateral and fore-aft dynamics of the last two cells of Fig. 8B have been replotted in Fig. 9 along with the estimated dynamics that would occur for stimulation along the maximum and minimum sensitivity directions. The maximum sensitivity vector was computed to be closely aligned (but reversed in orientation) to the lateral motion direction for cell d53f (left) and the fore-aft direction for cell p90e (right). Because of the spatiotemporal properties of 2-D neurons, the phase of the minimum sensitivity vector always differed 90° from that of the maximum sensitivity vector at each frequency (Fig. 9, compare □ and ■; see also Angelaki 1991, 1993a,b).

Because many of the central neurons had different response dynamics for different directions of movement, further examination of the frequency dependence of the sensitivity and phase was limited to only maximum sensitivity vector responses. Mainly cells whose responses were obtained for two or more movement directions in a minimum of three different frequencies were examined. A few cells whose dynamics were measured at a single orientation (lateral or fore-aft), but their maximum sensitivity direction was found to be less than 6°10° of the lateral or fore-aft directions, were also included for analysis. For the 23 central otolith neurons studied, groups of cells with three distinctly different response dynamics were observed. As shown in Fig. 10 (left), the majority of cells (13/23, 57%), termed high-pass neurons, had gains that increased with frequency and phases that significantly lagged linear acceleration at low frequencies (phase, less than -60° at frequencies of up to 0.5 Hz). A second group of cells (7/23, 30%; Fig. 10, middle), termed flat neurons, were characterized by relatively constant sensitivities and phase lags (ranging from -55 to -0°) for all stimulus frequencies. A third group of central otolith neurons (3/23, 13%; Fig. 10, right) exhibited maximum sensitivities that decreased with frequency and phase lags that increased with frequency. We refer to these cells as low-pass neurons.

The difference in the response dynamics between these groups of central neurons and in relation to those of primary otolith afferents is better illustrated in Fig. 11 where mean sensitivity (normalized to unity at 0.5 Hz) and phase have been plotted versus frequency. It is apparent that although there is a large range in central otolith dynamics, none of the three groups have responses that are characteristic of primary otolith afferents. The changes in sensitivity as a function of frequency were usually more extreme and phase lags were larger than those of otolith afferents at nearly all frequencies. The large diversity in the low frequency dynamics among the three different groups of central otolith neurons explains the wide
phase distribution observed across the larger central cell population sampled at 0.5 Hz (Fig. 7, top). Conversely, at high frequencies, the phase for all central cells was more similar, as evidenced by the tighter phase distribution observed at 5 Hz (Fig. 7, bottom).

**Transfer functions**

To quantitatively describe the central neuron response dynamics, several functions were fit to the average gain and phase data for each group of afferent and central otolith neurons. This analysis was performed merely to specify the simplest function that would describe the maximum sensitivity vector dynamics of the central neurons and was not intended to define functional parameters related to specific temporal filtering (as will be discussed later, such a concept cannot be applicable for spatiotemporal processing of signals). Initially, the simplest model that would qualitatively describe the frequency dependence was tried. Then, the complexity of the model was increased guided by two goodness of fit measures, the VAF and the MSE (see METHODS). The complexity of the model was increased only if it resulted in an increase of VAF and a decrease of MSE.

For primary otolith afferents, the simplest function used was a first-order model that corresponded to the peripheral mechanics of the otolith system (Grant and Cotton 1990), cascaded by a frequency-independent adaptation operator ($s^0$). However, the simple model did not provide good fits for either the gain or phase of regular afferents (Table 1, 1st row). In fact, the variance of the model’s fit error was larger than the variance of the data (as indicated by the negative value of VAF). Making the adaptation operator frequency-dependent yielded positive VAF values but only slightly improved the MSE (Table 1, 2nd row). A function consisting of only zeros and no poles was equally bad in adequately describing the frequency dependence of primary otolith afferents (Table 1, 3rd row). However, when a first-order function consisting of one pole and two cascaded, fractional adaptation operators was used, the model satisfactorily described the regular afferent data (Table 1, 4th row; see also Fig. 11, dashed lines). The same results were also obtained when describing irregular otolith afferent dynamics (Table 1).

For both afferent groups, increasing the model complexity further did not significantly increase VAF while concurrently keeping constant or reducing MSE.

For the low-pass central neurons, the simplest model allowed was a first-order function. Even though the first-order model could account for 77% of the gain and 64% of the phase variance, MSE values were quite large for both (Table 2C). When the order of both the numerator and denominator was increased simultaneously, the goodness of fit was improved, yet a significant portion of the dynamics was unexplained (VAF values of 88% for gain and 63% for phase). A third-order model (Table 2C) was the best in describing the dynamics of low-pass neurons (Fig. 11, solid cyan line). Further increasing the order and the parameters of the model did not improve the goodness of fit.

For the other two groups of central otolith neurons, identifying a function that would adequately describe the dependence of both gain and phase on frequency was more difficult. Unlike the dynamic behavior of otolith afferents, the flat and high-pass neurons exhibited frequency dependencies of phase that did not parallel those of the gain. For example, flat gains

![Fig. 10. Sensitivity (in spikes·s⁻¹·G⁻¹), phase (in °) and orientation (in °) of the maximum sensitivity vector as well as the tuning ratio (minimum/maximum) as a function of frequency for 13 high-pass, 7 flat, and 3 low-pass central otolith neurons. A phase of 0° (linear acceleration) and 90° (linear velocity) has been illustrated with ∙∙∙.](http://jn.physiology.org/)
would usually be accompanied with nearly zero phase values across all frequencies. In contrast, flat neurons were characterized by significant phase lags, which could be as large as 50–60° (Figs. 10, middle, and 11, ●). Similarly, the gain increases observed in high-pass neurons would usually also be accompanied by small phase leads rather than large phase lags (Figs. 10, left, and 11, ●). Dissociation between gain and phase in this manner is referred to as nonminimum phase system behavior. Nonminimum phase system behavior could be explained by a term of the form $(1 - \tau s)/(1 + \tau s)$, which is characterized by unity gain and a phase that equals $-2 \tan^{-1}(2\pi f\tau)$ (varying between 0 and $-180^\circ$ as a function of frequency) (cf. Ogata 1980). This simple nonminimum phase function was used to best describe the dynamics of flat neurons with a large time constant that was outside the frequency range tested (thus fixed to $\tau = 100$ s). Since the largest phase lags observed did not exceed 90°, a fractional exponent had to be incorporated (Table 2).

For the high-pass neurons, it was necessary that a nonminimum phase system term be present. Within a decade of frequency, the phase of these cells changed more than 90° (in some neurons the change was closer to 180°; see Fig. 10, left). A minimum phase system function would require that the gain also increase with frequency with a very steep slope (larger than unity). As shown in Figs. 10 and 11, the gain for high-pass neurons usually increased with a lesser slope. Therefore the same nonminimum phase term used to describe the flat neurons was also utilized for the high-pass neurons with a preset time constant of 100 s (Table 2). The transfer function also included additional high-pass terms with corner frequencies more than 2 Hz that reproduced the high-frequency gain and phase properties. A single high-pass term was sufficient to explain the gain changes, but two high-pass terms were necessary to reproduce the phase behavior (Table 2). Whereas the function used is sufficient to adequately account for the high-frequency behavior, it probably falls short of describing the neural properties at low frequencies (less than 0.3–0.5 Hz). In the few neurons tested at 0.16 Hz, gain continues to drop with decreasing frequency (Fig. 10, left), whereas the transfer function used to fit the data asymptotes to a flat gain at low frequencies. Since insufficient data were available at low frequencies, the present analysis cannot specify the low-frequency transfer function of these neurons.

**Maximum and minimum vector distributions**

The distribution of the maximum vector directions for the 56 central otolith cells and 18 primary otolith afferents that were tested at different orientations are shown in Fig. 12. Four groups of central otolith neurons have been plotted. High-pass neurons ($n = 25$) included the 13 cells shown in Fig. 10, plus 12 additional neurons that had phase lags at least 60° at 0.5 Hz (but were not tested across a broad enough frequency range to be included in the transfer function analysis). Flat and low-pass central neurons were those displayed in Fig. 10 ($n = 7$ and $n = 3$, respectively). The remaining ($n = 21$) central otolith neurons were tested at only one or two frequencies and had sensitivity and phase values that would not allow sufficient characterization in terms of response dynamics. They were thus termed “unidentified central OTO neurons.”

As shown in Fig. 12, the majority of the afferent and central cells had vectors pointing toward the contralateral ear. As a general rule, the high-pass and the few low-pass neural vectors were split between ipsilateral and contralateral. In contrast, the vectors of flat central neurons tended to point mostly contralaterally. We did not encounter any neuron whose maximum sensitivity direction was pointing within ±15° from the ipsilateral ear.

**Responses during static and dynamic pitch tilts**

Fourteen otolith afferents and 12 central otolith-only cells were also tested during dynamic pitch oscillations at 0.5 Hz ($\pm 10^\circ$). These pitch oscillations elicited a sinusoidally varying gravitational acceleration along the animal’s naso-occipital axis with a peak amplitude of 0.17 G. The peak firing rates of these cells during pitch oscillation has been plotted versus that during fore-aft translation (0.5 Hz, $\pm 0.2$ G) in Fig. 13. Data points for both afferents and central neurons were closely aligned with a 0.87-slope line (corresponding to the ratio of peak fore-aft gravitational acceleration during pitch over peak fore-aft translational acceleration). These results show that central otolith-only neurons respond during dynamic tilting of the head exactly the same as during translation. Therefore similar to primary otolith afferents, central otolith-only neurons do not discriminate between the gravitational and translational components of linear acceleration.
characterized by phase leads relative to linear acceleration. The majority of central neurons still exhibited phase lags. In contrast, most primary otolith afferents are tuned 2-D spatial tuning to linear acceleration. In addition, otolith neurons were found to distinguish between the gravitational and inertial components of linear acceleration. However, otolith afferents nor central otolith neurons were found to be frequency-independent adaptation operator and (1 + τs) is responsible for the high-frequency (>2 Hz) phase leads. Assuming that the mechanics term is common to all afferents, the pole corner frequency of the irregular afferents could be restrained to be the same as that of the regular cells (τ1 = 0.07). In this case, the function fitted was (**)

\[
\begin{align*}
\text{Regular afferents:} & \quad 0.82 \frac{s^{0.15}}{(1 + 0.027s)^{1.41}} \\
\text{Irregular afferents:} & \quad 0.70 \frac{s^{0.07}}{(1 + 0.0013s)^{1.12}} \\
\text{Irregular afferents:} & \quad 0.68 \frac{s^{0.35}}{(1 + 0.045s)^{2.21}} \\
\end{align*}
\]

To examine if central otolith neurons responded during static tilt of the head, 21 of the central otolith cells were also tested in three static head orientations: upright, 30° nose-up and 30° nose-down. Two of three low-pass neurons and 4/7 of the flat neurons changed their sustained firing rate as a function of static head tilt. None of the high-pass exhibited any systematic dependence on static pitch tilt.

**DISCUSSION**

We have investigated the spatial tuning and temporal dynamics of primate primary otolith afferents and central otolith neurons that responded exclusively to linear accelerations of the head. As expected, neither otolith afferents nor central otolith neurons were found to distinguish between the gravitational and inertial components of linear acceleration. However, unlike primary otolith afferents, central otolith neurons exhibited 2-D spatial tuning to linear acceleration. In addition, central otolith neurons exhibited distinct response dynamics, all of which differed from the afferent population. The majority of central otolith neurons responded in phase with linear head velocity (i.e., they significantly lagged linear acceleration) at low frequencies. Similar results were also previously reported for vestibular-only cells during 0.5-Hz eccentric rotation in monkeys (Tomlinson et al. 1996). At high frequencies, the phase of the neuronal responses shifted toward linear acceleration, although the majority of central neurons still exhibited phase lags. In contrast, most primary otolith afferents are characterized by phase leads relative to linear acceleration. The implications of these findings will be discussed in detail in the following text.

**Otolith spatiotemporal convergence and 2-D spatial tuning to linear acceleration**

Given the well-known diversity in primary otolith afferent responses (Fernandez and Goldberg 1976c), we have previously proposed that it is likely that second- and higher-order neurons receive convergent inputs from otolith afferent fibers that differ in both spatial and temporal properties (Angelaki et al. 1992, 1993). Theoretical studies have demonstrated that if spatiotemporal convergence occurred in the central vestibular system, higher-order neurons would code the spatial and temporal aspects of a linear acceleration stimulus in an independent manner. That is, the neuronal temporal properties would vary as a function of the spatial configuration of the linear acceleration stimulus (Angelaki 1993a,b). A mathematical analysis of these interactions provided results that propose that otolith neurons may exist in the CNS that are characterized by two (rather than a single) sensitivity vectors (Angelaki 1991; Hess and Angelaki 1993; Schor and Angelaki 1992). The present results extend previous observations in decerebrate rats (Angelaki et al. 1992, 1993; Bush et al. 1993) and suggest that 2-D spatial tuning might be more common than 1-D spatial tuning in central otolith neurons of alert, behaving primates. In fact, 2-D tuning has also been recently reported in prepositus/medial vestibular nucleus cells in alert gerbils (Kaufman et al. 2000). Recent electrophysiological experiments in cats have shown...
that extensive convergence of primary otolith afferents from the two labyrinths, as well as from the two sides of the striola, exists on single vestibular nuclei neurons (Uchino et al. 1999). Specifically for the utricular-activated secondary vestibular neurons, 44% received commissural inhibition and 3% commissural excitation. In a different group of central otolith cells, 40% received cross-striolar inhibition. Cells that were monosynaptically activated by afferents located on one side of the striola were polysynaptically inhibited by afferents located in the opposite side of the striola. An additional 20% of the cat otolith neurons received cross-striolar inputs of the same polarity. The remaining 40% received inputs from afferents originating only from the medial side of the utricular neuroepithelium (Uchino et al. 1999). The spatiotemporal convergence suggested by the present results could be a consequence of afferent convergence from either the same or opposite sides of the ipsilateral striola. In addition, 2-D tuning could also be the result of convergence of afferents innervating the two opposite labyrinths.

We have previously investigated the theoretical predictions of spatiotemporal convergence, assuming idealized afferent transfer functions (Angelaki 1992, 1993a,b). We have shown that spatiotemporal summation makes specific predictions regarding the change in neuron dynamics as a function of stimulus orientation. Specifically, those simulations have demonstrated that spatiotemporal convergence is equivalent to a spatially selective temporal filter whose properties depend on the relative dynamics of the converging neurons and could exhibit nonminimum phase behavior. Since both afferent and central neuron dynamics were studied here, it might be interesting to directly investigate if spatiotemporal convergence of afferents could be consistent with central otolith neuron dynamics.

For this, we implemented and simulated the simplest model of spatiotemporal convergence. Accordingly, it was assumed that a hypothetical central neuron receives inputs from two otolith afferents whose dynamics are described by the mean sensitivity and phase of the regular and irregular afferent population (Fig. 11). Summation was assumed to be linear and frequency independent (i.e., no temporal filtering), with k_{RR} and k_{IR} being the relative strengths of the two inputs and θ the angle between the polarization vectors of the two converging afferents. The simulated response parameters (i.e., maximum sensitivity and phase, vector orientation and tuning ratio) of the hypothetical target cell for θ = 170° and three different values of k_{RR} and k_{IR} have been plotted in Fig. 14. Depending on the relative strength of projections from the “regular” and “irregular” afferent inputs, two main response patterns result. 1) When the regular input is stronger, the maximum response sensitivity of the simulated target cell is relatively flat, whereas the tuning ratio increases with frequency, suggesting that the minimum sensitivity vector increases with frequency (Fig. 14,

**Table 2. Transfer function fits for central otolith neurons**

<table>
<thead>
<tr>
<th></th>
<th>VAF</th>
<th>MSE</th>
<th>Parameters Fitted</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Gain (s)</td>
<td>Phase (°)</td>
<td></td>
</tr>
<tr>
<td><strong>A. High-Pass Neurons</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$p \left[ \frac{1 - \tau_1}{1 + \tau_3} \right](1 + \tau_5)$ (3)</td>
<td>0.91</td>
<td>0.83</td>
<td>$\tau_1 = 0.07$ s (2.3 Hz)</td>
</tr>
<tr>
<td>$\left(\ast\right) p \left[ \frac{1 - \tau_1}{1 + \tau_3} \right](1 + \tau_5)(1 + \tau_3)$ (4)</td>
<td>0.91</td>
<td>0.91</td>
<td>$\tau_1 = 0.06$ s (2.6 Hz)</td>
</tr>
<tr>
<td>$\left(\ast\right) p \left[ \frac{1 - \tau_1}{1 + \tau_3} \right]$ (2)</td>
<td>0.00</td>
<td>-0.01</td>
<td>$k = 0.13$</td>
</tr>
<tr>
<td><strong>B. Flat Neurons</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$p \left[ \frac{1 - \tau_1}{1 + \tau_3} \right](1 + \tau_5)$ (2)</td>
<td>0.77</td>
<td>0.64</td>
<td>$r = 2$</td>
</tr>
<tr>
<td>$\frac{1 + \tau_5}{1 + \tau_3}(1 + \tau_5)$ (4)</td>
<td>0.88</td>
<td>0.63</td>
<td>$r = 0.91$ s (3.6 Hz)</td>
</tr>
<tr>
<td>$\frac{1 + \tau_5}{1 + \tau_3}(1 + \tau_5)$ (6)</td>
<td>0.96</td>
<td>0.71</td>
<td>$\tau = 100$ s (fixed)</td>
</tr>
<tr>
<td>$\left(\ast\right) p \frac{s(1 + \tau_5)}{(1 + \tau_3)(1 + \tau_5)}$ (4)</td>
<td>0.96</td>
<td>0.71</td>
<td>$\tau = 100$ s (fixed)</td>
</tr>
<tr>
<td><strong>C. Low-Pass Neurons</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$p \left[ \frac{1 - \tau_1}{1 + \tau_3} \right](1 + \tau_5)$ (2)</td>
<td>0.77</td>
<td>0.64</td>
<td>$r = 1.2$</td>
</tr>
<tr>
<td>$\frac{1 + \tau_5}{1 + \tau_3}(1 + \tau_5)$ (4)</td>
<td>0.88</td>
<td>0.63</td>
<td>$\tau = 0.23$ s (0.71 Hz)</td>
</tr>
<tr>
<td>$\frac{1 + \tau_5}{1 + \tau_3}(1 + \tau_5)$ (6)</td>
<td>0.96</td>
<td>0.71</td>
<td>$\tau = 0.13$ s (3.6 Hz)</td>
</tr>
<tr>
<td>$\left(\ast\right) p \frac{s(1 + \tau_5)}{(1 + \tau_3)(1 + \tau_5)}$ (4)</td>
<td>0.96</td>
<td>0.71</td>
<td>$P = 4.2$</td>
</tr>
</tbody>
</table>

For each model, the number of parameters fitted is indicated in parenthesis next to the model structure. The goodness of fit was determined through two different measures that were computed separately for gain and phase: the VAF and the MSE. For neurons with flat response dynamics, the choice of fitted function was only based on MSE (since there was no frequency dependence of either gain or phase, VAF is an insensitive measure of the goodness of fit). (*) Function that was used to generate the lines plotted in Fig. 11.
2) When the irregular input is weighted similarly or stronger than that of the regular contribution, the maximum response sensitivity of the simulated target cell increases with frequency, whereas the tuning ratio is either flat or decreases with frequency (Fig. 14, □ and ○). The phase dependence on frequency is either flat or phase lags are predicted to increase with frequency.

Neither group of central otolith response dynamics encountered in the central otolith neurons of the present study was identical to these simulations. Interestingly, however, these simulated dynamics were nearly identical to those previously described in decerebrate cats (e.g., compare the simulations of Fig. 14 with the data illustrated in Fig. 2 of Schor et al. 1985) and decerebrate rats (Angelaki et al. 1993). The reasons behind this difference are unknown, but at least two possibilities could be discussed. First, the underlying assumptions for the model simulations are clearly extreme oversimplifications of the real distributed properties of the system. In fact, none of the simplified assumptions for these simulations might be valid. 1) Central otolith neurons do not necessarily receive inputs from only two otolith afferents. 2) Primary afferent dynamics represent a continuum and the mean sensitivity and phase of the regular and irregular otolith afferents (from Fig. 11) and whose vector orientation differed by 170°. The only parameter varied in the illustrated simulations is the relative strength of the “regular” and “irregular” inputs to the target cell (kRE and kIRR, respectively). A phase of 0° (linear acceleration) and −90° (linear velocity) has been illustrated with ···.

FIG. 12. Distribution of the maximum sensitivity vectors in the horizontal plane. Different symbols and colors are used for the different groups of central neurons (high-pass, flat, and low-pass). Cells whose dynamics could not be identified have been labeled as unidentified central OTO neurons. Afferent vectors are shown with □ and ○. “Contralateral” refers to acceleration toward the contralateral ear (corresponding to an ipsilateral head tilt).

FIG. 13. Peak neural firing rates of primary otolith afferents and central otolith neurons during 0.5 Hz (±0.2 G) fore-aft translation and 0.5 Hz (±10°) pitch tilt. The pitch oscillations elicited a sinusoidally varying gravitational acceleration along the animal’s naso-occipital axis with a peak amplitude of 0.17 G. Data points were closely aligned with a 0.87 (0.17/0.2)-slope line (dashed lines). A linear regression through all central neuron data points had a slope of 0.88 (straight lines). The slope for the afferent data was 0.90 (regression not plotted). High-pass (●), flat (●), low-pass (●), unidentified central neurons (○), and primary otolith afferents (□).

FIG. 14. Simulated sensitivity (Smax), phase (in °) and orientation (in °) of the maximum sensitivity vector as well as the tuning ratio (minimum/maximum) as a function of frequency. The model simulated was the simplest example of spatiotemporal convergence of two cells (e.g., Angelaki 1993a,b) whose dynamics were described by the mean normalized sensitivity and phase of the regular and irregular otolith afferents (from Fig. 11) and whose vector orientation differed by 170°. The only parameter varied in the illustrated simulations is the relative strength of the “regular” and “irregular” inputs to the target cell (kRE and kIRR, respectively). A phase of 0° (linear acceleration) and −90° (linear velocity) has been illustrated with ···.
cific distribution of the afferent vector orientations (Angelaki 1992). Despite all of these oversimplifications that will definitely be important in predicting central otolith neuron dynamics, we cannot exclude the possibility that the central processing of otolith signals might also be more complex in alert primates (compared with decerebrate preparations).

**Response dynamics of central otolith neurons**

Three groups of central otolith neurons were identified based on their dynamic properties along the maximum sensitivity direction, including high-pass, flat, and low-pass cells. An attempt was made to characterize these dynamic properties using the simplest possible functions. Among these groups of dynamics, only low-pass cells could be described by a simple function with minimum phase characteristics. In contrast, both the high-pass and flat cells exhibited nonminimum phase behavior and larger phase lags than predicted by their gain dependence on frequency. The presence of these large phase lags necessitated the use of a nonminimum phase term with a fractional exponent. This term was adequate to describe the frequency dependence of flat neurons. Functions describing high-pass neuron dynamics required additional terms (Table 2). It is interesting to note that neither group of central neurons that was characterized by low-frequency phase lags that resembled linear velocity (high-pass and flat cells) could be satisfactorily described by functions that resembled or included a neural integrator.

In considering these functions used to describe central neuron dynamics, it should be emphasized that it would be inappropriate to interpret the dynamics of 2-D neurons using the traditional temporal filtering concepts. As explained above, and as shown in Fig. 14, significant (spatially specific) “filtering” would be expected even in the case of the simplest filter-free spatiotemporal summation of afferent response dynamics. Thus without a careful analysis and model of the responses, the terms used to describe the dynamics of 2-D neurons need not necessarily correspond to actual temporal processing.

Studies of primate central neuron responses to linear acceleration have been limited. In addition, neural responses during off-axis rotations that co-activate semicircular canal and otolith afferents have usually been restricted to a single spatial direction (Chen-Huang and McCrea 1999; McConville et al. 1996; Tomlinson et al. 1996). Considering only stimulus orientations along the interaural axis, the vestibular-only responses reported by Tomlinson et al. (1996) at two frequencies (0.5 and 3 Hz) are similar to those of high-pass neurons of the present study. Responses were reported to lag linear acceleration by 30–60° at 0.5 Hz but be nearly in phase (small phase lags) at 3 Hz. The sensitivity of the majority of the cells was reported to increase between 0.5 and 3 Hz (Tomlinson et al. 1996), similar to the high-pass neurons reported here.

The majority of previous studies of vestibular nuclei neuron responses to linear acceleration along different directions have been in anesthetized or decerebrate animals (Angelaki et al. 1993; Bush et al. 1993; Schor 1974; Schor and Miller 1982; Schor et al. 1984, 1985, 1998; Xerri et al. 1987). The present results are not easily comparable with these previous studies, not only because of different preparations and species, but also because of potentially different neural populations investigated. In the majority of previous studies, recorded neurons were located more laterally and caudally within the vestibular nuclear complex than those in the present study. For example, in the Deiter’s nucleus and the caudal aspects of the medial and inferior vestibular nuclei, “otolith” neurons were reported to have maximum sensitivity vectors directed along the roll and not the pitch axis (Endo et al. 1995; Kasper et al. 1988; Schor et al. 1984; Wilson et al. 1990). In the present study, central neurons had a wide vector distribution, including orientations along both the roll and pitch axes. The response dynamics encountered in the rostrally located neurons of the present study were also different from those reported in the lateral vestibular nuclei of decerebrate, canal-plugged cats (Schor et al. 1985).

**Central otolith neurons do not discriminate for tilt and translation**

It has always been assumed that primary otolith afferent neurons provide identical responses during head tilts relative to gravity and during translational movements (Dickman et al. 1991; Fernandez and Goldberg 1976a–c; Fernandez et al. 1972; Loe et al. 1973; Si et al. 1997). Despite indiscriminate primary otolith afferent information, horizontal VOR responses, at least for frequencies higher than 0.16 Hz, have been shown to be specific for the translational (rather than the resultant) acceleration (Angelaki et al. 1999a). The fact that central otolith neurons responded similarly during pitch and fore-aft translations (Fig. 13) suggests that the computations to discriminate between the two types of motion do not occur at the level of otolith-only central vestibular nuclei neurons. The inability of central otolith neurons to discriminate between translation and tilt might not be surprising, given the recent results that demonstrate a fundamental role for the semicircular canal signals in this computation (Angelaki et al. 1999a; Merfeld et al. 1999). Thus it is likely that convergent otolith-canal (rather than otolith-only) central neurons participate in the tilt versus translation discrimination task.

**Large differences in response dynamics between the afferent and central otolith populations: can conclusions be drawn from previous rotational studies?**

Perhaps one of the most important results of the present study is the observation that central otolith dynamics are very different from those of the afferent population. To verify that this was not simply the result of different approaches, exactly the same alert preparation, stimuli, and analysis techniques were used to investigate the response properties of both central and primary afferent neurons. It is astonishing that not a single central neuron in our data sample exhibited dynamic properties that were similar to those of the afferent population. This observation, coupled with the facts that the majority of central otolith neurons phase lagged linear acceleration by ~60–110° at 0.5 Hz and that central otolith-only neurons respond similarly to tilt and translation, raises serious concerns about previously made assumptions regarding vestibular nuclei neuron responses.

More specifically, a number of investigations have utilized sinusoidal earth-horizontal or off-vertical axis rotations to study central vestibular responses (Bolton et al. 1992; Endo et al. 1994, 1995; Fukushima et al. 1990, 1999; Graf et al. 1993;
Iwamoto et al. 1996; Kasper et al. 1988; Perlmutter et al. 1998, 1999; Wilson et al. 1990, 1996). During such rotations, both semicircular canal and otolith afferents are simultaneously activated. Since stimuli were not discretely activating an afferent group, assumptions had to be often made to describe central vestibular responses. For example, Kasper et al. (1988) (as well as several other studies since e.g., Bolton et al. 1992; Endo et al. 1994, 1995; Perlmutter et al. 1999; Wilson et al. 1990, 1996) have classified central neurons “by comparing their response dynamics with the known dynamics of canal and otolith afferents.” An implicit assumption in classifying central neurons in this manner is that central neurons exhibit the same dynamics as their respective afferents. The data presented here clearly demonstrate that such an assumption is invalid. For example, in the present study, neurons were observed that responded exclusively to linear motion yet exhibited gains that increased with frequency and phase values that significantly lagged linear acceleration at low frequencies (i.e., were closely in phase with velocity; e.g., Figs. 10 and 11). Using the classification scheme of Kasper et al. (1988), these central otolith neurons would most likely have been described as either “canal” or “canal + otolith” (but unlikely “otolith-only”) cells. To demonstrate this point, Fig. 15 directly compares the data from Kasper et al. (1988) with the mean gain and phase of the present population of otolith-only neurons with “high-pass” properties. For a direct comparison, our data have been expressed in the same units as those of Kasper et al. (1988), i.e., both gain and phase have been plotted relative to the corresponding head tilt position. It is obvious that the high-pass neurons of the present study are more similar in terms of both the slope of gain increase as a function of frequency and the phase values to what was classified as canal or canal + otolith neurons in previous studies. Therefore if otolith-only cells in the more caudal vestibular nuclei are characterized by significant phase lags relative to linear acceleration (as the present more rostrally-located population), then the cell classification in these previous studies would need to be seriously reconsidered.

A similar concern also applies to another set of studies that have used a combination of earth-horizontal and -vertical axis rotations to study the spatial transformations between the semicircular canal and motoneuron coordinate frames (Fukushima et al. 1990; Graf et al. 1993; Iwamoto et al. 1996; Perlmutter et al. 1998). In fact, the concern is more important in these later studies because the quantitative conclusions would be seriously affected by the underlying assumption that any neural response with a phase within ±45° of velocity at 0.5 Hz was considered to be canal-generated (e.g., Fukushima et al. 1990). Thus the maximum-activation-directions computed (including the evidence for orthogonal canal/canal convergence) might not necessarily reflect the semicircular canal activation vectors but rather a global vestibular activation that could be partly due to canal and partly due to otolith responses (or even exclusively due to otolith responses).

A similar problem arises from previous interpretations of the nature and degree of spatiotemporal convergence in central neurons receiving otolith inputs. For example, spatiotemporal convergence (STC) and 2-D spatial tuning has been reported using earth-horizontal axis rotation in the vestibular nuclei (Baker et al. 1984; Perlmutter et al. 1999) and the reticular formation (Bolton et al. 1992; Fagerson and Barmack 1995). These STC responses were often described as a result of a misalignment of the otolith and semicircular canal maximum sensitivity directions (Baker et al. 1984; Endo et al. 1995; Fukushima et al. 1990; Graf et al. 1993; Iwamoto et al. 1996; Kasper et al. 1988; Perlmutter et al. 1998, 1999; Wilson et al. 1990). However, these studies also classified central neurons as canal, otolith, and canal + otolith according to their resemblance of afferent-like dynamics. Since the present results raise a sincere doubt to this assumption, the incidence of otolith STC might have been strongly underestimated in previous rotational studies. Therefore conclusions regarding the type of afferent input and convergence should be made with caution, unless distinct stimuli that selectively activate only semicircular canal or otolith afferents are used.

**Functional implications: why such a diverse dynamic behavior in central otolith neurons?**

One of the most striking observations in the present study is the vast diversity in the dynamics of central neurons in response to linear acceleration. Neurons were identified in the rostral portions of the vestibular nuclear complex that exhibited high-pass, flat, and low-pass filter behaviors. These dynamics, coupled with those previously observed from neurons in more caudal parts of the vestibular nuclear complex (see the preceding text) point to perhaps one of the most important characteristics of the otolith system: its diversity in function. This could be partly due to the fact that the otolith system serves a...
dual role: to detect the linear acceleration components of movement as well as to detect and compensate for the force of gravity.

In the present study, the output projections of the central otolith neurons were not identified. Utricular and saccular signals have been shown to make disynaptic or polysynaptic connections with spinal cord motoneurons (Bolton et al. 1992; Ikegami et al. 1994; Wilson et al. 1977). Vestibular projections to the spinal cord have been shown to include neurons in the lateral vestibular nucleus as well as the rostral half of both the medial and descending vestibular nuclei (cf. Wilson and Schor 1999). Some of the neurons whose properties were described here could send axons in the medial vestibulospinal tract. In addition, some of these neurons could be interneurons that mediate connectivity between different brain stem structures. For example, some of the presently identified central otolith neurons could provide a disynaptic input to the prepositus hypoglossi, as postulated in a recent model (Green and Galiana 1998), or participate in the commissural inhibition that has been shown in the cat (Uchino et al. 1999). Since most of our recordings were concentrated in the rostral vestibular nuclei, it is less likely that many of the recorded neurons were flocculus-projecting neurons. Flocculus- and nodulus-projecting neurons have been reported to lie in the more caudal regions of the medial and inferior vestibular nuclei (Brodal 1974; Langer et al. 1985).

Electrolytic and kainic acid lesions have suggested that vestibulo-sympathetic and vestibulo-respiratory pathways originate from a relatively small portion of the vestibular nuclear complex, comprising regions in the caudal medial vestibular and inferior nuclei, just caudal to the Deiter’s nucleus (Pan et al. 1991; Uchino et al. 1970; Yates and Miller 1994; Yates et al. 1993). Even though our anatomical reconstructions were not accurate enough to eliminate the possibility, the recording locations of the present study appear to be more rostral that the vestibulo-sympathetic region.

*Can central otolith neuron dynamics explain the temporal properties of the translational VOR?*

One of the most well-understood otolith-motor responses are the eye movements generated during head translation (translational VOR). Like the rotational vestibuloocular reflex driven by the semicircular canals, the otolith-driven translational VOR functions to stabilize targets during head movement. Perhaps one of the most challenging questions, that is yet unresolved, is the temporal processing that is necessary to convert primary otolith afferent activity, which is in phase with linear acceleration (Fig. 11) (see also Fernandez and Goldberg 1976b) to an eye position signal. Because eye velocity is in phase with linear head velocity during translations between 0.5 and 10 Hz (Angelaki 1998; Angelaki et al. 2000b; Paige and Tomko 1991; Telford et al. 1997), a double integration has been postulated. There is little dispute that the velocity-to-position neural integrator (cf. Robinson 1981) performs one of these integrations. However, because of the high-pass filter properties in the translational VOR dynamics, the existence and implementation of the second integration remains in question. One proposal is based on a central processing that resembles that of the semicircular canals. That is, otolith signals could be centrally integrated to yield a linear head velocity signal that can then be combined with the rotational head velocity signal arising from the semicircular canals. The combined vestibular velocity signal would subsequently be commonly processed by the premotor circuits and eye plant (Paige and Tomko 1991; Raphan et al. 1996; Telford et al. 1997). However, a traditional double neural integration is not sufficient to produce the behavioral observations. A neural high-pass filter has then been suggested either in combination with the integrator (Telford et al. 1997) or independently (Angelaki et al. 1993). Such a high-pass filtering was proposed to arise at least partly through spatiotemporal convergence (Angelaki 1993a,b; Angelaki et al. 1993, 1999b). Recently, the dynamics of the eye plant have been proposed as an interesting alternative to the second neural integration model (Green and Galiana 1998). Rather than being neurally compensated, as is the case for the rotational VOR, the eye plant dynamics were proposed to provide the second low-pass filtering of otolith signals in the translational VOR (Green and Galiana 1998). When this conceptual model was fitted to the sensitivity and phase of the translational VOR data, a complex high-pass filter processing with nonminimum phase characteristics (similar to the dynamics of the presently identified cells) was predicted for the central otolith pathways (Angelaki 1998).

As explained in the preceding text, the central otolith dynamics identified here should not be considered as representing integrated afferent signals. Even though the phase distribution of the majority of central otolith neurons suggest that linear acceleration signals might have been centrally integrated (e.g., Fig. 7), this was shown not to be the case when response dynamics were evaluated across a wide frequency range (e.g., Fig. 11). The approximately 90° phase lags observed at low frequencies are not the result of a neural integration but rather the effect of nonminimum phase behavior, possibly arising at least partly, but probably not exclusively, through spatiotemporal convergence (Angelaki 1993a,b; Angelaki et al. 1999b).

**Conclusions**

The 2-D spatial tuning in the majority of central otolith neurons suggest that extensive spatiotemporal processing might exist in the primate central otolith system. This finding suggests that spatial and temporal channels of information do not appear to be parallel and independently processed by the central vestibular system. It should be noted that interdependence of spatial and temporal signal processing exists and might be a common form of processing in multiple sensory and motor systems. In addition to the 2-D tuning of otolith signals in the vestibular nuclei (Angelaki et al. 1993; Bush et al. 1993; present study) as well as vestibular and neck signals in the anterior cerebellar vermis (Manzoni et al. 1999; Pompeiano et al. 1997), spatiotemporal interactions have been shown to be fundamental in visual processing (Cai et al. 1997; DeAngelis et al. 1993; Hamilton et al. 1989; McLean and Palmer 1989; Reid et al. 1991). More recently, evidence for spatiotemporal processing and 2-D tuning has been provided for neurons in the auditory midbrain (Koch and Grothe 2000) as well as shown to
characterize Purkinje cell responses during smooth pursuit eye movements (Leung et al. 2000). Thus it is tempting to speculate that 2-D spatiotemporal interactions might represent a common neural organization in directionally tuned sensorimotor processing.

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