Vestibular Convergence Patterns in Vestibular Nuclei Neurons of Alert Primates

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INTRODUCTION

Perception and control of motion, spatial orientation, and motion-centered neuromotor behavior all depend on rapid accurate detection of the orientation and movement of the head and body, processes that are largely dependent on vestibular system function. Vestibular afferents innervating each semicircular canal are homogeneously spatially tuned to provide a three-axis head reference frame representing rotational motion (Dickman 1996; Estes et al. 1975; Goldberg and Fernandez 1971a,b; Rabitt 1999; Reisine et al. 1988). Otolith afferents are each uniquely tuned to linear accelerations along specific directions, with the population of afferents being heterogeneously distributed throughout three-dimensional (3D) space (Fernandez and Goldberg 1976a–c). However, otolith afferents cannot distinguish between changes in the orientation of the head relative to gravity and translational motion (Angelaki and Dickman 2000; Dickman et al. 1991; Fernandez and Goldberg 1976a–c; Fernandez et al. 1972; Loe et al. 1973; Si et al. 1997; Tomko et al. 1981). Somehow, vestibular central neurons must synthesize and process afferent information to correctly detect the amplitude and direction of not only rotational but also translational motions as well as elicit appropriate compensatory eye movement and postural motor reflexes (Angelaki et al. 1999; Merfeld and Zupan 2002; Paige and Tomko 1991; Telford et al. 1997; Young 1974).

Recording studies using nerve branch electrical stimulation have attempted to identify the nature and extent of signal convergence from the different canal and otolith receptors onto single vestibular nuclei (VN) neurons, with the general consensus being that ~30–40% of VN cells respond to multiple receptor signals (Markham and Curthoys 1972; Ono et al. 2000; Uchino et al. 2000; Searles and Barnes 1977; Wilson and Felpel 1972; Zakir et al. 2000). Other investigations employing discrete rotational and/or translational motion stimuli have shown that the prevalence of signal convergence onto VN neurons is higher (Bush et al. 1993; Markham and Curthoys 1971; Tomlinson et al. 1996). Some studies, however, have attributed the velocity-sensitive responses of central neurons during earth-horizontal axis rotations (EHA) to semicircular canal (SCC) activation exclusively and not to otolith inputs (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. 1990, 1999; Merfeld and Zupan 2002; Paige and Tomko 1991; Telford et al. 1997; Young 1974).
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1988; Perlmuter et al. 1998, 1999; Wilson et al. 1990, 1996). In effect, these investigations expected that central oto\linebreak
lith neuron responses should reciprocate the responses observed in primary oto\linebreak
lith afferents (i.e., exhibit responses in phase with head position during rotation). However, responses from cen\linebreak
tral neurons elicited by pure translational motion stimuli clearly indicated that this expectation was incorrect (Bush et al.

More recently, observations during translation in reduced preparations have been replicated and expanded with VN
neuron recordings in alert rhesus monkeys. A clear demonstration of many differences between central neuron and oto\linebreak
lith afferent responses was found (Angelaki and Dickman 2000). Speci\linebreak
fically, the spatial response properties to translation differed widely for VN cells, from being narrowly tuned (similar to afferents) to being responsive to broad directions of motion (Angelaki and Dickman 2000; Angelaki et al. 1993; Bush et al. 1993). In addition, although VN neuron dynamics to transla\linebreak
tion exhibited great variability, all central gain and phase behaviors as a function of frequency were distinctly different from the relatively stereotypic frequency dependence of primary oto\linebreak
lith afferents. Finally, the majority of the central neurons modulated in phase with head velocity rather than linear acceleration during 0.5-Hz translation (Angelaki and Dickman 2000). If in fact, it was observed that pure oto\linebreak
lith-only central neurons (i.e., cells without any rotational sensitivity when tested with earth-vertical axis (EVA) rotations in any head orientation) responded during EHA rotations in phase with head velocity and exhibited dynamic behavior that was indistinguishable from a pure canal-only cell. As a result, conclusions regarding the 3D distribution of rotational maximum sensitivity vectors in previous studies may be confounded in that many cells characterized as canal-only could, in fact, have been convergent oto\linebreak
lith + canal or purely oto\linebreak
lith-only neurons.

The direction of maximum sensitivity to rotation reported previously in decerebrate rats was found to be congruent with that during translation (Angelaki et al. 1993). Thus the sensit\linebreak
ivity of vertical canal neurons to linear acceleration was “aligned” with that of their major SCC input, such that the cell’s canal and oto\linebreak
lith responses would be complementary for maximum modulation during EHA rotations. These results were interpreted as the neural correlate of the behavioral observation that, during both translation and off-vertical axis rotation, the function of oto\linebreak
lith-driven eye movements in the rat is to complement SCC activation in achieving gaze stability during EHA rotations (Hess and Dieringer 1990, 1991).

Such a functional role for oto\linebreak
lith/canal convergence might not, however, be easily extendable to primates. Linear acceleration and oto\linebreak
lith-driven eye movements in primates seem to provide binocular gaze stability during translational movements rather than contribute in gaze stabilization during head tilts (Angelaki 1998; Angelaki et al. 2000b; Miles 1993) as is the case in lateral-eyed species. As a consequence of the increased functional demand and high behavioral relevance for binocular gaze stability during translation in primates (Miles 1993, 1998), the primate VOR has, in fact, evolved the unique ability to discriminate between translation and tilts relative to gravity (Angelaki et al. 1999). This tilt/translation discrimination ability seems to operate for frequencies higher than that corresponding to the SCC time constant (Angelaki et al. 1999; Merfeld and Zupan 2002; Mergner and Glasauer 1999). As a result, simultaneous oto\linebreak
lith system activation during mid- and high-frequency EHA rotations in primates results in identical oculo\linebreak
motor responses as those elicited during EVA, when only SCC afferents are dynamically activated (Angelaki and Hess 1996; Merfeld and Young 1995; Tweed et al. 1994). In contrast, in lateral-eyed species, oto\linebreak
lith-driven oculo\linebreak
motor responses are the same during translation and EHA rotations (Baarsma and Collewijn 1975; Barmack and Pettrorossi 1988; Dickman and Angelaki 1999; Hess and Dieringer 1990, 1991).

Recent efforts to understand the mechanisms underlying tilt versus translation discrimination in primates have shown that oto\linebreak
lith sensory information must be combined centrally with SCC signals to correctly distinguish between the two types of linear acceleration (Angelaki et al. 1999; Merfeld 1995; Merfeld and Zupan 2002). Where and how these oto\linebreak
lith/SCC interactions take place is unknown, but afferent signal convergence onto VN cells presents a likely source. Thus tilt/transla\linebreak
tional discrimination could represent one of the functional roles for canal/oto\linebreak
lith convergence in primates. In a previous study where we compared the properties of central oto\linebreak
lith-only neurons with those of primary oto\linebreak
lith afferents, we have reported that none of the recorded central nonconvergent cells discriminated tilt from translation (Angelaki and Dickman 2000). The present study represents an extension of those findings to include neurons that were either only sensitive to EVA rotations (canal-only neurons) or sensitive during both EVA rotation and translations (oto\linebreak
lith + canal neurons).

Thus the goals of the present study were threefold: 1) to compare the properties of all three central populations of neurons insensitive to eye movements (canal-only, oto\linebreak
lith + canal, and oto\linebreak
lith-only cells), 2) to re-examine the 3D distributions of rotational maximum sensitivity vectors of central neurons using only EVA rotations, such that canal activation would not be accompanied by oto\linebreak
lith activation, and 3) to examine the pattern of convergence in oto\linebreak
lith + canal neurons by comparing EVA rotation and translation responses to those during EHA rotation. For the latter two, specific hypotheses were investigated. First, whether the recorded EHA responses could be predicted from a linear combination of EVA rotation and translation responses. If true, central oto\linebreak
lith + canal convergent neurons, similar to primary oto\linebreak
lith afferents and central oto\linebreak
lith-only cells, respond equivalently to the translational and gravitational components of linear acceleration stimuli. Second, responses could be equivalent during EVA and EHA rotations, suggesting that convergent neurons are not encoding linear acceleration components that are due to head tilting relative to gravity. If true, convergent cells would encode an accurate estimate of the translational component of the imposed motion by selectively discriminating and excluding the linear acceleration components due to gravity. Preliminary results of this work have appeared in abstract form (Angelaki and Dickman 2002).

METHODO

Three juvenile rhesus monkeys (Macaca mulatta) were chronically implanted for head stabilization with a circular delrin ring using stainless steel inverted T-bolts that were secured to the skull with dental acrylic. A guide tube platform (3 x 3 x 0.5 cm) constructed of delrin was stereotaxically secured to the skull inside the head ring.
The platform had a staggered array of holes (spaced 0.8 mm apart) that extended from the midline to the area overlying the vestibular nerves bilaterally. All animals were implanted with search coils on both eyes, and two of the animals were also implanted with labyrinthine-stimulating electrodes (Angelaki et al. 2000a). All surgical procedures were performed under sterile conditions in accordance to institutional and National Institutes of Health guidelines.

During experiments, the monkeys were seated in a primate chair with their heads statically positioned 18° nose-down, which approximately aligned the major plane of the utricle and horizontal canals with an earth-horizontal plane. The primate chair was then secured inside the inner frame of a vestibular turntable consisting of a 3D rotator on top of a 2-m linear sled (Acutronics). The linear acceleration of the head was measured with a three-axis accelerometer mounted on the head ring support structure. For each recording session, the eye-coil signals, the three output signals of the linear accelerometer, as well as velocity tachometer and position feedback signals 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 for off-line analysis.

Extracellular recordings from single VN neurons were obtained with epoxy-coated tungsten microelectrodes. Electrodes were inserted into 26-gauge guide tubes, advanced through a predrilled hole in the recording platform, then manipulated vertically with a remote control microdrive. Neural activity was amplified, filtered (300 Hz to 6 kHz) and passed through a BAK Instruments dual time-amplitude window discriminator. Single-unit spikes triggered acceptance pulses (BAK window discriminator) that were stored on computer using the event channel of a Cambridge Electronics Design (model 1401) data-acquisition system. Stimulus protocols and data acquisition were computer-controlled with the 1401 using scripts written for the Spike2 (CED) software environment.

**Experimental procedure**

Initially, recording tracks were performed to identify the location of the abducens nucleus. Once the abducens nuclei were located bilaterally, penetrations explored areas of the VN that extended 0–4.5 mm lateral to the midline and 0–4.5 mm posterior to the abducens nucleus (Fig. 1A). The electrode track locations shown in Fig. 1A were taken from all three animals and then placed onto the nuclear outlines traced from a single animal and collapsed in the horizontal plane. The overlapping borders of the VN represent regions in the dorsoventral axis where nuclear regions overlap.

In the two animals that were implanted with bilateral labyrinthine-stimulating electrodes, the location of the VN was also guided by vestibular field potentials evoked with electrical stimulation of the ipsilateral vestibular nerve (0.1-ms monophasic pulses, 50–400 μA). Approximately one-fourth of the recorded cells were also tested for mono- or polysynaptic inputs from the ipsilateral labyrinth based on orthodromic activation with monophasic single pulses (0.1-ms duration, 50- to 400-μA amplitude) delivered at a frequency of 2 or 5 Hz (Fig. 1B).

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 tasks and visually guided saccades, were first obtained. Only cells that did not exhibit any eye-velocity or eye-position sensitivity (non-eye movement, NEM, neurons) (e.g., Scudder and Fuchs 1992) were further studied with the stimuli outlined in the following text.

**Translational stimuli**

Neurons were tested during translation at different frequencies (0.16 and 0.2 Hz, ±0.1 G; 0.3 and 0.5 Hz, ±0.19 G; 1–5 Hz, ±0.2–0.3 G) and along different directions in the horizontal plane (due to technical limitations, no vertical plane translations were delivered). Each cell was typically tested at a minimum of three different frequencies and two different orientations (lateral and fore-aft motion). In addition, cells were tested for static tilt sensitivity in pitch, roll, or additional head planes. All cells that were judged to be unresponsive to translation (canal-only neurons) did not significantly change their steady-state firing rates during either translation or static head tilts.

**Rotational stimuli**

Responses were obtained from all neurons during 0.5 Hz (±10°) EVA rotations. EVA rotations were used to avoid simultaneous dynamic otolith activation and to observe any rotational sensitivity due to activation of the SCCs. EVA rotations were delivered with the animal positioned upright, pitched 30° nose-up and pitched 30° nose-down. These rotations produced either a horizontal or combinations of horizontal and torsional VOR. If neural isolation was maintained, EVA rotations in additional planes were delivered by re-orienting the animal relative to the axis of
rotation. These included EVA rotations in 30° right and left ear-down positions (eliciting combinations of horizontal and vertical VOR), as well as in 30° tilted positions in the plane of the left anterior-right posterior (LARP) and right anterior-left posterior (RALP) canals. The largest vertical tilt used (relative to the axis of rotation) was 45°.

Based on the responsiveness of the neurons during EVA rotations (Duensing and Schaeffer 1958), an initial characterization of cells as type I HC, type II HC, and VC neurons was performed during the recording session. Neurons whose firing rate increased approximately in phase with ipsilateral head velocity during standard yaw rotation and yaw rotation in both the nose-up and -down orientations were characterized as “type I HC” cells. Neurons whose firing rates increased approximately in phase with contralateral head velocity during standard yaw rotation as well as during yaw rotation in nose-up and nose-down orientations were characterized as “type II HC” cells. Neurons whose firing rates changed from being in phase with ipsilateral head velocity to being in phase with contralateral head velocity during rotation in any of the three planes were characterized as “VC” cells (Estes et al. 1975). This initial on-line characterization was used for consistency with many previous studies of vestibular neurons. However, as will be shown in RESULTS, such a characterization becomes largely irrelevant for otolith + canal convergent neurons because of the large scatter and mostly uniform distribution of rotational maximum sensitivity vectors throughout the 3D space.

Responses from VN neurons were also obtained during 0.5 Hz (±10°) rotations about EHA, including the pitch, roll, RALP, and LARP planes (as well as other in-between head-vertical planes). During these motions, both SCC and otolith afferents were dynamically activated. Specifically, during these EHA rotations, there was a component of gravity in the horizontal head plane that modulated sinusoidally with peak amplitude of (sin10°) = 0.174 G. As this peak amplitude was close to that of the translational stimuli (at 0.5 Hz, peak translational amplitude was ~0.19 G), a direct comparison between these responses was possible (see Data analyses). Completion of the entire stimulation protocol required a recording period of >1.5 h. Therefore for each cell a single stimulus of either 0.5-Hz yaw rotation or lateral translation was delivered several times throughout the experimental protocol. Only neurons that maintained nonsignificant differences in discharge pattern and response gain for the repeated stimulus presentation were included in the analyses.

In addition to the central neurons, recordings were also obtained from primary vestibular afferent fibers as they entered the brain stem proximal to Scarpa’s ganglion. These afferent data have only been used here in a direct comparison with the central neuron response gain and phase at 0.5 Hz (Table 1). A more detailed presentation of the afferent responses has been included elsewhere (for otolith afferents: Angelaki and Dickman 2000; for SCC afferents: Dickman et al. 2002).

After the completion of all recording experiments, the animals were utilized for additional anatomical studies involving neural tracer experiments. Following appropriate transport times, the animals were deeply anesthetized (pentobarbital sodium) and perfused transcardially with 2% paraformaldehyde/2% glutaraldehyde solution. The brain was removed, sectioned (80 μm), and counterstained. 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 (Fig. 1A).

Data analyses

All data analyses were performed off-line using custom-written scripts in Matlab (Mathworks). 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. The neural response amplitude 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).

For rotational stimuli, neural “sensitivity” (also referred to as “gain”) was expressed as spikes/s per °/s, whereas phase was expressed as the difference (in degrees) between peak neural activity and peak head velocity. The maximum rotational sensitivity (3D tuning) for each neuron was computed based on a cosine-tuning spatial model. Accordingly, the response gain along each spatial direction tested was modeled as the projection of the maximum sensitivity vector onto the respective direction (defined by its direction cosines). The gain and orientation of the maximum sensitivity vector (3 parameters) were then computed by minimizing (Levenberg-Marquardt method) the difference between the actual and computed gains along multiple spatial directions. For this analysis, it was assumed that the rotational sensitivity for each neuron was not dependent on the static orientation of the head relative to gravity. Validity for this assumption arises from the fact that the rotational VOR does not depend on static head orientation relative to gravity during mid and high-frequency rotations (although it does below ~0.05 Hz) (see Angelaki et al. 1995). Further, the cosine-fitting procedure assumes that no spatiotemporal convergence (STC; i.e., convergence of regular and irregular afferents from orthogonal canals) exists in the central convergence of SSC signals [although the opposite is true for otolith convergence (Angelaki and Dickman 2000; Angelaki et al. 1992, 1993; Bush et al. 1993) and canal/otolith interactions; (Baker et al. 1984)]. Although we have not systematically tested for STC through convergence of SSC signals, no experimental or theoretical evidence exists to date to suggest that it occurs.

The validity of the cosine-fitting procedure for computing the 3D rotational sensitivity vectors of the neurons was based on two goodness-of-fit criteria, the mean square error (MSE) and variance accounted for (VAF). The MSE was computed as MSE = Σ [model(v) − data(v)]²/(N − P), where data(v) represents the gain values experimentally measured at each stimulus direction v, model(v) the corresponding values estimated from the fit, N the number of different stimulus directions tested and P = 3, the number of model parameters (maximum sensitivity and the 2 direction cosines defining the orientation of a unity-length vector corresponding to the maximum sensitivity direction). VAF coefficients were computed as VAF = (1 − [var (model − data)/var (data)]). Only neurons whose fits had VAF values >80% (indicating that 80% of the gain variation as a function of stimulus orientation could be
accounted for by the cosine-tuning model) were included in the present analyses.

All computed maximum sensitivity directions (neural response vectors) were expressed in a right-handed, head-fixed coordinate system as defined in the standard 18° nose-down position, which approximately aligned the horizontal SCCs with the horizontal rotation plane. That is, the coordinate system used here is pitched relative to the stereotaxic coordinates through 18° nose-up. Positive directions for the x, y, and z axes were forward, left ear-out, and upward, respectively (see Figs. 4 and 5). For clarity, all vectors have been illustrated as if the cell was located in the left VN.

For translational stimuli, neural sensitivity (also referred to as gain) was expressed as spikes/s per g (with g = 9.81 m/s²). Unless otherwise stated, phase is reported as the difference (in degrees) between peak neural activity and peak linear velocity. The maximum sensitivity direction (spatial tuning) for each cell to translational motion in the horizontal plane was characterized by applying either a cosine-tuning function to gain only or a spatiotemporal model to both the gain and phase data simultaneously obtained at two or more orientations. The latter model is optimal for neural tuning without zero response sensitivity along any direction in the horizontal plane and response phase that exhibits a systematic dependence on stimulus direction. As described in detail in previous work (Angelaki et al. 1991; Angelaki and Dickman 2000; Bush et al. 1993), such gain and phase behavior can be modeled by two sensitivity vectors (rather than the single vector characterizing cosine-tuned neurons). The spatiotemporal model yielded consistently better VAF and MSE values than the cosineshaping model. As this issue has been dealt with in detail for the otolith-only neuron population (Angelaki and Dickman 2000), only the results from the spatiotemporal model are presented here. Similar to the rotational maximum sensitivity vectors, translation vectors were also adjusted for the left side of the brain.

To characterize the signal convergence in each neuron, the cell was considered to respond to either translation or rotation according to the following criteria (Angelaki and Dickman 2000; Angelaki et al. 2001): harmonic distortion (2nd harmonic) was <20% during rotation/translation in at least one stimulus direction; response gain was larger than a minimum (0.10 spikes/s per °/s for rotation and 15 spikes/s per g for translation) along the directions of minimum harmonic distortion. Because neurons were tested only during horizontal translation, the translational maximum sensitivity vectors were not computed in 3D but only in the horizontal x-y plane (corresponding approximately to the plane of the horizontal SCCs and the major plane of the utricle). Thus the present results mostly pertain to utricular activation. Cells with predominantly saccular inputs or cells with convergent utricular/saccular signals (Kushiro et al. 2000; Sato et al. 2000) would not have been identified as such in the present study. Thus it is possible that cells that were characterized as nonconvergent because they did not respond during horizontal plane translation do in fact receive saccular inputs.

Statistical comparisons on gain and phase values were based on two-tailed t-tests or ANOVAs. To evaluate whether neural responses to EHA rotations could be predicted according to a linear superposition of the respective responses during EVA rotations (SCC activation) and translations (otolith activation), the following analysis was performed. First, the projection of the 3D EVA response vector onto the horizontal plane and the two otolith response vectors during translation were computed. (The fitted 2-dimensional spatiotemporal model provided 2 linearly independent vector estimates, i.e., the minimum and maximum sensitivity axes in the horizontal plane. In general, each of these 3 vectors would have a different direction and a different phase.) We then used the spatiotemporal model (Angelaki 1991; Angelaki et al. 1992) to compute the direction of maximum sensitivity for each cell during EHA rotations assuming linear superposition of these three vectors (response amplitudes were adjusted to account for the ~0.015 g difference in response amplitudes between the linear acceleration stimuli during translation and head tilt relative to gravity). The computed direction, amplitude, and phase values were directly compared with the experimentally determined maximum sensitivity direction, gain, and phase of the neural response modulation during EHA rotations.

RESULTS

Responses were obtained from 268 NEM neurons located primarily in the rostral central VN. As shown in Fig. 1A, neurons were recorded in the central regions of the medial and superior VN as well as the medial portions of the lateral and rostral tip of the descending VN. Few electrode tracks were made in the caudal regions of the medial and descending or in the rostral superior or lateral regions of the VN complex. Three groups of neurons were encountered. One group of cells, termed “canal-only” neurons, responded to 3D motion stimuli similar to SCC afferents. As shown in Fig. 2, canal-only neurons exhibited no significant modulation during either horizontal or vertical smooth pursuit eye movements (Fig. 2, A and B) but were clearly modulated during both EVA and EHA rotations (Fig. 2, C and D, respectively). The cell illustrated in Fig. 2 exhibited a negligible response during yaw rotation, suggesting that it received little contribution from the horizontal SCCs. In contrast, as the head was tilted 30° up or down in the LARP canal plane (a stimulus that would put the RALP canals closer to the plane of rotation), clear responses with opposite phase were elicited (Fig. 2C, bottom). The cell also responded during pitch rotation (Fig. 2D, top), with a maximum modulation during oscillations in the RALP canal plane (Fig. 2D, middle) and null response during oscillations in the LARP plane. Similar directional tunings were true for all

![FIG. 2. Instantaneous firing rate (IFR) of a canal-only neuron in the right vestibular nuclei during various stimulus protocols. Responses during horizontal smooth pursuit (A); vertical smooth pursuit (B); earth-vertical axis rotation (EVA, C) with the animal positioned either upright (top), tilted 30° down (middle), or tilted 30° up (bottom) in the left anterior-right posterior (LARP) plane; and earth-horizontal axis (EHA, D) rotations in the pitch (top), right anterior-left posterior (RALP) (middle), or LARP (bottom) plane. EVA: earth-vertical axis; RALP: binocular horizontal (A) or vertical (B) eye position/velocity during 0.5-Hz pursuit. Positive eye movements are leftward and downward, respectively. H: angular head velocity (0.5 Hz). Positive head velocity is leftward (C) or downward (D). This cell (d51a) was classified as a type II RALP VC neuron.](http://jn.physiology.org/)

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canal-only neurons and resembled those of SCC afferents. The RALP canal-only neuron of Fig. 2 was located in the right VN and increased its firing rate with upward head velocity, a phase opposite to that of ipsilateral anterior canal afferents. Thus the cell was characterized as a type II RALP neuron. None of the canal-only cells modulated during translation (0.16–5 Hz) along any direction in the horizontal plane. In addition, when the head and body were tilted in different static positions relative to gravity, the firing rates of the canal-only cells exhibited only a transient response change and returned to their spontaneous level within a few seconds after the movement ceased. These responses were interpreted to be due to transient canal (and not due to otolith) activation.

The second group of neurons exhibited significant modulation in their firing rates during both translations and EVA rotations. Because only primary otolith afferents are activated during translation and only SCC afferents are dynamically activated during EVA rotations, these neurons were classified as "convergent" and referred to as "otolith + canal" neurons. Responses during yaw oscillation and lateral/fore-aft translation for two otolith + canal neurons are illustrated in Fig. 3. Both cells were monosynaptically activated during electrical stimulation of the ipsilateral labyrinth. The cell in Fig. 3A, located in the left VN, was excited during ipsilateral (leftward) head rotation in upright, 30° nose-up and 30° nose-down positions and was characterized as a type I HC neuron. The cell in Fig. 3B, located in the right VN, was excited during contralateral (leftward) head motion for all three positions and was characterized as a type II HC neuron. Both cells exhibited a large response modulation during lateral/fore-aft translation, indicating a strong convergent otolith input. The majority of canal + otolith neurons also exhibited static tilt sensitivity although these responses were not systematically examined.

The third group of neurons (classified as "otolith-only" cells) changed their firing rates during translation but did not modulate during EVA rotations for any head position. The spatiotemporal properties from a subgroup of these neurons were previously described in detail (Angelaki and Dickman 2000). In the present study, additional otolith-only neurons were obtained for comparison with the other cell groups to provide for a comprehensive evaluation of the multidimensional properties of all NEM neurons.

Of the 268 recorded NEM neurons, 226 cells were isolated sufficiently to be characterized during both EVA rotations and translations in multiple planes and directions. Of these 226 neurons, 50 (22%, canal-only cells) only responded during rotations, 63 (28%, otolith-only cells) only responded during translations, and 113 (50%, canal + otolith cells) exhibited sensitivity during both rotational and translational motion. These three groups of NEM neurons were scattered throughout the rostral VN (Fig. 1). Cells that were positively identified as receiving monosynaptic inputs from the ipsilateral labyrinth belonged to all three classes.

Responses to rotation

The 3D maximum sensitivity directions to rotational motion were calculated for 40 canal-only and 48 otolith + canal neurons where sufficient EVA 0.5-Hz oscillation protocols about multiple directions were obtained. These unity-sensitivity orientation vectors were plotted as projections onto the three cardinal head planes, as shown in Figs. 4 and 5. Differences in the response vector distributions were striking with a statistically significant difference in the rotational maximum sensitivity vector directions for canal-only and otolith + canal neurons [F(3,83) = 12.0, P < 0.01]. As shown in Fig. 4, canal-only neurons that did not respond during translation had maximum sensitivity vectors that were closely aligned with those of the SCC afferents. For comparison, the mean vector orientations of the horizontal canal (HC), anterior canal (AC), and posterior canal (PC) afferents in rhesus monkeys were also plotted (Fig. 4; red, green, and cyan lines, respectively) (Dickman et al. 2002). Of the 40 canal-only neurons in our sample, only 4 cells had vectors closely aligned with the HC. The majority of the sampled cells that did not respond to translation received inputs from only the vertical canals. Of these, 14 cells had vectors that were closely aligned with the ipsilateral AC, 20 cells had vectors closely aligned with the ipsilateral PC, and 2 cells exhibited type II AC responses (i.e., their vectors were aligned with the contralateral AC).

As shown in Fig. 5, the distribution of rotational maximum sensitivity vectors of the otolith + canal convergent neurons was substantially more dispersed than canal-only cells. When viewed in total as a group, these neurons had vectors that were uniformly distributed throughout the 3D space. During the recording sessions, an attempt was made to qualitatively characterize neurons as type I HC, type II HC, and VC neurons (depending on their excitability and phase during yaw rotations in upright, as well as nose-up and nose-down orientations; see METHODS). This on-line characterization is reflected in the color, lines, and symbols used in the plots of Fig. 5. As expected, HC-type convergent neurons generally lay within 45° of the z axis. Conversely, VC neurons had vectors mostly located within 45° of the x-y plane. However, because we found no difference in any of the response properties (including the gain,
phase of either rotational or translational responses as well as in the relationship between rotational and translation responses; \( P > 0.05 \) among type I HC, type II HC, and VC neurons, all cells were lumped together as otolith + canal neurons for further analyses.

Canal-only and otolith + canal cell populations differed not only in their maximum sensitivity directions but also in their sensitivity and phase to rotational motion. Specifically, the canal-only neurons had higher sensitivities and smaller phase leads as compared with the convergent neurons, as shown in Table 1. Only the phase but not the gain difference, however, reached statistically significant levels (gain: \( t_{56} = 1.7, P > 0.05 \); phase: \( t_{46} = 8.5, P < 0.01 \)). The range of rotational response gains and phases for the nonconvergent and convergent central VN populations is shown in Fig. 6. For comparison, the means \( \pm \) SD data of regular and irregular SCC afferents whose responses were obtained using identical stimuli and analyses have also been illustrated (Fig. 6, solid- and dashed-line rectangles, respectively). Differences between the central and afferent populations in both peak sensitivity and phase were observed. For example, the gains of both convergent and nonconvergent VN cells were higher than regular (but not irregular) SCC afferents (nonconvergent cells: \( t_{66} = 5.1, P < 0.01 \); convergent cells: \( t_{74} = 2.9, P < 0.01 \)). The rotational

![Figure 4: Distribution of rotational maximum sensitivity vectors for 40 canal-only neurons.](image1)

![Figure 5: Distribution of rotational maximum sensitivity vectors for 48 otolith + canal convergent neurons.](image2)
and lower than that of the irregular SCC afferents (t66 = 30.0, P < 0.01). This comparison was made only for otolith-only afferents, which lead head velocity by ∼20° (Fig. 8B), compare solid circles with the rectangles illustrating the means ± SD of the otolith afferent responses). Similar observations were also made for the nonconvergent otolith-only neurons (Fig. 8A) (see also Angelaki and Dickman 2000).

As the frequency of translational motion was varied, otolith + canal neurons exhibited a wide variety of response dynamics, as shown in Fig. 9. Because spatiotemporal (as opposed to cosine-) tuned cells in general exhibit different dynamics along different directions of motion (e.g., Angelaki and Dickman 2000), only the gain and phase values obtained for translation along the maximum sensitivity directions have been illustrated here. Response gains remained either flat, decreased, or increased as a function of stimulus frequency (Fig. 9). Response phase differed greatly at low frequencies (see also Fig. 8) and was typically in between velocity (∼90°, Fig. 9) and acceleration (0°, Fig. 9) at high frequencies. Neurons with large decreasing phase lags versus frequency (from approximately −180° to −90°) had increasing, decreasing or relatively flat gains (Fig. 9A). Neurons whose phase remained contrary to otolith-only cells (Angelaki and Dickman 2000), there was no clear preference for contralateral versus ipsilateral receptor orientations for otolith + canal neurons. The spatial tuning for the large majority of otolith + canal neurons to translation exhibited two-dimensional spatiotemporal properties. Because such a comparison between cosine- and spatiotemporal tuning has been presented in detail for otolith-only neurons before (Angelaki and Dickman 2000) and because otolith + canal cells were similar in this regard, these properties will not be further discussed here.

In contrast to rotational phase that varied little among neurons (SD < ±20°; see Table 1 and Fig. 6), neural response phase to translation (computed along the maximum sensitivity direction) exhibited a large range of values, as shown in Fig. 8 (see also Table 1). The wide phase distribution of the central otolith + canal neurons contrasts with that observed for primary otolith afferents, which lead head velocity by ∼90° (Fig. 8B), compare solid circles with the rectangles illustrating the means ± SD of the otolith afferent responses). Similar observations were also made for the nonconvergent otolith-only neurons (Fig. 8A) (see also Angelaki and Dickman 2000).

Responses to translation

The distribution of the translational maximum sensitivity vectors for the translation-sensitive neurons was determined using 0.5-Hz sinusoidal motion along different directions in the horizontal plane. As shown in Fig. 7, translational response vectors for otolith + canal convergent neurons were distributed throughout the horizontal plane with a preference for sensitivity to lateral head movements. Only six (7%) and five (6%) otolith + canal convergent cells exhibited maximum sensitivity directions within ±30° of the forward and backward motion directions, respectively. Such a preference for lateral motion and absence of tuning for fore-aft directions has also been observed for otolith-only neurons (Angelaki and Dickman 2000) as well as previously reported for decerebrate cats and rats (Bush et al. 1993; Schor et al. 1984, 1998). However,
relatively constant between linear velocity and acceleration tended to have relatively flat gains (Fig. 9B). Finally, approximately one-third of the neurons exhibited gains that decreased with frequency and phase behavior that varied greatly (Fig. 9C). These response characteristics are similar to those previously reported for otolith-only cells (Angelaki and Dickman 2000) and suggest that the spatiotemporal processing of vestibular signals during head translation are similar for otolith-only and otolith + canal neurons.

Despite the similarities between otolith-only and otolith + canal neurons in terms of the presence of spatiotemporal (non-cosine) tuning, response dynamics, and the wide distributions of phase and maximum sensitivity vectors to translation, otolith + canal convergent neurons differed from otolith-only neurons in sensitivity. Specifically, otolith + canal neurons were more sensitive than otolith-only cells (t(134) = 39.8, P < 0.01, Table 1). In addition, the otolith + canal neurons exhibited higher sensitivities to translation when compared with either the regular or irregular primary otolith afferent populations (P < 0.01).

**Relationship between rotational and translational response sensitivity vectors**

To examine if the maximum sensitivity directions for translation and EVA rotation would be congruent (i.e., complementary) during vertical plane EHA rotations for the otolith + canal convergent neurons, the following analysis was performed. First, a “canal vector angle” was calculated as the angle formed between the projection of the 3D rotational sensitivity vector onto the horizontal x-y plane and the positive x axis. Next, an “otolith rotation vector angle” was also computed as the axis of rotation about which the head had to be rotated in a vertical plane to place the translational sensitivity vector of the cell in the plane of rotation (computed by rotating the translational maximum sensitivity vector of the cell through 90°). The relationship between the computed otolith rotation vector angle and the canal vector angle for all otolith + canal cells is illustrated in Fig. 10. If the translational and rotational directional tunings for each cell were complementary for maximum congruent activation during EHA rotations, the data should fall along the unity-slope (—) line. For most of the otolith + canal convergent neurons, no such relationship between the two angles was observed. In fact, for only 9/44 (20%) cells were the computed angles within ±30° of the unity-slope line. These findings in primate VN neurons appear to be different from that previously reported for lateral-eyed species (Angelaki et al. 1993), suggesting that otolith/canal...
convergence in primates might subserve a different function (see DISCUSSION).

Responses during EHA rotations

By comparing EVA rotation and translation responses to those during EHA rotation, it is possible to further examine the patterns of convergence in otolith + canal neurons. Two specific hypotheses could be directly investigated. First, whether the recorded EHA data could be predicted from a linear combination of EVA rotation and translation responses (hypothesis 1). If so, we would conclude that central otolith + canal convergent neurons, similar to primary otolith afferents, respond equivalently to the translational and gravitational components of linear acceleration stimuli. Second, whether the recorded EHA responses could be exclusively predicted by the cell’s responses to EVA rotation (hypothesis 2). If so, we would conclude that convergent cells encode a true estimate of the translational component of the imposed motion by selectively discriminating and excluding the linear acceleration components that are due to head tilting relative to gravity.

This analysis, performed in the horizontal head plane, is first presented using an example (Fig. 11). The response tuning of this particular otolith + canal cell during EHA rotations, along with the corresponding spatiotemporal model fit, have been plotted as red circles and lines in Fig. 11. The cell of Fig. 11 was maximally sensitive during pitch EHA rotation (90° direction). Because the EVA vector was computed in 3D, the dashed green line represents the projection of the 3D EVA maximum sensitivity onto the horizontal head plane. Thus, this cell was maximally sensitive during EVA rotation about an axis approximately half way between pitch and roll (Fig. 11; 125° orientation). Finally, the amplitude and phase during translation along different directions in the horizontal plane, along with the spatiotemporal model fit are shown as blue squares and lines in Fig. 11. During translation, the cell was maximally sensitive during lateral motion (stimulus direction of 180°, corresponding to roll).

Given that the maximum translational (otolith) response was at ~180° and the maximum EVA rotational (canal) response was at ~125°, linear addition would predict an EHA response with a maximum at ~155° (Fig. 11, black lines), ~65° away from the actually measured maximum EHA response orientation. In addition, the predicted amplitude was approximately double that actually measured experimentally (Fig. 11, compare red with black lines). Thus the linear addition model (hypothesis 1) is not a good predictor of the response properties of the convergent cell during EHA rotation. The actual EHA response gain and phase measured experimentally were, in fact, closer to those computed by projecting the EVA response vector onto the horizontal plane (hypothesis 2) rather than the linear addition model (hypothesis 1).

Similar comparisons between predicted and actual EHA response maximums were performed for 29 otolith + canal neurons that were sufficiently tested during multiple directions of translation, as well as EVA and EHA rotations (Fig. 12). In only 3/29 cells were the EHA gains within 30%, as well as the EHA phases and vector orientations within ±40° of values predicted by the linear addition model (hypothesis 1; Fig. 12A, red diamonds). A larger number of neurons (8/29) complied with hypothesis 2, with EHA gains within 30%, as well as phases and orientations within ±40° of the EVA rotation values (Fig. 12B, red diamonds). Thus more central VN neurons seemed to correctly encode translation rather than “afferent-like” sensitivity to any linear acceleration regardless of source. Interestingly, the property to encode translational motion was independent of the cell’s dynamics to translation, as two of these neurons exhibited high-pass, two neurons exhibited flat, and three cells were characterized by low-pass gain dependence on frequency (Fig. 9, A–C, respectively).

DISCUSSION

The goals of the present study were threefold: first, to identify and quantitatively compare the properties of separate central neural populations insensitive to eye movements according to their sensitivity to passive 3D rotational and two-dimensional translational movements. Using distinct stimuli that selectively activate otolith versus SCC afferents (translations and EVA rotations, respectively), three different populations of NEM cells were identified (canal-only, otolith + canal, and otolith-only cells). Second, to re-examine the 3D distributions of maximum sensitivity vectors of central neurons by alleviating the limitations of previous studies, i.e., by explicitly testing if neurons exhibited sensitivity to translation and by restricting the stimuli used to compute the 3D SCC maximum sensitivity vector to only EVA rotations for otolith/canal convergent neurons. According to this 3D analysis, the two neural populations sensitive to rotation (canal-only and otolith + canal cells) were for the first time shown to have distinctly

![Image](https://www.jn.org/)
A differentiation of canal-only and otolith-only neurons in the central vestibular nuclei (VNs) was investigated. The canal-only neurons exhibit similar properties to SCC afferents, whereas the otolith-only neurons are more sensitive to translational than rotational movements. The otolith-only neurons appear to encode a true estimate of the translational component of the imposed motion by selectively excluding the linear acceleration components that are due to head tilting relative to gravity. However, the majority of central otolith + canal neurons (63%) behaved in between, whereby gravity was neither encoded equivalently as translation nor totally discriminated and ignored.

**Canal-only neurons**

Only approximately one-fourth of the cells recorded in the rostral VN of alert primates responded exclusively to SCC activation (canal-only neurons) as determined by the fact that these neurons modulated their firing rates during neither translation nor static head tilts. Even though canal-only neurons encoded 3D rotation in SCC coordinates, they differed from primary SCC afferents in both sensitivity and response dynamics. Higher central neuron response sensitivities to rotational motion as compared with SCC afferents have been reported in other species (Melvill Jones and Milsum 1970, 1971; Shinoda and Yoshida 1973), although results in alert monkeys have been unclear (because cell response characterization was not typically in their maximum response plane) (Cullen and McCrea 1993; Fuchs and Kimm 1975; Keller and Kamath 1975). The increased sensitivities of central vestibular neurons might arise through commissural inhibition as previously suggested for both the horizontal and vertical systems (Kasahara and Uchino 1974; Kasahara et al. 1968; Shimazu and Precht 1965, 1966; Uchino et al. 1986).

Differences in response dynamics to rotation between central and afferent SCC neurons have been more salient (Buettner et al. 1978; Fuchs and Kimm 1975). Typically, central rotation-sensitive neurons in alert animals (including some neurons in the present study) were found to differ from both regularly and irregularly firing SCC afferents at both high and low frequencies (Dickman et al. 2002). During high-frequency rotation, central responses were characterized by larger gain increases and larger phase leads as compared with primary SCC afferents. At low frequencies, central responses exhibited smaller phase leads than those of irregularly firing SCC afferents. Nevertheless, it should be noted that these differences between central and afferent SCC response dynamics were small, particularly when compared with those between central and afferent otolith responses (see following text). Thus central rotational responses continue to remain largely in phase with head velocity and exhibit small variability that is only slightly larger than that of the afferent SCC population (Fig. 6).

Among the three NEM cell groups identified here, the canal-only population is perhaps the one with the clearest function. Being characterized by low variability, high sensitivity responses, canal-only neurons probably provide the main rotation-selective conduit of 3D motion. Whereas a direct role in vestibulococular pathways is questionable (McCrea et al. 1987; Scudder and Fuchs 1992), canal-only neurons would be ideally suited to directly participate in vestibulospinal reflexes. In fact, discrete canal-specific activation of spinal motoneurons and neck muscles has been previously established (Isu et al. 1988; Shinoda et al. 1997; Wilson and Maeda 1974). In addition,
canal–only neurons could provide robust passive rotational signals to other structures, like cerebellum and thalamo-cortical pathways.

**Otolith-only neurons**

Another one-fourth of the recorded neurons were sensitive to head translation in the horizontal plane and were characterized as otolith-only neurons. During rotations, these neurons only responded when the axis of rotation was earth-horizontal and the head was changing orientation relative to gravity (but not when the axis of rotation was earth-vertical). Despite the fact that these neurons seemed to mainly receive otolith inputs, their properties differed from primary otolith afferents in several respects. First, the majority of central neurons were not cosine-tuned like primary otolith afferents (Angelaki and Dickman 2000). Second, because of the spatiotemporal tuning, many central neurons exhibited different dynamics during translation along different directions. Third, even when restricted to the maximum sensitivity direction, there was great variability among central neurons in terms of both response phase at a single frequency and response dynamics (Fig. 8). Finally, many central otolith-sensitive neurons were in phase with head velocity and not linear acceleration. However, because gain typically increased or remained flat as a function of frequency, these dynamics were not consistent with a central integration process (Angelaki and Dickman 2000). In fact, central otolith dynamics exhibited nonminimum phase behavior, where neurons were characterized by larger phase lags than would be expected based on the frequency dependence of the gain. Either spatiotemporal convergence (Angelaki 1992; Angelaki and Dickman 2000) and/or parallel pathways with opposite phase (Schor et al. 1985) could be responsible for the observed dynamic behaviors.

Despite the noted differences between central otolith-only and primary otolith afferent neurons, there were some similarities. Both primary otolith afferents and central otolith-only cells responded similarly during head translation and an equivalent head tilt (i.e., EHA rotation) of comparable amplitude and frequency (Angelaki and Dickman 2000). Thus central otolith-only neurons do not exclusively encode the translational motion of the head. Similarly to otolith afferents, they only encoded the resultant gravitoinear acceleration. Because of this ambiguity, the function of otolith-only central neurons remains elusive. If these cells are not local interneurons but project outside the VN, their functional roles would have to be suited to this ambiguity, possibly being involved in functions where either tilt/translation discrimination is unimportant or where additional downstream processing would be required to separate the two sources of linear acceleration.

**Otolith/canal convergent cells**

The most abundant and perhaps most interesting group of neurons identified here is the otolith + canal cells. Other than the tilt/translation issue (see following text) and higher sensitivities, the spatiotemporal properties of otolith + canal cells during translational motion were similar to those of otolith-only neurons. In contrast, the spatial properties of otolith + canal cells during rotation were different from those of canal-only neurons. Whereas canal-only cell maximum sensitivity directions were confined to the SCC planes, a wide distribution of rotational sensitivity vectors characterized otolith + canal convergent cells. To our knowledge, such a complete segregation of rotational vector distributions according to whether the cell exhibited translational motion sensitivity or not is a novel finding. In fact, other than a few reports where both rotational and translational motion stimuli were used to test the responsiveness of VN neurons (e.g., Angelaki et al. 1993; Bush et al. 1993), most previous VN studies were restricted to rotational stimuli. In these cases, determining the degree of otolith/canal convergence was based on the presumption that central otolith-related responses would appear afferent-like, i.e., modulate in phase with linear acceleration (or, equivalently, head position during rotation) and/or exhibit flat response sensitivities as a function of frequency (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). However, this presumption has been shown to be invalid, as central otolith responses are not afferent-like in multiple aspects. First and perhaps most important is the finding that many otolith-only neurons modulate during translation in phase with head velocity (rather than linear acceleration) and exhibit sensitivity increases as a function of frequency (Angelaki and Dickman 2000) (see also Fig. 9). Thus during EHA rotations otolith-driven modulations can often be mistaken for canal-mediated responses.

Thus direct comparison between the present results and previous studies that have used such afferent-like assumptions is impossible. Several studies, for example, reported on the maximum rotational sensitivity vector distributions of central vestibular neurons in cats (Fukushima et al. 1990, 1999; Graf et al. 1993; Iwamoto et al. 1996; Perlmutter et al. 1998, 1999). However, neural responses during multiple EHA rotations were combined vectorially with those during yaw EVA rotations, under the assumption that, because responses were closely in phase with head velocity, all cells were “canal-only” neurons. However, as already pointed out, these neurons could have been otolith + canal convergent or even otolith-only cells. Thus the maximum sensitivity vectors previously reported by combining EVA and EHA rotation data do not necessarily represent “SCC activation patterns.” Rather, these vectors most likely represent a directional sensitivity to head rotation produced by unknown afferent convergence.

Other findings in the present work appear more directly comparable with previous studies. For example, the high percentage of otolith/canal convergent neurons presently observed is consistent with previous neurophysiological studies using discrete rotational and translational motion stimuli (Bush et al. 1993; Lannou et al. 1980). In contrast, smaller convergence ratios have been reported using electrical stimulation of individual nerve branches (Uchino et al. 2000; Wilson and Felpel 1972; Zakir et al. 2000; Zhang et al. 2001). The implied orthogonal canal convergence evident in the present results by the wide distribution of 3D rotational vectors of otolith + canal neurons was also more extensive than what was previously suggested from electrical stimulation studies of select nerve branches (Kasahara and Uchino 1974; Markham and Curthoys 1972; Wilson and Felpel 1972). These differences could likely be due to polysynaptic pathways subserving convergence that
are typically not sufficiently activated with electrical stimulation in anesthetized or decerebrate preparations.

Functional significance for otolith/canal convergence in the primate VN

Previous investigations examined the VN responses during both 3D rotational and 2D translational motion stimuli in decerebrate rats, where a striking relationship between the rotational and translational preferences of the cells was found (Angelaki et al. 1993; Bush et al. 1993). Specifically, rat VN neurons receiving their major SCC input from the posterior or anterior SCCs were also maximally activated during linear accelerations in horizontal directions within the plane of the respective canal. Thus activation patterns would be synergistic and congruent for maximum modulation of the cell during EHA rotations from upright. These results were interpreted as the neural correlate for the behavioral observation that, during both translation and off-vertical axis rotation, the function of otolith-driven eye movements in the rat is to complement SCC-activation in achieving gaze stability during EHA rotations (Hess and Dieringer 1990, 1991).

No such congruent relationship was seen in the present population of primate VN cells, where maximum sensitivity to translation was not generally spatially aligned (in the sense of an equivalent tilt) with the cell’s major SCC input, contrary to the findings in rats. The reason for this difference could lie on the different functional roles of otolith/SCC activations during tilting movements relative to gravity in primates and laterally-eyed species. For example, “tilt” otolith reflexes are well developed in lateral-eyed species, like rats, rabbits, and birds (Baarsma and Collewijn 1975; Dickman and Angelaki 1999; Hess and Dieringer 1990, 1991), but negligible in primates and humans (Angelaki 1998; Paige and Tomko 1991; Telford et al. 1997). Moreover, otolith-driven oculomotor responses in lateral-eyed species are the same during translation and EHA rotations (Baarsma and Collewijn 1975; Barmack and Pettorossi 1988; Dickman and Angelaki 1999; Hess and Dieringer 1990, 1991), suggesting that generation of compensatory eye movements during translation is not a primary goal of the gaze stabilization system in these species (Miles 1993).

In contrast, binocular gaze stability during translation has emerged as an important function of the VOR in primates (Miles 1993, 1998). Thus primate VN have also developed a unique ability to use multisensory integration and extra-otolith signals to discriminate head translation from tilts relative to gravity, at least for high frequencies of motion when binocular gaze stability is of functional importance for foveal vision and stereovision (Angelaki et al. 1999). Because the primate rotational VOR gain is close to ideal, there would anyway be little need for otolith-driven tilt signals to augment SCC-activation during natural tilts from upright. Thus although it might be functionally beneficial for otolith and canal neural activations to be complementary during EHA rotations in lateral-eyed species, there might be little such advantage for the primate brain.

Convergence patterns of otolith and SCC signals: sensory discrimination for tilt and translation

Recent theoretical and experimental studies have provided clear evidence that otolith/canal convergence is an important aspect in the ability to effectively use extra-otolith, multisensory signals to decipher translational motion from other types of linear acceleration (Angelaki et al. 1999; Merfeld and Zupan 2002). In the present study, we directly tested whether the central convergent cells appropriately encoded head translation per se by comparing neural responses obtained with EHA rotations to those observed during EVA rotations and translations. We reasoned that if central convergent neurons appropriately encoded the translational component of the movement by being insensitive to the linear acceleration stimuli associated with changes in the orientation of the head relative to gravity, neural responses to EVA and EHA rotations should be indistinguishable. Alternatively, if convergent neurons did not discriminate translational from other sources of linear accelerations, responses to EHA rotation should be predicted as a vectorial sum of the neuron’s sensitivities to translation and EVA rotation.

We found that, contrary to otolith-only VN cells (Angelaki and Dickman 2000), very few otolith + canal neurons exhibited similar responsiveness to the two types of linear acceleration. In fact, the responses of approximately one-third of the convergent cells were consistent with a specific encoding of translational motion. However, the large majority of the otolith + canal neurons (65%) exhibited intermediate properties, where the accelerations associated with tilts relative to gravity were neither ignored nor encoded indiscriminately to translational accelerations. Thus the complex response properties of otolith + canal neurons and the simultaneous activation during both rotational and translational movements suggest that these cells might represent intermediate stages in the processing of otolith/canal interactions for the correct detection of head translation (Angelaki et al. 1999; Bos and Bles 2002; Glasauer and Merfeld 1997; Merfeld et al. 1999; Zupan et al. 2000, 2002). In agreement, a recent model of otolith/canal interactions for the generation of the translational VOR has predicted the existence of central neural populations with properties similar to those observed in the present study (Green and Angelaki 2002; Green et al. 2002). Accordingly, nonconvergent canal-only neurons with spatial selectivities aligned with those of SCC afferents and convergent otolith + canal neurons characterized by extensive orthogonal canal convergence, as well as another class of NEM VN neurons sensitive to head tilt (not encountered in the present study) (but see Zhou et al. 2000), are important cell types within a postulated brain stem network that effectively encodes head translation. In this formulation, an extensive orthogonal canal convergence is the direct consequence of a highly interconnected central network using vertical canal signals to generate a central estimate of head tilt within the horizontal motion pathway (Green and Angelaki 2002; Green et al. 2002).

The present results and recent demonstrations of differences between vestibular neuron modulation for active and passive yaw rotations (McCrea et al. 1999; Roy and Cullen 2001) clearly demonstrate the extensive processing of signals in the VN. Neck proprioceptive information gated by efference copy signals during active head movements are thought to converge afferent to reafferent sensory rotational information (Roy and Cullen 2001). When considered in relationship to 3D movement sensitivities and otolith/canal convergence, multiple functional issues are raised. For example, it is tempting to speculate that such a reafference computation is restricted to...
the nonconvergent canal-only population. In contrast, the otolith + canal neurons, whose function we postulate to be tilt/translation discrimination, might encode both the active and passive components of rotational movements. Alternatively, if the otolith + canal neurons also encode the rotational reafference signal, the actual motor commands would need to be taken into account in the resolution of translational head movements. This alternative remains plausible given that extra-vestibular information, including visual, proprioceptive, and motor command signals, is probably also involved in the difficult task of providing the best-possible estimate of inertial head and body movements.

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