An Integrative Neural Network for Detecting Inertial Motion and Head Orientation

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Green, Andrea M. and Dora E. Angelaki. An integrative neural network for detecting inertial motion and head orientation. J Neurophysiol 92: 905–925, 2004. First published March 31, 2004; 10.1152/jn.01234.2003. The ability to navigate in the world and execute appropriate behavioral responses depends critically on the contribution of the vestibular system to the detection of motion and spatial orientation. A complicating factor is that otolith afferents equivalently encode inertial and gravitational accelerations. Recent studies have demonstrated that the brain can resolve this sensory ambiguity by combining signals from both the otoliths and semicircular canal sensors, although it remains unknown how the brain integrates these sensory contributions to perform the nonlinear vector computations required to accurately detect head movement in space. Here, we illustrate how a physiologically relevant, nonlinear integrative neural network could be used to perform the required computations for inertial motion detection along the interaural head axis. The proposed model not only can simulate recent behavioral observations, including a translational vestibulocular reflex driven by the semicircular canals, but also accounts for several previously unexplained characteristics of central neural responses such as complex otolith–canal convergence patterns and the prevalence of dynamically processed otolith signals. A key model prediction, implied by the required computations for tilt–translation discrimination, is a coordinate transformation of canal signals from a head-fixed to a spatial reference frame. As a result, cell responses may reflect canal signal contributions that cannot be easily detected or distinguished from otolith signals. New experimental protocols are proposed to characterize these cells and identify their contributions to spatial motion estimation. The proposed theoretical framework makes an essential first link between the computations for inertial acceleration detection derived from the physical laws of motion and the neural response properties predicted in a physiologically realistic network implementation.

INTRODUCTION

The vestibular system plays a critical role in spatial perception and motor compensation for head movement. As in any inertial guidance system, vestibular information about the angular and linear components of head motion is provided by distinct types of sensors. The semicircular canals act as integrating angular accelerometers to provide the brain with an estimate of rotational head velocity (Fernandez and Goldberg 1971), whereas the otolith organs behave as linear accelerometers that sense net gravito-inertial force (Angelaki and Dickman 2000; Fernandez and Goldberg 1976a,b). Because everyday activities such as locomotion give rise to both translations and rotations within a gravitational field, integration of both sets of vestibular signals is vital for motion detection.

Among the most important and well-studied functions of the vestibular system is its contribution to gaze stabilization. Vestibular stimulation elicits short-latency compensatory ocular responses to head motion known as the vestibuloocular reflexes (VORs) that ensure the ability to maintain ocular stability and thus high visual acuity while moving. Early investigations of the VOR focused mainly on the sensorimotor transformations associated with rotational motion [rotational VOR (RVOR)]. More recently, compensatory responses to translation [translational VOR (TVOR)] have been investigated (Angelaki 1998; Busettini et al. 1994; Paige and Tomko 1991a,b; Paige et al. 1998; Schwarz and Miles 1991; Schwarz et al. 1989; Telford et al. 1997).

Linear acceleration information is provided to the brain by primary otolith afferents. However, linear accelerometers (including the otoliths) respond similarly to inertial and gravitational accelerations (Einstein’s equivalence principle; Einstein 1908). Thus, otolith afferents provide inherently ambiguous sensory information, given that the encoded acceleration could have been generated during either actual translation or a head reorientation relative to gravity (Angelaki and Dickman 2000; Fernandez and Goldberg 1976a,b). Yet, behavioral responses to tilts and translation are different. In the oculomotor system, for example, lateral translation elicits horizontal eye movements (Angelaki 1998; Paige and Tomko 1991a; Schwarz et al. 1991; Telford et al. 1997), whereas roll tilt generates mainly ocular torsion (Angelaki and Hess, 1996; Crawford and Vilis 1991; Haslwanter et al. 1992; Seidman et al. 1995). The integration of available sensory information to ensure that otolith signals are correctly processed to generate appropriate perceptual or motor responses thus represents an essential task for the central nervous system.

It has long been proposed that the brain integrates information from both otolith and semicircular canal afferents to differentiate translation from tilt (Guedry 1974; Mayne 1974; Young 1984). Theoretically, the canals should then also contribute to driving the TVOR (Glasauer and Merfeld 1997; Merfeld 1995; Merfeld and Zupan 2002; Mergner and Glasauer 1999; Zupan et al. 2002). This has been confirmed experimentally by examining oculomotor responses to simultaneous roll tilt and translation stimuli, carefully matched to ensure that the gravitational and translational components of acceleration along the interaural head axis cancelled one another out. Despite the absence of a net lateral acceleration stimulus to the otoliths, horizontal oculor responses appropriately directed to compensate for the translational component of motion were

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The contribution of semicircular canal cues to the generation of these horizontal eye movements was directly demonstrated by the fact that they were no longer evoked in canal-plugged animals (Angelaki et al. 1999). Recently, it has been shown that these canal-driven responses represent an extra-otolith driven TVOR that exhibits dynamic properties and a dependency on viewing distance similar to those of the purely otolith-driven reflex (Green and Angelaki 2003). Quantitative analyses demonstrated that the horizontal eye velocity profile associated with this extra-otolith driven TVOR was best correlated with angular head position, suggesting that angular velocity signals from the semicircular canals are processed by an additional neural integrator in the TVOR pathways. It was proposed that the integrative network known as the “velocity storage integrator” might perform this function (Green and Angelaki 2003).

These experimental results are consistent with the predictions of several theoretical studies that propose that the brain explicitly constructs internal estimates of gravity and translational acceleration (Glasauer et al. 1997; Merfeld 1995; Merfeld and Zupan 2002; Merfeld et al. 1993b; Mergner and Glasauer 1999; Zupan et al. 2002). To do so, the brain must effectively solve a vector differential equation that relies on an angular head velocity signal to extract the translational component of the gravity vector, suggesting that angular head velocity information, in agreement with experimental observations (Green and Angelaki 2003). This gravity estimate can then be combined with the net gravito-inertial acceleration sensed by the otoliths to extract the translational component of acceleration. Although such models have provided computationally rigorous solutions to the problem that are consistent with many experimentally observed behaviors, they are difficult to relate directly to the response properties of individual neurons. Specifically, these models use 3-component vector representations to perform the calculations required to compute head orientation in 3-dimensions (e.g., vector cross-products), whereas the instantaneous firing rate of an individual neuron is a scalar quantity. Thus, although significant progress has been made in outlining the computational requirements for resolving the tilt–translation ambiguity problem, few predictions have been made regarding the types of neural responses expected from a network that effectively implements these calculations. Specifically, how could cells involved in these nonlinear vector computations be identified and what types of experimental and analytical approaches should be used to interpret their responses?

The goals of the current investigation were twofold: 1) to illustrate how an integrative network within the traditional VOR circuitry (Green and Angelaki 2003) could implement these abstract vector computations to distinguish head translations from reorientations relative to gravity; 2) to investigate the predictions of such a structure at the neural level, with the goal of elucidating experimental paradigms appropriate for identifying and characterizing the physiological response properties of neurons involved in inertial motion detection. Preliminary versions of these results have been presented in abstract form (Green and Angelaki 2002; Green et al. 2002).

**MODEL DEVELOPMENT**

**General framework**

The general framework for the current theoretical investigation was previously proposed (Green and Angelaki 2003) and is summarized in the schematic of Fig. 1, which illustrates a feedforward model for the VOR. The classical model for sensorimotor transformations in the RVOR (Robinson 1981; Skavenski and Robinson 1973) consists of a parallel set of pathways (labeled as RVOR in Fig. 1) that convey angular head velocity signals (\(\omega_h\)) sensed by the semicircular canals, \(C(s)\), to extraocular motoneurons (Mn) both “directly” (i.e., via the short latency 3-neuron–arc VOR pathways) and “indirectly” via the oculomotor neural integrator \(N_L\) (e.g., Cannon and Robinson 1987). The bottom projection (labeled as TVOR in Fig. 1) represents a proposal for the dynamic processing of linear acceleration signals (\(\omega_t\)) sensed by the otoliths, \(O(s)\), during translation (Angelaki et al. 2001a; Green and Galiana

![Fig. 1. Overview of sensorimotor processing in the vestibuloocular reflexes. Schematic illustrates a classical feedforward diagram for the rotational vestibuloocular reflex (RVOR) (Skavenski and Robinson 1973) extended to incorporate the contributions of both otolith and semicircular canal signals to the translational VOR (TVOR) (Green and Angelaki 2003).](http://jn.physiology.org/Download/fig1.png)
A second neural integrator, \(NI_1\), accounts for the recently established contribution of integrated semicircular canal signals to the TVOR (Angelaki et al. 1999; Green and Angelaki 2003). This integrative network, which could be the so-called velocity storage integrator (Raphan et al. 1977, 1979), computes a dynamic estimate of head orientation relative to gravity that, when combined with otolith sensory signals, could be used to extract the component of linear acceleration due to translation (i.e., on cell VO\(_T\)) (Green and Angelaki 2003).

In general, the semicircular canal signals that must be combined with otolith information to extract translational acceleration depend on current head orientation. For example, both roll rotation from upright and yaw rotation from supine positions cause a reorientation relative to gravity that stimulates the otoliths along the head’s interaural axis. The extra-otolith signals required to ensure that reorientations relative to gravity are not incorrectly interpreted as translation must therefore arise mainly from vertical canals in the upright orientation, yet from the horizontal canals in the supine orientation. Thus, the circle labeled with an X at the input of \(NI_1\) illustrates a required head-orientation–dependent modulation in the coupling between semicircular canal sensory signals [i.e., at the output of \(C(s)\)] and this integrative network. The result of such a nonlinear (multiplicative) coupling of semicircular canal signals to integrator \(NI_1\) is the construction of an internal dynamic estimate of head reorientation relative to gravity (or equivalently a dynamic estimate of the gravity vector in a head-fixed reference frame), as described below.

**Mathematics of tilt–translation discrimination**

Several theoretical studies have proposed models for tilt–translation discrimination that combine otolith and canal sensory information in 3 dimensions (3D) to extract the component of linear acceleration that is due to translation from that due to head reorientation relative to gravity (Angelaki et al. 1999; Glasauer and Merfeld 1997; Merfeld 1995; Merfeld and Zupan 2002). All are based on the premise that canal information about angular velocity is used to keep track of changes in orientation of the gravity vector relative to the head (in which the vestibular sensors are fixed), as described by the first-order differential equation (Goldstein 1980)

\[
\frac{d\vec{g}}{dt} = -\vec{\alpha} \times \vec{g}
\]

where \(\vec{g}\) and \(\vec{\alpha}\) are vector representations of gravity and angular velocity, respectively, in head-fixed coordinates and \(x\) denotes a vector cross-product. Using the additional information that the net acceleration sensed by the otoliths is the vectorial difference of translational (\(\vec{f}\)) and gravitational (\(\vec{g}\)) components

\[
\vec{a} = \vec{f} - \vec{g}
\]

the translational acceleration component can be easily computed by solving the vector differential equation resulting from the combination of Eq. 1 and 2 (Angelaki et al. 1999; Hess and Angelaki 1997; Viéville and Faugeras 1990)

\[
\frac{d\vec{f}}{dt} = \vec{\omega} \times \vec{a} + \frac{d\vec{a}}{dt} - \vec{\omega} \times \vec{f}
\]

Equivalently, the same basic equations have been used to postulate that the otolith measurement of gravito-inertial force is explicitly resolved into central estimates of gravitational and translational accelerations (e.g., Glasauer and Merfeld 1997; Merfeld and Zupan 2002). Specifically, an internal 3D estimate of the gravity vector in head coordinates is obtained from Eq. 1 (i.e., \(\vec{g} = -\vec{f} \times \vec{\omega},\) assuming a known set of initial conditions). The translational acceleration component can be subsequently obtained from Eq. 2. These implementations are mathematically equivalent (Angelaki et al. 2001b). Both involve a central (nonlinear) neural integration of angular velocity, a theoretical prediction that is consistent with recent experimental observations (Green and Angelaki 2003).

Although vector Eqs 1 and 2 can be used to discriminate tilt from translation in 3D, a key focus of the current study is to predict the responses of central neurons whose firing rates are scalar quantities. Thus, to simplify the problem we have chosen to examine tilt–translation discrimination along only the interaural head axis. In particular, we can expand the vector cross-product in Eq. 1 into components as

\[
\frac{d\vec{g}}{dt} = -\vec{\alpha} \times \vec{g} = -\left[ (\vec{\omega}_x, -\vec{\omega}_z, \vec{\omega}_y), (\vec{\omega}_z, -\vec{\omega}_y, \vec{\omega}_x), (\vec{\omega}_y, -\vec{\omega}_x, \vec{\omega}_z) \right]
\]

where \(i, j, k\) are unit vectors in a right-handed coordinate system along the \(x\) [nasooccipital (NO)], \(y\) [interaural (IA)], and \(z\) [dorsoventral (DV)] axes, respectively. Integration of each vector component in Eq. 4 yields the gravitational acceleration along the \(x\), \(y\), and \(z\) axes, as illustrated in Fig. 2.

**FIG. 2.** Schematic illustration of the computations necessary to calculate the gravitational component of acceleration in a head-fixed reference frame as the head reorients relative to gravity (i.e., \(\vec{g} = -\vec{f} \times \vec{\omega}\); also see Eq. 4). Computations involve multiplications between the vector components (i.e., \(x\)-, \(y\)-, and \(z\)-axis components) of angular velocity signals \(\vec{\omega}\) (solid lines) and gravitational accelerations \(\vec{g}\) (dashed lines), followed by integration. Notice that calculation of the gravitational acceleration along any particular axis depends on the components of gravitational acceleration along the 2 other axes, illustrating the requirement for coupled integrative networks in 3D. Here we consider tilt–translation discrimination along only the interaural axis (i.e., \(y\)-axis) and thus focus on the computation of \(g_y\) (shaded region). To simplify the problem we decouple computation of \(g_y\) from its dependency on \(g_x\) and \(g_z\) by assuming that \(x\)- and \(z\)-axis translational accelerations are small (i.e., \(f_x = f_z = 0\)) such that \(g_y \approx -\vec{\alpha}_y\) and \(g_z \approx -\vec{\alpha}_z\) (see MODEL DEVELOPMENT).
Because we restrict consideration to tilt–translation discrimination along the interaural axis (i.e., y-axis associated with unit vector $j$) we focus on the calculation of $g_y$ (shaded region in Fig. 2)

$$g_y = -\int (\omega_{y\dot{z}} - \omega_{y\dot{x}})dt = -\int [\omega(f_x - \alpha_x) - \omega(f_z - \alpha_z)]dt$$

According to Eq. 5, calculation of the gravity component, along the interaural axis (y-axis) requires estimates of the components of gravitational acceleration along the other 2 axes, illustrating the 3D nature of the problem (i.e., coupled integrative networks in Fig. 2). However, the solution can be simplified if we decouple computation of $g_y$ from its dependency on $g_x$ and $g_z$ by limiting consideration to conditions where $x$- and $z$-axis translations are small (i.e., $f_x = f_z = 0$). Under these conditions, where $g_x \approx -\alpha_x$ and $g_z \approx -\alpha_z$, $g_y$ can be approximated as

$$g_y \approx \int [\omega \alpha_z - \omega \alpha_x] dt$$

The preceding equation indicates that, for the restricted conditions we consider here, the component of gravity along the interaural head axis can be computed by integrating estimates of yaw and roll head velocities that have been premultiplied by the net instantaneous accelerations sensed by otolith afferents along the nasooccipital and dorsoventral axes, respectively.

**Proposed network for tilt–translation discrimination**

**GENERAL DESCRIPTION.** Figure 3A illustrates one of many possible integrative networks (representing $N_{1,4}$ expanded from Fig. 1) that could perform the computations of Eq. 2 and 6. Circles in the schematic represent summing junctions that are used to represent different vestibular-only (VO; i.e., eye-movement–insensitive) cell populations, whereas boxes repre-

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**FIG. 3.** Proposed model for detecting head orientation and translation. A: implementation of the integrative network $N_{1,4}$ (illustrated in Fig. 1). Circles labeled VO1 through VO5 represent different populations of VO cells. Box labeled $C_{o}(s)$ represents a low-pass internal model of the semicircular canals [$C_{o}(s) = 1/(T_{o} s + 1)$]. Inputs to the model include yaw and roll velocities, $\omega_{x}$ and $\omega_{z}$, sensed by the horizontal and vertical canals [$C_{o}(s) = 1/(T_{o} s + 1)$], respectively, and interaural acceleration $\omega_{z}$, sensed by the otolith organs [$O_{x}(s) = 1/(T_{o} s + 1)$]. X’s indicate a multiplicative modulation in the strengths of the projections from cells VO1 and VO2 onto cell VO4 by nasooccipital and dorsoventral accelerations, $\alpha_x$ and $\alpha_z$, respectively. Note that these multiplications implement the head-orientation–dependent modulation illustrated in Fig. 1 at the input to $N_{1,4}$. Here, this nonlinear signal interaction is incorporated as part of the network. Parameters associated with different pathways represent the strength or weight of the projection. B: previously proposed implementation of the premotor network for the RVOR and TVOR consisting of a feedforward loop around an internal model [$F(s) = K_f(T_f s + 1)$] of the eye plant [$P(s) = K_p(T_p s + 1)$] (Angelaki et al. 2001a; Green and Galiana 1998). Semicircular canal signals project directly onto eye-contra–sensitive premotor vestibular neurons (EMC) that represent the key interneurons in the shortest-latency RVOR pathways. Eye-ipsi–sensitive premotor neurons (EMP) are proposed to mediate the shortest-latency TVOR pathways (Angelaki et al. 2001a) and receive projections from cell VO3 in A. Separate but structurally identical premotor networks were assumed to simulate horizontal and torsional eye movements. Model parameters are: $p_{0} = 1$, $p_{0} = 2.568$, $p_{0} = 0.56$, $p_{0} = 2.568$, $q_{1} = 0.25$, $q_{2} = 0.22$, $q_{3} = 0.1975$, $K_{o} = 0$, $K_{x} = 0$, $K_{y} = 1$, $K_{z} = 0$, $K_{y} = 0.1$, $K_{z} = 0.1$, $K_{x} = 0.061$, $K_{y} = 1.6$, $K_{z} = 2.75$, $a = 0.19$, $b = 0.75$, $d_{1} = 0.21$, $d_{2} = 1$, $T_{o} = 6$, $T_{x} = 0.0159$, $T_{y} = 2.81$, $T_{z} = 1$, $T_{o} = 0.25$, $T_{x} = 0.25$. Parameters $\omega_{x}$, $\omega_{z}$, $\alpha_{x}$, and $\alpha_{z}$ are used to represent the gravity component, along the interaural axis. The preceding equation indicates that, for the restricted conditions we consider here, the component of gravity along the interaural head axis can be computed by integrating estimates of yaw and roll head velocities that have been premultiplied by the net instantaneous accelerations sensed by otolith afferents along the nasooccipital and dorsoventral axes, respectively.

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sent dynamic elements or filters. These include first-order dynamic approximations of the semicircular canals, \( C(s) = T_s/(T_s + 1) \) (Fernandez and Goldberg 1971) and the otolith organs, \( O(s) = 1/(T_s + 1) \) (Fernandez and Goldberg 1976b) as well as the neural filter, \( C_{LP}(s) \), which represents a low-pass internal model of the semicircular canals \[ C_{LP}(s) = 1/(T_s + 1) \].

For the simplified case of tilt–translation discrimination along the interaural axis considered here \( (Eq. 6) \), inputs to the model include interaural acceleration, \( \alpha_i \), sensed by the otoliths (mainly the utricles), and yaw and roll head velocities, \( \omega_b \) and \( \omega_s \), sensed mainly by the horizontal and vertical semicircular canals, respectively. The 2 orthogonal accelerations, \( \alpha_i \) and \( \alpha_b \), are proposed to modulate the strengths of semicircular canal projections onto the network. Specifically, by multiplying the yaw and roll head velocity projections onto VO4 by either \( \alpha_i \) or \( \alpha_b \), the network effectively implements \( Eq. 6 \). Accordingly, cell VO5 encodes \( g_y \). The network output arises from cell VO3, which performs the addition implied by \( Eq. 2 \) to extract translational acceleration \( (i.e., f_y = \alpha_i + g_y) \). VO3 then projects directly into the downstream premotor TVOR pathways.

We focus here on an integrative network of VO neurons for two reasons: 1) populations of VO neurons have recently been observed that code mainly for either translation (vestibular and fastigial nuclei; Angelaki et al. 2003) or tilt (vestibular nuclei; Zhou et al. 2000); 2) the ability to distinguish head tilts and translations is important for both perceptual and motor responses. Both observations suggest that a network for distinguishing tilt versus translation occurs upstream of the premotor oculomotor networks of eye-movement–sensitive neurons \( (i.e., \text{network in Fig 3B}) \). In keeping with a previous proposal that the required integrative network could represent that known as the velocity storage integrator (Green and Angelaki 2003), we assume a model structure that is based on a feedback implementation of this integrative network originally proposed by Robinson (1977). Accordingly, neurons that receive direct vestibular sensory projections \( (i.e., \text{cells VO1, VO2, and VO3}) \) are each interconnected in a feedback loop with an assumed common internal low-pass canal model, \( C_{LP}(s) \), to form a distributed integrative neural network. Potentially, many other model structures could be used to implement the requirements for tilt–translation discrimination described by \( Eq. 2 \) and 6. All such networks, however, will be common in the requirements for 1) performing a central neural integration of canal signals and 2) implementing a head-orientation–dependent coupling between canal and otolith-derived sensory information. The key arguments to be made in this study focus on the implications of these common requirements and therefore are largely independent of the particular model structure. In the example network proposed here, the required integration is a distributed network property implemented by positive feedback loops through the low-pass filter, \( C_{LP}(s) \), whereas the head-orientation–dependent sensory coupling is implemented by the multiplicative interactions, denoted by X’s, in Fig. 3A.

The premotor oculomotor network used to simulate compensatory VOR responses is illustrated in Fig. 3B. It represents a feedback implementation of the “neural integration and eye plant compensation network” of Fig. 1 and was previously described in detail (Angelaki et al. 2001a; Green 2000; Green and Galiana 1998). For simplicity, we assume separate, but structurally identical, premotor networks for driving horizontal and torsional eye movements.

**DYNAMIC PROCESSING OF SENSORY SIGNALS.** The goal in this section is to illustrate the relationship between the dynamic computations performed by the model in Fig. 3A and the necessary computations for tilt–translation discrimination presented above. In particular, we will demonstrate that the network can perform the computations described by \( Eq. 6 \) to construct an internal estimate of dynamic head orientation relative to gravity on cell VO5. For descriptive purposes we will express this cell’s response in the Laplace domain. Note, however, that because canal-related projection weights onto cell VO4 \( (i.e., \text{projections from cells VO1 and VO2}) \) modulate as a function of \( \alpha_i(t) \) or \( \alpha_b(t) \), the system is nonlinear. Laplace domain descriptions thus cannot generally be used here to predict response trajectories over time. However, they can approximate the dynamic characteristics of the system for small movements about an average static head orientation \( (i.e., \text{a given operating point}) \) when the system exhibits close to linear performance. In particular, for small head movements around a given pitch orientation we can assume static approximations to the linear accelerations along the NO and DV axes \( (i.e., \alpha_i = -\sin \phi \text{ and } \alpha_b = \cos \phi \text{ in units of } g) \) where angle \( \phi \) describes the pitch angle from upright. At mid-high frequencies \( (>0.1 \text{ Hz}) \), where semicircular canal cues were previously confirmed to play a crucial role in resolving ambiguous otolith sensory information (Angelaki et al. 1999), the response of cell VO5 can then be approximated as

\[
VO_5(s) \approx \frac{G_{VOH}(s)}{s} \left( a_0(s) - \frac{\alpha_i}{s} - \frac{\alpha_b}{s} \right)
\]

where \( G_{VOH} \) and \( G_{VOV} \) are static gain terms \( (G_{VOH} = p_3 K_1 K_3/T_c \text{ and } G_{VOV} = p_4 K_2 K_3/T_c) \). \( Eq. 7 \) represents a high-frequency, small-angle approximation to the general expression for cell VO5 that assumes model parameters chosen to ensure close to ideal tilt–translation discrimination (see APPENDIX).

Because \( 1/s \) is the Laplace domain description of an integrator, \( Eq. 7 \) illustrates that the network integrates angular velocity signals, \( \alpha_i \) and \( \alpha_b \), that have been multiplied by \( \alpha_i \) or \( \alpha_b \) as required to construct an internal estimate of the gravitational acceleration component along the interaural axis \( (i.e., \text{compare Eq. 7 with Eq. 6}) \). Given an internal \( (\text{scaled}) \) estimate of \( g_y \), on cell VO5, \( Eq. 2 \) predicts that the translational component of the acceleration, \( f_y \), can be obtained by combining this estimate with the net interaural acceleration signal, \( \alpha_i \). In the model this occurs on cell VO3 \( (i.e., VO3(s) = q_i a_i(s) + \sum K a_i(s) + g(s)) \). Note that, although the analytical expressions presented in this section are valid only for small dynamic head reorientations relative to gravity, the model can simulate appropriate responses even for large tilts in all pitch head orientations, assuming that any concurrent translational acceleration is mainly directed along the y-axis of the head \( (i.e., f_x = f_z = 0; \text{ see above}) \). Further details of the Laplace domain descriptions of cell and motor responses are provided in the APPENDIX.

**Model simulations**

The proposed model was implemented using the MATLAB simulation toolbox SIMULINK (MathWorks, Natick, MA).
All simulations were performed using a fixed-step Runge–Kutta numerical integration routine (ode4 in SIMULINK) with time steps fixed at 0.01 s. The model parameters provided in the caption of Fig. 3 were chosen to satisfy the criteria outlined in the Appendix.

RESULTS

The basic predictions of the model in Fig. 3 will be explored during pure rotations and translations in different head orientations as well as for combinations of rotational and translation motion stimuli that have recently been used to investigate tilt and translation responses. To begin, we will illustrate the ability of the model to generate appropriate behavioral responses. We will then use the model to predict the neural response properties expected from the cell populations involved in estimating spatial orientation and inertial motion.

Behavioral responses

FREQUENCY RESPONSE PREDICTIONS. Figure 4 illustrates predicted horizontal and torsional ocular responses during yaw rotation, interaural translation, and small angle roll rotation (e.g., \(30^\circ\)) from upright orientation. Both yaw rotation and interaural translation are predicted to elicit large horizontal eye movements (Fig. 4, A and C; solid black curves), whereas head roll generates torsional ocular responses (Fig. 4B, solid gray curves), as required for gaze stabilization. Small torsional responses are also elicited in response to head translation, as observed experimentally (Fig. 4C, gray traces; Angelaki 1998; Paige and Tomko 1991a).

Although interaural acceleration-sensitive otolith afferents modulate similarly during both lateral translation and roll tilt, the horizontal ocular responses to these motions are quite different. Ambiguous sensory otolith information has therefore been appropriately combined with integrated semicircular canal signals in the model to ensure that dynamic head tilts do not give rise to a TVOR. This is explicitly illustrated in Fig. 4D where tilt and translation responses are both expressed relative to the acceleration stimulus; the horizontal eye velocity sensitivity to interaural linear acceleration during roll tilt is clearly attenuated compared to that during translation across all frequencies (Fig. 4D). Notice, however, that at low frequencies the predicted horizontal ocular responses to small amplitude roll rotations are nevertheless significantly larger than those reported experimentally in rhesus monkeys (compare black traces with black circles in Fig. 4B; Angelaki et al. 1999). The difference between model predictions and experimental data is much smaller when large-amplitude roll rotations are simulated (e.g., \(90^\circ\) peak roll deviations, gray squares and dash–dot lines in Fig. 4B). This is the case because of the inherent nonlinearities associated with large reorientations relative to gravity.

The deterioration in model performance with decreasing frequency occurs because the semicircular canals cease to provide perfect estimates of head velocity. In fact, when the canals are assumed to be perfect transducers of head velocity [i.e., canal transfer function \(C(s) = 1\)] negligible horizontal responses to tilt are predicted across all frequencies (Fig. 4B, black dashed lines). In the absence of an accurate canal estimate of head velocity in the real physiological system, other strategies for distinguishing tilt from translation are required to achieve appropriate behavior at low frequencies (e.g., Mergner and Glasauer 1999; Paige and Tomko 1991a; Telford et al. 1997). In the following, we will focus on simulations of cell responses at frequencies above 0.1 Hz, where the semicircular canals provide reliable estimates of head velocity and the network appropriately discriminates tilts and translations.
SIMULATED BEHAVIORAL RESPONSES TO TILT–TRANSLATION COMBINATIONS. Novel combinations of translational and roll tilt movements have recently been used to investigate semicircular canal and otolith contributions to oculomotor responses (Angelaki et al. 1999; Green and Angelaki 2003). Similar stimulus combinations were used to simulate the performance of the model. Four protocols are illustrated at the top of Fig. 5A that consist of either lateral translation (Translation only), roll tilt (Roll tilt only), or combined lateral translation and roll tilt motion stimuli (Roll tilt + Translation motion and Roll tilt – Translation motion). Because the interaural acceleration ($\alpha_e$) stimulus to the otoliths was matched for Translation and Roll tilt motions (each set to a peak of 0.2 g at 0.5 Hz; Fig. 5A, bottom row), combined motion stimuli result either in a doubling of the interaural acceleration stimulus (Roll tilt + Translation) or zero acceleration (Roll tilt – Translation), depending on the relative directions of the two stimuli.

Simulations of the model output for the sinusoidal tilt–translation protocols are illustrated in Fig. 5A. Horizontal eye velocities (TVOR) of similar amplitude are predicted during all movements that include a translational component (Fig. 5A, solid black traces, top row). In addition, torsional eye velocity (RVOR) is elicited whenever the movement includes a roll component (Fig. 5A, dashed gray traces, top row). In contrast, no horizontal TVOR is predicted during pure roll tilt, despite the presence of an identical interaural acceleration stimulus to the otoliths (Fig. 5A, compare columns 1 and 2). Notice that an appropriate TVOR is elicited even in the absence of an interaural acceleration stimulus to the otoliths during Roll tilt – Translation motion. These predictions are compatible with recent observations in rhesus monkeys (Angelaki et al. 1999; Green and Angelaki 2003).

The model can also predict appropriate eye movement responses with the head in supine orientation (Fig. 5B). For example, roll rotation and lateral translation elicit torsional and horizontal responses, respectively (Fig. 5B, columns 1 and 2). More interesting is the case of supine yaw rotation that dynamically stimulates the otoliths along the interaural head axis (Fig. 5B, column 3). This stimulus condition presents a similar ambiguity problem to the case of roll tilt from upright. Specifically, because the otoliths are dynamically stimulated during supine yaw rotation, horizontal eye velocity could potentially reflect a combination of TVOR and RVOR response components. If otolith signals were not appropriately interpreted by the brain, supine yaw rotation would elicit significantly smaller horizontal responses than upright yaw rotation.

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**Fig. 5.** Simulated behavioral responses. A: horizontal and torsional eye velocity responses ($E_{\text{hor}}$, solid black; $E_{\text{tor}}$, dashed gray) to 4 tilt–translation stimulus paradigms at 0.5 Hz (i.e., Translation only, Roll tilt only, Roll tilt + Translation, and Roll tilt – Translation; Angelaki et al. 1999; Green and Angelaki 2003). B: ocular responses during Supine Roll, Supine Translation, Supine Yaw, and Upright Yaw motions. Bottom 2 traces in A and B illustrate the stimuli: roll and horizontal angular velocities ($\alpha_e$, solid black; $\alpha_s$, dashed gray lines); net and translational components of the interaural acceleration ($\alpha_e$, solid black; $f_{\text{y}}$, dashed gray lines).
whereas larger horizontal eye velocities would be predicted in the prone orientation. However, model simulations result in identical horizontal eye movements during both upright and supine yaw rotations (Fig. 5B; compare columns 3 and 4). Thus, just as in the case of roll tilt from upright, interaural accelerations attributed to a head reorientation relative to gravity during supine yaw rotation are appropriately distinguished from translation.

Neural response predictions and simulations

Given a model that predicts appropriate behavioral responses, we may now address the predicted response properties of different average neural populations within such a network. First, we will illustrate the frequency response predictions for each cell type during pure roll tilts and translations, as well as their responses to earth-vertical–axis rotations in different pitch head orientations when the canals are stimulated in isolation. We will show that in the integrative network proposed here, traditional interpretations of the responses to these stimuli embed assumptions that can lead to incorrect conclusions with respect to the signals encoded by central neurons. The goals of this section will be to illustrate this point and then to consider experimental protocols appropriate to reveal the underlying properties of the network.

FREQUENCY RESPONSE AND EARTH-VERTICAL–AXIS ROTATION PREDICTIONS. Neurons VO1 and VO2 exhibit the expected characteristics of semicircular-canal–sensitive cells, coding for head rotation in head coordinates (Fig. 6). In both upright and supine orientations, cell VO1 modulates in phase with angular yaw velocity but does not respond during roll rotation (Fig. 6, B and C, black traces), whereas cell VO2 responds exclusively to roll rotations (Fig. 6, B and C, gray traces). Neither cell group modulates during a pure translational stimulus (Fig. 6A). The canal afferent-like behavior of cells VO1 and VO2 also holds for earth-vertical–axis rotations at different static pitch orientations (Fig. 6, D and E). Cell VO1 responds maximally during earth-vertical–axis rotation in the upright orientation (i.e., during yaw rotation for a pitch angle = 0°), exhibiting a sensitivity that drops off with the cosine of pitch angle from upright, as predicted for a dominantly horizontal canal-sensitive cell. Similarly, cell VO2 exhibits no modulation during earth-vertical–axis rotation with the head upright and maximal

![FIG. 6. Predicted responses for cell populations VO1 and VO2. A–C: frequency response predictions for cells VO1 (black) and VO2 (gray) during (A) translation, (B) roll rotation, and (C) yaw rotation in upright (solid curves) and supine (dashed curves) orientations. Cell response sensitivities and phases are expressed relative to head velocity. D–E: predicted responses for cells (D) VO1 and (E) VO2 during earth-vertical–axis (EVA) rotations at 0.5 Hz in different static pitch orientations (0°, upright; 90°, prone; −90°, supine).](http://jn.physiology.org/doi/10.1152/jn.011005.0912)
responses in the prone and supine positions (i.e., pitch angles of ±90°) consistent with this cell receiving mainly vertical semicircular canal inputs (Fig. 6E). Accordingly, the properties of VO1 and VO2 are consistent with cells described as “canal-only” neurons (Dickman and Angelaki 2002).

Cells VO3 and VO4 reflect a more complicated processing of sensory information. These neural populations exhibit strong modulations during high frequency translation, in phase with either ipsilaterally or contralaterally directed linear acceleration in both upright and supine head orientations (i.e., phase of ±90° relative to head velocity; Fig. 7A). Their activities thus reflect high-pass responses to translational velocity. Although the robust translational responses of cells VO3 and VO4 clearly demonstrate an otolithic sensory contribution to their activities, there is no evidence for a canal contribution during earth-vertical–axis rotations (Fig. 7D and E). Nonetheless, cell VO4 exhibits a robust response at high frequencies during roll tilt from upright or yaw tilt from supine orientations (solid gray curves in Fig. 7B and dashed gray curves in Fig. 7C, respectively) that is in phase with angular head velocity (i.e., phase of −180° during upright roll and 0° during supine yaw).

In contrast, cell VO3 exhibits little modulation during high frequency head reorientations relative to gravity despite the presence of a gravitational stimulus to the otoliths. Thus, as predicted, cell VO3 distinguishes between inertial and gravitational accelerations, coding selectively for translational accelerations. The response of this model cell population is compatible with those of cells in the vestibular and fastigial nuclei that have been shown to preferentially encode the translational component of linear acceleration (Angelaki et al. 2003).

In contrast to cells VO3 and VO4, VO5 does not respond during translation (Fig. 8A). It also exhibits no response during earth-vertical–axis rotations (not shown) but modulates in phase with angular position (−180° or 0° phase) during roll or yaw rotations when the rotation involves a dynamic head reorientation relative to gravity (Fig. 8, B and C). Thus in agreement with theoretical predictions (see Model Development), cell VO5 encodes angular head position relative to gravity or tilt (more generally, g; see Appendix). Although we focus here on responses at mid-high frequencies (>0.1 Hz) it is relevant to note that VO5 is also predicted to respond to
static head tilt. Cells that respond robustly to both static and dynamic head tilts from upright but not to high-frequency translation have been observed in the vestibular nuclei (Zhou et al. 2000).

In summary, the idealized model predicts several average cell populations that are compatible with those observed experimentally, including cells that respond exclusively to canal stimulation (i.e., cells VO1 and VO2) as well as cells that preferentially encode either head translation (cell VO3) or tilt (cell VO5). Yet, using the stimuli described in Fig. 6 through 8, incorrect conclusions would likely be reached regarding the sensory contributions to their responses. In particular, because cells VO3, VO4, and VO5 fail to modulate during earth-vertical–axis rotations, it might be concluded that their activities do not reflect canal signal contributions (a conclusion that is incorrect). Neither can their responses be directly correlated with the sensory otolith signal because none of these cell groups encodes the net gravito-inertial acceleration. As a result, their responses during earth-horizontal–axis rotations (i.e., combined otolith and canal stimulation) do not reflect a simple summation of their activities during translation (estimated otolith contribution) and earth-vertical–axis rotations (estimated canal contribution).

This observation has in fact been made for many central translation-sensitive vestibular neurons (Dickman and Angelaki 2002) and was used to suggest that the activities of such neurons might reflect intermediate processing stages in distinguishing between head tilt and translation. Yet the question of how this distinction is made remains unanswered. The model proposed here provides an explanation. Specifically, the responses of cells VO3, VO4, and VO5 differ from those of sensory otolith signals because their activities do indeed reflect the contribution of semicircular canal inputs (Fig. 3A). However, these cells do not code for rotation in the head-fixed reference frame of the canal sensors. Because of the multiplicative canal–otolith interactions at the input to cell VO4, the activities of these cells instead reflect spatially referenced canal signal contributions aligned with the earth-horizontal axis (e.g., vertical canal signals during tilts from upright and horizontal signals during tilts from supine head orientations). They thus encode only the component of rotation orthogonal to gravity that is not observed during earth-vertical–axis rotations. Such a postulated canal-derived signal would nevertheless be difficult to detect because it contributes only under conditions that typically simultaneously stimulate the otoliths. In the following section, we will address how the proposed “hidden” semicircular canal signal contribution to the responses of these neurons can be isolated.

SIMULATED RESPONSES TO COMBINED TILT–TRANSLATION STIMULI. To isolate the contribution of semicircular canal signals to the neural activities of cells VO3, VO4, and VO5 we may investigate the simulated responses of the model neurons for the same set of stimulus combinations employed to examine behavioral responses (Fig. 9). As expected based on the analytical predictions in Figures 6 through 8, cells VO1 and VO2 code for horizontal and roll head velocity, respectively, regardless of head orientation (Fig. 9, A and B). In contrast, VO3 exhibits negligible responses to roll and yaw rotations, in both upright and supine head orientations (e.g., Fig. 9C, columns 2 and 5) but encodes the translational component of acceleration (Fig. 9C, similar responses in columns 1, 3, and 4). Cell VO5, on the other hand, codes specifically for head tilt relative to gravity, responding during either upright roll (Fig. 9E, columns 2, 3, and 4) or supine yaw (Fig. 9E, column 5) but not during pure translation. Finally, cell VO4 exhibits a more complex behavior, being sensitive to both translation and head reorientation relative to gravity.

Although earth-vertical–axis rotations do not reveal the contribution of semicircular canal signal inputs to cells VO3, VO4, and VO5 (e.g., Fig. 7, D and E), notice that all 3 cell populations modulate with sinusoidal responses during Roll tilt – Translation motion (Fig. 9, column 4). This observation is relevant because during this unique protocol there is no net linear acceleration along the interaural head axis and thus no sensory stimulus along this axis to the otoliths (Fig. 9G, column 4). Therefore, the modulation in the firing rates of these cells must be attributed to semicircular–canal–derived signals. Specifically, during the upright Roll tilt – Translation proto-
col, VO4 cell responses are entirely driven by vertical semicircular canal signals. These signals are subsequently integrated by the network to produce the head tilt position responses of cell VO5. It is a scaled version of this same integrated canal signal that appears on cell VO3 (Fig. 9C, column 4) and is subsequently used to drive compensatory responses to translation during Roll tilt – Translation motion, even in the absence of an appropriate dynamic otolith stimulus. Thus, the Roll tilt – Translation motion paradigm unmasks a semicircular canal contribution to the activities of these cells that might otherwise remain “hidden” during earth-vertical–axis rotations in all head orientations.

Variability in individual cell responses

Using a particular model structure and parameter set chosen to achieve ideal tilt–translation discrimination we have illustrated the response properties of several average cell populations within this network. However, in contrast to these idealized model cells, the majority of experimentally observed translation-sensitive neurons do in fact exhibit responses to earth-vertical–axis rotations that reflect the sensory contribution of signals from multiple orthogonal canals (Dickman and Angelaki 2002). Furthermore, relatively few cells have been isolated that respond exclusively to tilt or translation (Angelaki et al. 2003; Zhou et al. 2000), suggesting that these variables may be encoded mainly as population averages (i.e., as represented by our average model neurons).

In the following sections we will explore the effects of varying particular parametric assumptions in the model with two key goals: 1) to examine a more realistic representation of the properties of individual neurons that contribute to the average population responses; 2) to further explore the implications of the most fundamental properties of the proposed model that must be shared by any neural network that effectively implements Eq. 4. These include its function as a neural integrator and the requirement for a coordinate transformation of canal signal contributions. To illustrate these issues we will consider how changes in the coupling of semicircular canal and otolith signals onto the network impact on the expected properties of individual neurons and their compatibility with experimental observations.

VARIABLE SEMICIRCULAR CANAL-RELATED PROJECTION WEIGHTS. To achieve close to ideal tilt–translation discrimination in the proposed model we assumed that the net projections from each canal onto cell VO4 (i.e., indirect projections from cells VO1 and VO2) were equal in strength and entirely

FIG. 9. Simulations of model cell responses. A–E: firing rate modulation of cells VO1 through VO5 during the 4 tilt–translation protocols in the upright orientation (columns 1–4; see Fig. 5 legend and text) and for supine yaw rotation (column 5). F: angular roll and yaw velocities (ωr, solid black; ωθ, dashed gray lines). G: net and translational interaural accelerations (αz, solid black; fzz, dashed gray lines).
head-orientation–dependent (i.e., \( K_{VH} = K_{2H} \) and \( K_{VH} = K_{2V} = 0 \) in Fig. 10A and Fig. 3A; see Fig. 3 legend). Average cell populations VO3, VO4, and VO5 were then predicted to exhibit no response during earth-vertical–axis rotations (e.g., solid black trace with zero gain in Fig. 10B; see also Fig. 7, D and E). Using the VO4 cell population as an example, we will now examine the effect of relaxing these parametric assumptions to explore the expected range of responses from individual neurons within this population.

We may begin by examining what happens if there is a head-orientation–independent canal component to an individual VO4 cell’s response (i.e., \( K_{VO} \neq 0 \) and/or \( K_{2O} \neq 0 \)). For example, in addition to head-orientation–dependent projections (still assumed to be equal at this point), a VO4 neuron could also receive small head-orientation–invariant horizontal and vertical canal contributions (\( K_{1o} = 0.2, K_{2o} = 0.2 \)). Under these conditions, the cell would exhibit the cosine-type tuning during earth-vertical–axis rotations expected for a neuron equally sensitive to horizontal and vertical canal inputs, thus demonstrating evidence for orthogonal canal–canal convergence (Fig. 10B, solid gray curve). The tuning exhibited by the cell is nonetheless clearly different from the responses that would be observed if all sensory canal projections were invariant to head orientation (Fig. 10B; compare dotted black and solid gray curves). Although the cell would no longer be classified as an “otolith-only” neuron, a significant component of the canal contribution to its response would remain hidden unless somehow explicitly unmasked (e.g., during Roll tilt – Translation motion).

More fundamental to the arguments here are the predictions made when the assumption of equal orientation-dependent horizontal and vertical canal-related projections is relaxed (i.e., \( K_{1o} \neq K_{2o} \)). In this case, the predicted responses no longer reflect simple cosine tuning patterns, but rather exhibit second harmonic spatial tuning properties (e.g., solid black and gray curves in Fig. 10C) indicative of head-orientation–dependent canal signal contributions (see Appendix for details). Notably, such spatial tuning might not be apparent for small pitch angles, given that these curves could appear similar to those of a neuron that receives exclusively orientation-independent vertical canal signals (Fig. 10C, compare solid black and dotted traces). Examination of cell response properties over a large range of static tilt angles (e.g., \( \pm 90^\circ \)) is therefore likely to be necessary to reveal the presence of head-orientation–dependent rotational sensitivities.

More generally, individual neurons are likely to receive different combinations of orientation-dependent and -independent canal projections, giving rise to a range of response patterns during earth-vertical–axis rotations that reflect different degrees of convergence from multiple orthogonal canal sensors, as observed experimentally (Fig. 10D; Dickman and Angelaki 2002; Siebold et al. 2001). When examined over a larger range of head orientations than those typically used (\( \pm 30^\circ \); e.g., Dickman and Angelaki 2002; Siebold et al. 2001), however, their responses are expected to differ considerably from the simple cosine-tuned behavior that has traditionally been assumed for vestibular neurons. Such response patterns do not simply reflect the particular model structure chosen here but would be expected in any network in which head-orientation–dependent canal- and otolith-derived signals converge to distinguish tilts and translations according to the requirements implied by Eq. 2 and 4. Hence, although these complex tuning properties have yet to be observed experimentally, they represent a fundamental model prediction that remains to be tested.

VARIABLE OTOLITH SIGNAL PROJECTION WEIGHTS. Otolith signals couple onto the model network not only through cell VO3, but also through sensory projections directly onto cell population VO4 (projection with weight \( q_2 \)) and into the neural filter \( C_{LP}(s) \) (projection with weight \( q_3 \)). The weights of these parameters were chosen both to set particular cell sensitivities to translation and to ensure that cell VO3 exhibits high-pass filtered responses to otolith stimulation with a minimal response to static head tilt (see Appendix). With the chosen parameter set the average neural populations responsive to translation (i.e., cells VO3 and VO4) were predicted to modulate closely in phase with head acceleration (Fig. 7). However, a consistent, yet so far unexplained, experimental observation is that eye-movement–insensitive vestibular neurons exhibit dynamic responses to translation that are highly variable and often quite different from those of otolith afferents (Angelaki and Dickman 2000; Chen-Huang and Peterson 2002; Dickman and Angelaki, 2002; Musallam and Tomlinson 2002; Tomlinson et al. 1996). Next we will illustrate that by changing a single parameter, weight \( q_3 \), individual neurons with a wide range of dynamic responses to head translation are predicted in the proposed model. Changes in this single parameter are
sufficient to illustrate a large range of response gains and phases during translation without affecting the integrative properties of the network.

Figure 11 illustrates distributions of the predicted gains and phases (relative to translational acceleration) of neural populations VO3, VO4, and VO5 at 0.5 Hz when weight $q_3$ was randomly varied according to a Gaussian distribution about its nominal value (see Fig. 11 legend). Notice that both populations VO3 and VO4 can exhibit a broad distribution of response phases reflecting either lags relative to ipsilaterally directed or leads relative to contralaterally directed acceleration (Fig. 11, A and B). This is particularly evident in the case of the VO3 population that exhibits a phase distribution peak more closely aligned with translational velocity ($\pm 90^\circ$) than acceleration ($0^\circ$ or $-180^\circ$). In addition, whereas with the nominal parameter set cell VO5 was predicted to respond only to head tilt, with changes in weight $q_3$ the cell may also exhibit responses to translation. Notice, however, that these translational responses are always in phase with either ipsilaterally or contralaterally directed translational velocity ($\pm 90^\circ$; Fig. 11C).

These points are further emphasized in Fig. 11D where the response gains and phases for cells VO3, VO4, and VO5 are plotted as a function of frequency for an example case where $q_3 = 1$. Each cell population now exhibits distinct dynamic characteristics such that at 0.5 Hz a range of response phases relative to translational acceleration are evident, consistent with experimental observations (Dickman and Angelaki, 2002). Notably, cell VO5 modulates in phase with translational velocity, exhibiting low-pass response characteristics relative to translational acceleration. This observation is consistent with the dynamic properties of cells shown to predominantly encode head tilt at high frequencies (Zhou et al. 2000).

It should be noted that because the characteristics of cell population VO3 are quite sensitive to changes in $q_3$, varying this parameter in isolation alters the VO3 population response and hence the average model behavior. This is indicated by the stars in Fig. 11A, which compare the mean gains and phases of cell population VO3 using the nominally chosen parameter set (gray stars) with the average response characteristics after varying parameter $q_3$ (black stars). Behavioral performance identical to that illustrated previously is nonetheless possible if inputs to the premotor TVOR pathways (i.e., onto cell EMl in Fig. 3B) are presumed to include a weighted combination of direct sensory otolith projections in addition to inputs from cell VO3 (assuming also appropriate adjustments in canal projection weights onto network Nl1). Indeed, a contribution of direct sensory projections to the TVOR is compatible with the neuroanatomical observation that the shortest latency, although weak, sensory otolith projections to the abducens are monoand disynaptic (Uchino et al. 1994).

Most relevant to the investigation here is the fact that the framework provides a functional rationale for the wide range of
central response dynamics observed during translation (Angelaki and Dickman 2000; Chen-Huang and Peterson 2002; Dickman and Angelaki 2002; Musallam and Tomlinson 2002; Tomlinson et al. 1996; Zhou et al. 2000, 2001). Although such dynamic characteristics could appear consistent with a low-pass versus high-pass filtering strategy for distinguishing tilts and translations (Paige et al. 1991a; Telford et al. 1997), they arise here as the result of coupling otolith sensory signals to an integrative network that combines otolith and canal sensory information to solve the differential equations necessary to detect head orientation in space.

DISCUSSION

The detection of motion in a gravitational field poses particular computational demands on the central nervous system because inertial and gravitational linear accelerations are sensed equivalently by the otoliths. To accurately distinguish between the two requires an estimate of changes in head orientation, implying the requirement for an integration of information from multiple sensory organs (Guedry 1974; Mayne 1974; Young 1984). Indeed, recent experimental studies of perception and oculomotor behavior have confirmed not only that tilts and translations are appropriately discriminated in the frequency range where the canals provide accurate estimates of head velocity, but that information from these angular sensors (in the absence of nonvestibular cues) is essential to resolve the ambiguity (Angelaki et al. 1999; Green and Angelaki 2003; Merfeld et al. 2003; also see Merfeld et al. 1999). Furthermore, both experimental observations (Green and Angelaki 2003) and theoretical predictions (Angelaki et al. 1999; Bos and Bles 2002; Glasauer and Merfeld 1997; Hess and Angelaki 1997; Merfeld 1995; Merfeld and Zupan 2002; Mergner and Glasauer 1999; Viéville and Faugeras 1990; Zupan et al. 2002) imply that resolution of the problem involves a temporal integration of angular velocity information.

Here, we have illustrated an integrative network that can compute an internal estimate of head orientation relative to gravity along the interaural head axis at mid-high frequencies (e.g., >0.1 Hz). In conjunction with net linear acceleration signals provided by the otoliths, the translational acceleration component can then be extracted to provide an appropriate drive to motor and perceptual systems. Our investigation here is novel in that we explore the problem in a physiologically relevant (albeit limited) context, where the scalar firing rate activities of different populations of neurons can be predicted. We illustrate that the computations for discriminating tilt and translation can be performed by an integrative network in which the strengths of canal signal projections modulate non-linearly (i.e., in a multiplicative sense) as a function of current head orientation. The most important feature of the approach is that it implies the existence of cells that respond to rotational stimuli from the canals differently depending on head orientation. As described below, this observation has important implications both for the characterization of cell responses and for identifying their contributions to spatial motion estimation.

Comparison of model predictions with experimentally observed neural response properties

The properties of populations of neurons likely to be involved in inertial motion estimation have been characterized during rotation and/or translation in several brain areas including the vestibular nuclei (Angelaki and Dickman 2000; Angelaki et al. 1993; Baker et al. 1984a,b; Brettler and Baker 2001; Bush et al. 1993; Chen-Huang and Peterson 2002; Dickman and Angelaki 2002; Endo et al. 1995; Fukushima et al. 1990; Graf et al. 1993; Iwamoto et al. 1996; Kasper et al. 1988; Musallam and Tomlinson 2002; Perlmuter et al. 1998, 1999; Schor et al. 1984, 1985; Wilson et al. 1990, 1996; Yakushin et al. 1999) and the rostral fastigial nucleus of the cerebellum (Siebold et al. 1997, 1999, 2001; Zhou et al. 2001). However, despite extensive characterization of the spatial tuning characteristics of such neurons, in many studies otolith and canal signal contributions were not adequately distinguished (see below). Furthermore, the neural correlates for the computations underlying tilt–translation discrimination are only now beginning to be investigated. Thus, the data with which our model predictions can be directly compared are currently limited. Using one potential model structure that can perform the computations implied by Eq. 2 and 6 to distinguish tilts and translations, we have nonetheless illustrated the ability to predict distinct average cell populations that are compatible with those observed experimentally to date. These include neurons that respond mainly to head rotation (“canal-only” cells) with spatial response selectivities closely aligned with a particular canal plane (e.g., cells VO1 and VO2; Dickman and Angelaki 2002) as well as neurons that code explicitly for internal dynamic estimates of either translation (cell VO3; Angelaki et al. 2003) or tilt (cell VO5; Zhou et al. 2000).

Most central translation-sensitive neurons, however, encode neither exclusively translation nor tilt (Angelaki et al. 2003). In fact, the most consistent experimental observation is a wide distribution of response properties that are difficult to interpret (Angelaki and Dickman 2000; Chen-Huang and Peterson 2002; Dickman and Angelaki 2002). As will be elaborated on below, two particular aspects of the framework explored here are not only compatible with general characteristics of experimentally observed responses, but lend particular insight as to the strategies likely used by the brain to estimate spatial orientation and motion.

A first general experimental observation is that the dynamic characteristics of central responses to translation are highly variable and typically quite different from those of sensory otolith afferents (Angelaki and Dickman 2000; Chen-Huang and Peterson 2002; Dickman and Angelaki 2002; Musallam and Tomlinson 2002; Tomlinson et al. 1996; Zhou et al. 2001). Cells with a wide range of response phases relative to the sensory stimulus have been observed during 0.5-Hz translations, and many modulated more closely in phase with translational velocity than acceleration (Angelaki and Dickman 2000; Dickman and Angelaki 2002). Although the contribution of an integrative element to their response dynamics was apparent (Angelaki and Dickman, 2000; Dickman and Angelaki 2002; also see Musallam and Tomlinson 2002) its origin and functional role remained unexplained. The current model provides a potential functional rationale for this observation. Both a variability in response phase and a tendency toward encoding head velocity at midrange frequencies (e.g., 0.5 Hz) are not only predicted but in fact almost inevitable consequences of coupling otolith sensory signals to an integrative network for detecting head orientation (e.g., Fig. 11).
A second general observation is that neurons sensitive to dynamic otolith stimulation in the vestibular and fastigial nuclei exhibit either no response during earth-vertical–axis rotations or complex spatial tuning properties with characteristics of orthogonal canal–canal convergence (Dickman and Angelaki 2002; Siebold et al. 2001). A functional significance for this experimental observation is also provided by the framework proposed here. We have illustrated that the ability to distinguish tilts and translations at mid-high frequencies implies a convergence of otolith information with sensory signals from multiple sets of canals (e.g., Figs. 3A and 10). Furthermore, because the problem of tilt–translation discrimination also implies a head-orientation–dependent coupling between canal and otolith signals, many central vestibular neurons may not encode rotational signals in the head-fixed reference frame of the canal sensors. As a result, any component of their responses aligned with an earth-horizontal axis would not be isolated during earth-vertical–axis rotations. This can account for the experimental observation that their responses during earth-horizontal–axis rotations (i.e., combined otolith and canal stimulation) often cannot be predicted by a vector summation of their activities during translation (estimated otolith contribution) and earth-vertical–axis rotations (estimated canal contribution; Dickman and Angelaki 2002).

In the following section, we consider how these two key features of the proposed model (i.e., its integrative properties and multiplicative canal–otolith interactions) expected to be common to any network that effectively solves Eq. 2 and 4, have an impact on the interpretation of neural activities and the protocols required to identify their functional contributions to the problem of distinguishing inertial and gravitational accelerations.

Implications for investigating neural response properties

The requirements for discriminating tilt and translation are relatively straightforward from a theoretical standpoint. However, the task of identifying how the brain actually uses the available sensory information to perform the required computations represents a much greater challenge because rotations that reorient the head relative to gravity stimulate both the canals and the otoliths simultaneously. Key to addressing how the required processing takes place is the question of how the contributions from each sensor should be identified.

Most studies to date have characterized cell responses only during purely rotational movements. The extent of canal–otolith convergence was often then estimated based on the assumption that the contributions from each sensor would mimic the dynamic characteristics of the corresponding afferent population. Specifically, whereas canal afferents encode angular velocity, otolith afferents modulate in phase with linear acceleration, a signal that appears proportional to angular head position during small angular reorientations relative to gravity (e.g., Fig. 12A, top). Experimental observations of large changes in response phase, including spatiotemporal convergence (STC) properties, have thus typically been attributed to a convergence of canal and otolith signals (Baker 1984b; Endo et al. 1995; Kasper et al. 1988;Perlmutter et al. 1998, 1999; Siebold et al. 1997, 1999;Wilson et al. 1990). Notably, however, studies in which the otoliths were stimulated in isolation have illustrated that such an assumption is invalid

(Angelaki and Dickman 2000; Bush et al. 1993; Dickman and Angelaki 2002; Schor et al. 1985). This is also suggested by the theoretical investigation here.

A key feature of the proposed model is that it performs a temporal integration of semicircular canal signals to construct an internal estimate of dynamic head tilt. If both the otoliths and canals converge on such a network, the respective contributions from each sensor may reflect signals in phase with either head position or velocity at various points within the circuit. As summarized in Fig. 12A, whereas the otolith- and canal-related signal contributions of cells at the input of such an integrative network would closely reflect the dynamic characteristics of the respective sensory signals, cells at the output end of such an integrator (e.g., cell VO5) would reflect apparently “opposite” dynamic characteristics (e.g., Fig. 12A, bot-
For example, the tilt responses of cell VO5 in phase with angular head position at mid-high frequencies arise almost exclusively from semicircular canal signal contributions, whereas any otolith sensory contribution to cell population VO5 is predicted to modulate in phase with translational velocity (e.g., Fig. 12, bottom, Fig. 11, C and D). Other cells may reflect sensory signals that have been dynamically processed to different extents. Clearly, therefore, response dynamics should not be used to dissociate otolith versus canal sensory contributions at central stages of vestibular processing.

Recent studies of central vestibular neurons have alternatively examined cell responses during earth-vertical–axis rotations to isolate the canal contributions to cell responses in the absence of a dynamic stimulus to the otoliths (Dickman and Angelaki 2002; Siebold et al. 2001). A key assumption in employing this approach, however, is that central sensitivities to canal signals are invariant to head orientation (e.g., Fig. 12B, top). Again, the present investigation emphasizes that this approach may be invalid. The vector cross-product computations required to solve Eq. 4 imply that the brain constructs spatially referenced central estimates of head velocity aligned with an earth-horizontal axis (e.g., Fig. 12B, middle). In the proposed model this transformation occurs on cell VO4 with the result that particular cell populations (i.e., neurons VO3, VO4, and VO5) code mainly for the component of rotation orthogonal to gravity. Thus, their activities reflect a canal-derived signal that can be observed only under conditions that typically simultaneously activate the otolith organs. This implies that previous characterizations of the 3D central neural sensitivities to canal stimulation during earth-vertical–axis rotations may have been inaccurate, potentially leading to inaccurate estimates of dynamic otolith contributions.

Validation of the hypothesized existence of cells that encode head velocity at least partially in a spatially referenced coordinate frame is fundamental to understanding how the brain constructs central estimates of head orientation and motion. Here we have illustrated that a “hidden” canal component to cell activities can be unmasked when canal and otolith sensory contributions are combined to cancel the net interaural acceleration stimulus to the otoliths (i.e., during Roll tilt – Translation motion; Angelaki et al. 1999; Green and Angelaki 2003). However, to verify the existence of a head-orientation–dependent canal component to cell responses during earth-vertical–axis rotations to different static head orientations may be sufficient to reveal head-orientation–dependent canal signal contributions.

In particular, we have illustrated that these could be identified by a significant second harmonic component in the cell’s spatial tuning properties during earth-vertical–axis rotations (Fig. 12B, bottom; Fig. 10; also see APPENDIX). However, to validate this model prediction, cell responses must be characterized over a broad range of head orientations (e.g., ±90°; Yakushin et al. 1999) much larger than those that have typically been used to date (±30°; e.g., Dickman and Angelaki 2002; Siebold et al. 2001).

Relationship to velocity storage

We previously speculated that the network involved in constructing internal estimates of head orientation and motion might be that known as the “velocity storage integrator” (Green and Angelaki 2003). In particular, both the problem of tilt–translation discrimination and “velocity storage” behavior require the presence of central integrative networks. At least a subset of the central cells in each network are thus expected to reflect these integrative properties by exhibiting improved responses to low frequency rotations compared to those predicted from the dynamic characteristics of the semicircular canals (e.g., Fig. 13). Such extended low frequency rotational dynamics are prevalent in the activities of vestibular nuclei neurons (Buettnert et al. 1978; Dickman and Angelaki 2003; Reisine and Raphan 1992; Waespe and Henn 1977, 1978, 1979). However, it remains to be addressed whether subsets of these same neurons participate in the computations surrounding tilt–translation discrimination.

A second link between the proposed integrative network and that traditionally associated with velocity storage relates to their 3-dimensional properties. It has been shown that the ocular nystagmus elicited by constant velocity rotation of either the subject or the visual surround tends to align with gravity or the net gravito-inertial vector (Angelaki and Hess 1994; Dai et al. 1991; Harris 1987; Merfeld and Young 1995; Merfeld et al. 1993a; Raphan et al. 1992; Wearne et al. 1999). This observation has led to the proposal that the velocity

![Graph](image-url)
storage network constructs an estimate of rotational motion in a space-fixed (inertial) reference frame (Angelaki and Hess 1994, 1995; Angelaki et al. 1995). Yet, this is exactly what we have argued here is required to distinguish tilt from translation. Further insight as to the relationship between the two networks may be provided by examining how modifications of the spatial and/or dynamic characteristics of velocity storage, associated with lesions of the nodulus and ventral uvula (Angelaki and Hess 1995; Waespe et al. 1985; Wearne et al. 1998) or sectioning the commissural fibers in the region of the rostral medial vestibular nuclei (Katz et al. 1991; Wearne et al. 1997), impact on the ability to discriminate tilts and translations. Intimately related to this issue is the extension of the model to address the problem of inertial motion detection at low frequencies where the semicircular canals do not provide accurate estimates of head velocity and other strategies including frequency segregation (Paige and Tomko 1991a; Telford et al. 1997) and/or the use of otolithic-based estimates of head rotation (Angelaki 1992a,b; Angelaki and Hess 1996; Correa and Mone 1970; Hain 1986; Harris 1987; Kushiro et al. 2002; Raphan and Schnabolk 1988) may make a contribution. As illustrated in Fig. 2, extension of the framework to 3 dimensions implies coupling of interdependent integrative networks that is expected to lend further insight as to the relationship between tilt-translation discrimination and the complex 3D spatial characteristics of velocity storage (Angelaki and Hess 1994, 1995; Dai et al. 1991; Hess and Angelaki 1997; Raphan and Sturin 1991; Wearne et al. 1998, 1999).

In conclusion, estimation of head orientation and inertial motion in space is a fundamental task of the vestibular system, yet one that remains to be understood at the neural level. Here we propose, for the first time, a physiologically relevant implementation of the theoretical relationships derived from the physical laws of motion, necessary to distinguish tilts and translations. Average neural populations that encode internal neural estimates of dynamic translational and gravitational accelerations are shown to emerge within such a network. Yet, the high degree of variability and complex patterns of otolithic–canal convergence observed in central neurons responsive to translation are not only difficult to interpret, but suggest a distributed central coding of such internal estimates. Here we illustrate that these seemingly complex properties are consistent with those of an integrative network that implements the nonlinear canal–otolith interactions required to distinguish inertial and gravitational accelerations. A key prediction of this model is the existence of central neurons that encode semicircular canal signals at least partially in a space-fixed coordinate frame, rather than in the traditionally assumed head-fixed reference frame defined by the peripheral vestibular system. New experimental paradigms and alternative data interpretations that account both for the implied coordinate transformation and the integrative properties of the system will be required if the contributions of sensory vestibular signals to constructing internal estimates of head motion and orientation are to be elucidated.

APPENDIX

Analytical descriptions of cell and ocular responses predicted by the proposed model (Fig. 3) are summarized here. To describe the basic dynamic characteristics of the network, Laplace domain descriptions presented below can be used to approximate the dynamic characteristics of the network only for small head movements about a given operating point (i.e., a given average head orientation) when the system exhibits close to linear performance.

VO cell responses

GENERAL EXPRESSIONS. Assuming small head deviations for a given static pitch angle \( \phi \), the responses of the VO cells in Fig. 3A to yaw and roll head velocity signals \( (\omega_o \text{ and } \alpha_o) \), sensed by the canals, and to interaural linear acceleration signals \( (\alpha_i) \), sensed by the otoliths, can be described by the general Laplace domain equation

\[
G_{VOH}(s) = \frac{G_{VOL} \alpha_o (1 + \frac{1}{T_{VOH}} + \frac{1}{T_{VOL}} \alpha_o)}{1 + \frac{1}{T_{VOH}} + \frac{1}{T_{VOL}} \alpha_o}\]

where \( s \) represents the complex Laplace variable and \( n \) is used to denote the cell number. The common gain term \( G_{SN} \) can be written in terms of model parameters as

\[
G_{SN} = \frac{1}{1 + K_1 K_{10} + K_1 K_{20} - K_1 K_{20} K_{10}}
\]

The network time constant \( T_{NI} \) is given by

\[
T_{NI} = \frac{T_c}{1 + K_1 K_{10} + K_1 K_{20} - K_1 K_{20} K_{10}}
\]

Model parameters were adjusted to set time constant \( T_{NI} \) to a large value of 20 s in the upright orientation such that the network behaves as a leaky neural integrator. Notice that all response terms in Eq. A1 reflect this long time constant. VO cell responses are therefore predicted to embed the integrative properties of the network such that they may exhibit “velocity-storage” type characteristics (e.g., see Fig. 13).

Expression for gains \( G_{VOL}, G_{VOH}, G_{VOV} \), and \( G_{VOL} \) as functions of the model parameters are summarized in Tables A1 and A2, respectively, for each cell type. Note that most gain and time constant terms depend on some combination of weights \( K_1 \) and \( K_2 \) that vary as a function of \( \alpha_i(t) \) or \( \alpha_o(t) \), respectively [i.e., \( K_1(t) = K_{10} + K_{11} \alpha_o(t); K_2(t) = K_{20} - K_{22} \alpha_i(t) \)]. Thus these terms can be evaluated only for small deviations about a particular operating point where static approximations to weights \( K_1 \) and \( K_2 \) can be assumed. Specifically, the accelerations along the nasooccipital and dorsoventral head axes \( \alpha_i(t) \) and \( \alpha_o(t) \) can be approximated as static values \( \alpha_i \sim -\sin \phi \) and \( \alpha_o \sim \cos \phi \) for a given head pitch angle \( \phi \). Parameters \( K_1 \) and \( K_2 \) can then be approximated as static weights \( K_{10} = K_{10} \sin \phi \) and \( K_{20} = K_{20} - K_{22} \cos \phi \). To calculate the bode plots in Figs. 6 through 8 estimates of \( K_1 \) and \( K_2 \) for a given average pitch angle were substituted into the appropriate gain and time constant expressions (above and in Tables A1 and A2) and used to evaluate Eq. A1 for each VO cell population.

CHOICE OF MODEL PARAMETERS. Model parameters in the network of Fig. 3A were chosen to satisfy several criteria for ideal tilt-translation discrimination.
TABLE A1. Gains in Eq. A1 expressed as a function of model parameters

<table>
<thead>
<tr>
<th>Cell</th>
<th>$G_{VOH}$</th>
<th>$G_{V0V}$</th>
<th>$G_{VO5}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>VO1</td>
<td>$p_0(1 - K_{1a}K_{3a} + K_{2b})$</td>
<td>$-p_0K_{1b}$</td>
<td>$[-q_1K_{1b} + (q_2 - q_3)K_{10}]$</td>
</tr>
<tr>
<td>VO2</td>
<td>$-p_0K_{1b}$</td>
<td>$p_0(1 - K_{1a}K_{3a} + K_{2b})$</td>
<td>$[-q_1K_{1b} + (q_2 - q_3)K_{20}]$</td>
</tr>
<tr>
<td>VO3</td>
<td>$p_0K_{1a}K_{3a}$</td>
<td>$p_0K_{1a}K_{3a}$</td>
<td>$q_1(K_1 - q_3K_{3a}K_{1b} - (q_2 - q_3)K_{3a}K_{3b})$</td>
</tr>
<tr>
<td>VO4</td>
<td>$p_0K_{1a}$</td>
<td>$p_0K_{1a}$</td>
<td>$q_1K_{1b}K_{3b} - (q_2 - q_3)K_{1b}$</td>
</tr>
<tr>
<td>VO5</td>
<td>$p_0K_{1a}$</td>
<td>$p_0K_{1a}$</td>
<td>$q_1K_{1b}K_{3b} - (q_2 - q_3)K_{1b}$</td>
</tr>
</tbody>
</table>

translation discrimination at mid-high frequencies as well as to replicate particular properties of experimentally observed cell types. These conditions included: 1) network time constant $T_{V0H}$ of about 20 s in the upright head orientation (see Eq. A2); 2) “canal-only” type responses on cells VO1 and VO2 that differ only in the axis of rotation for which each cell population is maximally stimulated (small values for $K_{1b} = K_{2b}$ of 0.1, $p_0 = p_3$); 3) translation-selective responses on cell VO3 at mid-high frequencies ($G_{V0H} = G_{V0V} = q_0981\pi T/180$); 4) high-pass response to sensory otoilih signals on cell VO3 (i.e., close to zero static tilt sensitivity, $-1/T_{V0L3} = 0$); 5) sensitivities to acceleration during 0.5-Hz translation on cells VO3 and VO4 of 250 and 180 spikes$^{-1}g^{-1}$, respectively (Dickman and Angelaki, 2002); 6) close to ideal estimate of head orientation relative to gravity (i.e., g_z) on cell VO5 ($K_{1z} = K_{2z} = 0$; $K_{1a} = K_{3a}$, $G_{V0L5}$ small, $\approx 0$ in units of cm/s$^2$); 7) VO5 cell sensitivity to both high frequency dynamic and static tilts of approximately 0.7 spikes$^{-1}$deg$^{-1}$, similar to that observed experimentally for cells sensitive mainly to tilt (Zhou et al. 2000).

Because of condition 6 above, the most general expression for cell VO5, given by Eq. A1, simplifies at high frequencies and for small head movements around a given static pitch orientation, (i.e., $\phi$ = $\alpha_z = -\sin \phi$ and $\alpha_z \approx \cos \phi$ in units of g) to that presented in Eq 7 (see MODEL DEVELOPMENT)

$$VO5(s) = G_{V0H}(\omega(s)/s - \omega(s)/s - \alpha_z)$$

$$= -G_{V0H}(\omega(s)/s - \sin \phi - \omega(s)/s - \cos \phi)$$  \hspace{1cm} \text{(A4)}

Note that this equation approximates $g_z$ only for small dynamic head reorientations relative to gravity as it predicts that cell VO5 encodes angular tilt position. For example, during head roll from upright, cell VO5 is predicted to encode a scaled estimate of angular roll position, $\phi$, even though the actual interaural gravitational acceleration during roll is $g_z = -\sin \phi$ (in units of g). This occurs because $\alpha_z$ and $\alpha_z$ are assumed static (i.e., constant during a given head movement) for ease of a linear systems exposition. In the actual model, however, the signal inputs to cell VO4 are multiplied by real dynamic signals $\alpha_z(t)$ and $\alpha_z(t)$. As a result, the simulated response of cell VO5 closely approximates an internal scaled estimate of $g_z$ that is accurate even for large angles during rotation. In addition, notice that Eq. A4 implies that canal signals make the dominant contribution to the response of cell VO5 at high frequencies. In contrast, at very low frequencies (e.g., $<0.01$ Hz) otoilih signals dominate such that cell VO5 is also predicted to respond to static head tilts.

EARTH-VERTICAL–AXIS ROTATIONS. During earth-vertical–axis rotations only the semicircular canals are stimulated. For an earth-vertical–axis rotation velocity $\omega_x$, and pitch angle $\phi$, the yaw and roll components of velocity can be expressed as $\omega_x(s) = \omega_x(s)\cos \phi$ and $\omega_z(s) = -\omega_z(s)\sin \phi$, respectively. VO cell responses can then be described by the first two terms in Eq. A1 as

$$\text{VO}(s) = \frac{G_{V0H}G_{V0V}(T_{V0L3} + 1)}{T_{V0L3} + 1} \frac{T_s}{T_{V0H} + 1} \cos(\phi)$$  \hspace{1cm} \text{(A5)}

To illustrate why cells VO3, VO4, and VO5 fail to respond in the model during earth-vertical–axis rotations we may examine the example case of cell VO4. For a given pitch head orientation, $K_1 = K_{1z} = K_{1a}$ $\sin \phi$ and $K_2 = K_{2z} = K_{2a} \cos \phi$. The cell’s response can then be approximated at mid-high frequencies as

$$\text{VO4}(s) = \frac{-p_0K_{1a}sin(\phi)s\cos(\phi) + p_0K_{1a}s\cos(\phi)+p_0K_{1a}s\phi}{2}$$

$$-p_0s\sin(\phi) - \frac{p_0K_{1a}}{2} \sin(2\phi) + \frac{p_0K_{2a}}{2} \sin(2\phi) + p_0K_{1a}s\cos(\phi) - p_0K_{2a}s\phi$$  \hspace{1cm} \text{(A6)}

When $p_0K_{1a} = p_0K_{2a}$ and $K_{1z} = K_{2z} = 0$ (as for the chosen parameter set; see Fig. 3 legend) Eq. A6 illustrates that cell VO4 will not respond during earth-vertical–axis rotations. It can be shown that in this case the cell population only exhibits a sensitivity to canal signals along an axis orthogonal to gravity (i.e., earth-horizontal axis). However, more generally, if $p_0K_{1a} \neq p_0K_{2a}$, on an individual VO4 cell, the neuron will indeed respond during earth-vertical–axis rotations but is predicted to respond with second-harmonic tuning (i.e., associated with the 1st two terms in Eq. A6; e.g., see Fig. 10C). Any head-orientation–invariant canal contribution to the cell’s input (i.e., last two terms in Eq. A6 when $K_{1a} \neq 0$ and/or $K_{2a} \neq 0$) will contribute a first-harmonic component to the cell’s tuning. In general, on any given cell, both first- and second-harmonic tuning components are predicted to be

TABLE A2. Time constants in Eq. A1 expressed as a function of model parameters

<table>
<thead>
<tr>
<th>Cell</th>
<th>$T_{V0H}$</th>
<th>$T_{V0V}$</th>
<th>$T_{VO5}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>VO1</td>
<td>$T_r$</td>
<td>$0$</td>
<td>$0$</td>
</tr>
<tr>
<td>VO2</td>
<td>$0$</td>
<td>$T_r$</td>
<td>$0$</td>
</tr>
<tr>
<td>VO3</td>
<td>$0$</td>
<td>$0$</td>
<td>$q_1T_r$</td>
</tr>
<tr>
<td>VO4</td>
<td>$T_r$</td>
<td>$T_r$</td>
<td>$0$</td>
</tr>
<tr>
<td>VO5</td>
<td>$0$</td>
<td>$0$</td>
<td>$0$</td>
</tr>
</tbody>
</table>
Ocular responses

Horizontal and torsional ocular responses (for small head movements about an average pitch setpoint) can be expressed in the Laplace domain as

\[ E_{\text{ocular}}(s) = \frac{G_{\text{VOH}}(f) G_{\text{TVOR}}(T_{\text{TVOR}}/s + 1)}{(T_{\text{TVOR}}/s + 1)(T_{\text{hor}}/s + 1)} \alpha(s) \]

and

\[ G_{\text{TVOR}}(T_{\text{TVOR}}/s + 1) \alpha(s) \]

where

\[ T_{\text{TVOR}} = \frac{T_f}{1 - abK_f - d_0 d_1 K_f} \]

is the oculomotor neural integrator time constant (i.e., long time constant set to 20 s; Angelaki et al., 2001a; Robinson, 1981) and

\[ G_{\text{TVOR}} = 1 \frac{1 - abK_f - d_0 d_1 K_f}{1 - abK_f - d_0 d_1 K_f} \]

\[ G_{\text{VOH}} = \rho(\alpha + \epsilon)K_f \]

\[ G_{\text{VOV}} = q_0(\epsilon + \alpha h K_f + d_0 d_1 K_f) \]

\[ T_{\text{TVOR}} = \epsilon T_f \]

\[ T_{\text{TVOR}} = e + \alpha h K_f + d_0 d_1 K_f \]

where weights \( p_d, p_o, \alpha, \epsilon, e, \) and \( q_0, q_{d0}, q_{o0} \) differ slightly for horizontal versus torsional premotor eye movement networks (i.e., see Fig. 3 legend) to reflect differences in horizontal versus torsional RVOR gains and responses to interaural translation. Note that to achieve eye plant compensation in RVOR responses, Eq. A7 assumes that the neural filter, \( F(s) = K_f/(T_f/1 + 1) \), in Fig. 3B represents a scaled internal model of the eye plant, \( F(s) = K_f(T_f/1 + 1) \), where \( T_f = T_s \) (Galiana and Outerbridge 1984; Green and Galiana 1998) and that \( d_0 = d_1 \) (Angelaki et al. 2001a).

A more intuitive feel for the response predicted by Eq. A7 may be obtained by considering an approximation valid at mid-high frequencies [\( f \gg 1/(2\pi T_{\text{TVOR}}), f \gg 1/(2\pi T_{1/2}), f \gg 1/(2\pi T_{\text{TVOR}}) \)] that incorporates a simplified expression for cell VO3, valid for the chosen parameter set and for small head movements about a given static pitch orientation, \( \phi \).

\[ E_{\text{ocular}}(s) = \frac{G_{\text{VOH}}(f) G_{\text{TVOR}}(T_{\text{TVOR}}/s + 1)}{T_f} \alpha(s) - \frac{G_{\text{VOH}} G_{\text{TVOR}} \alpha(s)}{s} \sin \phi - \frac{G_{\text{VOH}} G_{\text{TVOR}} \alpha(s)}{s} \cos \phi + q_0 \alpha(s) \]

where \( G_{\text{VOH}} = p_1 K_f K_o K_s T_c \) and \( G_{\text{VOV}} = p_1 K_f K_o K_s T_c \). The first term in Eq. A13 predicts an eye velocity response proportional to angular head velocity. This corresponds to the RVOR component of ocular responses (either horizontal or torsional) driven by direct canal projections (associated with weights \( p_{d1} \) and \( p_{o1} \)) onto premotor cells sensitive to contralaterally directed eye movements (i.e., EMG cells in Fig. 3B). The second term reflects canal and otolith contributions to the TVOR component of the ocular response. These are conveyed from cell VO3 onto the premotor horizontal and torsional networks by projections onto cells sensitive to ipsilaterally directed eye movements (i.e., projection with weight \( q_0 \) onto EMG cells in Fig. 3B).

Details of the differences in dynamic processing that occur in the RVOR versus TVOR premotor pathways of the proposed model have been described previously (Angelaki et al. 2001a; Green and Galiana 1998). Model parameters \( a, b, d_1, d_2, K_f, \) and \( p_d \), \( p_o \), and \( e = e_2 \) in Fig. 3B are identical to those previously published (Angelaki et al. 2001a). Parameters \( q_{d0}, q_{o0}, \) and \( e \) were adjusted here in conjunction with weight \( q_0 \) (i.e., otolith sensory input to cell VO3) to approximate experimentally observed horizontal versus torsional ocular responses to interaural translation (Angelaki 1998; see data in Fig. 4C). In addition, weight \( p_{d1} \) was chosen to simulate a torsional RVOR gain during head roll of 0.76, slightly lower than the simulated horizontal RVOR gain of 0.88 (e.g., Angelaki and Hess 1996).

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