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Neural Processing of Gravito inertial Cues in Humans. III. Modeling Tilt and Translation Responses

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Received 12 June 2001; accepted in final form 21 September 2001

Merfeld, D. M. and L. H. Zupan. Neural processing of gravito inertial cues in humans. III. Modeling tilt and translation responses. *J Neurophysiol* 87: 819–833, 2002; 10.1152/jn.00485.2001. All linear accelerometers measure gravito inertial force, which is the sum of gravitational force (tilt) and inertial force due to linear acceleration (translation). Neural strategies must exist to elicit tilt and translation responses from this ambiguous cue. To investigate these neural processes, we developed a model of human responses and simulated a number of motion paradigms used to investigate this tilt/translation ambiguity. In this model, the separation of GIF into neural estimates of gravity and linear acceleration is accomplished via an internal model made up of three principal components: 1) the influence of rotational cues (e.g., semicircular canals) on the neural representation of gravity, 2) the resolution of gravito inertial force into neural representations of gravity and linear acceleration, and 3) the neural representation of the dynamics of the semicircular canals. By combining these simple hypotheses within the internal model framework, the model mimics human responses to a number of different paradigms, ranging from simple paradigms, like roll tilt, to complex paradigms, like postrotational tilt and centrifugation. It is important to note that the exact same mechanisms can explain responses induced by simple movements as well as by more complex paradigms; no additional elements or hypotheses are needed to match the data obtained during more complex paradigms. Therefore these modeled response characteristics are consistent with available data and with the hypothesis that the nervous system uses internal models to estimate tilt and translation in the presence of ambiguous sensory cues.

INTRODUCTION

All linear accelerometers (e.g., otolith organs) measure gravity and linear acceleration. The nervous system must process these cues to elicit appropriate responses during translation [e.g., translational vestibulo ocular reflex (VOR)] and tilt (e.g., postural control). It has been shown that neural processes of sensory integration are used to separate otolith measures of gravito inertial force to yield responses for both tilt and translation. For example, canal cues influence the processing of tilt (Hess and Angelaki 1999; Merfeld and Young 1995; Merfeld et al. 1999, 2001; Stockwell and Guedry 1970; von Holst and Grisebach 1951), which, in turn, influence the processing of translation (Angelaki et al. 1999, 2001; Merfeld and Young 1995; Merfeld et al. 1999; Zupan et al. 2000). In this study, we use modeling to show that the exact same neural mechanisms

can explain human responses to relatively simple motion stimuli (e.g., tilt alone, translation alone) as well as to more complicated motion stimuli (e.g., centrifugation, postrotary tilt, combined tilt and translation).

This report also shows that a “human” model can match human responses during motion paradigms that we have used to investigate tilt and translation processing, specifically centrifugation (Merfeld et al. 2001) and postrotatory tilt (Zupan et al. 2000). We then use this exact same model to make predictions about human responses during motion paradigms that combine roll tilt and interaural translation, as investigated in rhesus monkeys (Angelaki et al. 1999). To our knowledge, these combined tilt and translation experiments have not been performed with human subjects, so we are making true modeling predictions. These predictions can be verified or refuted by experiments.

In addition, data have shown that tilt responses tend to dominate during low-frequency stimulation of the otolith organs and translation responses (e.g., translational VOR) tend to dominate during high-frequency stimulation (e.g., Paige 1983; Telford et al. 1997). These data have been interpreted to indicate that the nervous system includes simple low-pass and high-pass filters to separate gravity from linear acceleration (Mayne 1974; Paige 1983). However, similar frequency characteristics can be predicted by this model, which does not include explicit low-pass or high-pass filtering of the gravito inertial cues. While not proving the veracity of the model, this does prove that caution must be taken when interpreting response dynamics. The model shows that investigations of response dynamics must be done in parallel with studies that investigate rotational influences on the responses (e.g., Angelaki et al. 1999; Merfeld et al. 2001; Zhou et al. 2000; Zupan et al. 2000).

Finally, it is known that monkey responses to certain motion stimuli (e.g., Angelaki and Hess 1994; Merfeld and Young 1995; Merfeld et al. 1993b; Raphan et al. 1981; Wearne et al. 1999), especially those that elicit interactions between the canals and otoliths (e.g., centrifugation, postrotatory tilt), differ substantially from human responses (e.g., Fetter 1996; Fetter et al. 1996; Lansberg et al. 1965; Merfeld et al. 2001; Zupan et al. 2000). One conclusion that might be drawn from these differences is that monkey responses are not applicable to human

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physiology. We use modeling to refute this suggestion. To investigate these known species differences, we compare and contrast human responses and simulations with monkey responses and simulations. We show that the same model can explain both human and monkey responses, thus uniting the species differences.

METHODS

This human model (Fig. 1) is similar to our monkey model (Merfeld 1995b; Merfeld et al. 1993a) but is altered to match human responses. These alterations required several parameter changes alongside one structural change to recent monkey versions of the model (Angelaki et al. 2000, 2001; Merfeld 1995b). A brief description is provided below; details are provided in the APPENDIX and in earlier descriptions (Merfeld 1995b; Merfeld et al. 1993a). The semicircular canals measure the angular velocity of the head (ω), while the otolith organs measure both linear acceleration of the head (\mathbf{a}) and gravity (\mathbf{g}). (Bold signifies a vector.) These are the three-dimensional (3D) model “inputs.” The 3D “outputs” are the neural representations (or estimates) of the same three quantities: angular velocity ($\hat{\omega}$), linear acceleration ($\hat{\mathbf{a}}$), and gravity ($\hat{\mathbf{g}}$). Each of the input/output vectors, as well as the intermediate quantities a expressed in head-fixed coordinates, since the vestibular system measures in a head reference frame. In our right-handed, orthogonal, coordinate system, the x-axis is aligned with the nasooccipital axis, the y-axis is

TABLE 1. Model feedback parameters

	Human	Monkey
k_ω	3	5
k_a	-2	-5
k_f	2	10
$k_{f\omega}$	2	100

aligned with the interaural axis, and the z-axis is orthogonal to both the x-axis and the y-axis. The positive directions are forward (x), toward the subject’s left (y), and toward the top of the head (z). Based on previous findings that the spatial organization of translational and angular visual motion cues are performed in a head-fixed, vestibular, coordinate frame (Graf et al. 1988; Wylie and Frost 1993; Wylie et al. 1998), we explicitly hypothesize that the neural calculations are performed in a head-fixed reference frame.

Model parameters and implementation

The human model parameters were held constant for all simulations presented herein. The values for the four feedback and two vestibuloocular reflex (VOR) parameters are presented below; other values are included in the APPENDIX.

FEEDBACK PARAMETERS. The model includes four free parameters (k_ω , $k_{f\omega}$, k_f , k_a) that feed back errors between the sensory measurements (α_{oto} , α_{scc}) and the sensory measurements predicted by the internal model ($\hat{\alpha}_{oto}$, $\hat{\alpha}_{scc}$). (See APPENDIX for more details.) The values for these four parameters were determined by trial and error; these four parameters are the only free parameters in this model. (See Table 1 for these parameter values.)

VOR CALCULATIONS. The focus of this modeling work remains the neural calculations and neural estimates of motion and orientation. Nonetheless, we also model the VOR to provide a direct comparison to available data. The modeled VOR (Fig. 1B) is the sum of an angular and a translational VOR (Sargent and Paige 1991). The angular VOR is simply the negative of estimated angular velocity. The calculation of the translational VOR is more complicated. First, the neural estimate of linear acceleration ($\hat{\mathbf{a}}$) is converted to linear velocity ($\hat{\mathbf{v}}$) via leaky integration¹ with a time constant of 0.1 s, roughly matching the published human translational VOR measured using transients that include high-frequency components (Busettoni et al. 1994). In addition, the translational VOR has been shown to depend on target distance and target orientation (Paige 1989; Paige and Tomko 1991; Schwarz and Miles 1991; Schwarz et al. 1989; Tomko and Paige 1992). To include these effects, we calculate the precise, compensatory, eye rotation required during translation using a cross product (Viirre et al. 1986), such that the translational VOR = $\hat{\mathbf{v}} \times \hat{\mathbf{p}}$, where $\hat{\mathbf{p}}$ is the estimated target proximity vector. If the gaze is straight ahead at an estimated target distance \hat{d} , the proximity vector is given as $\hat{\mathbf{p}} = (1/\hat{d}, 0, 0)$. The estimated target distance (\hat{d}) was 2 m.

All simulations were implemented using the MATLAB toolbox SIMULINK (The Mathworks, Natick, MA). All simulations were performed using a variable-step Dormand–Prince numerical integration algorithm (ode45 in SIMULINK). For all simulations shown below, we focus on the motion variables predicted by the model. These include neural representations of angular velocity ($\hat{\omega}$), gravity ($\hat{\mathbf{g}}$), and linear acceleration ($\hat{\mathbf{a}}$). In this study, we emphasize these predicted “average” neural responses, which remain a primary goal of this modeling effort.

¹ The dynamics of the oculomotor plant also affect the dynamics of the VOR (Green and Galiana 1998; Musallam and Tomlinson 1999), but this does not eliminate the need for some form of neural processing to yield perceived linear velocity from linear acceleration cues. Since the precise neural mechanisms by which the translational VOR integration is performed is not central to the sensory integration topics investigated with this model, it is not further addressed herein.

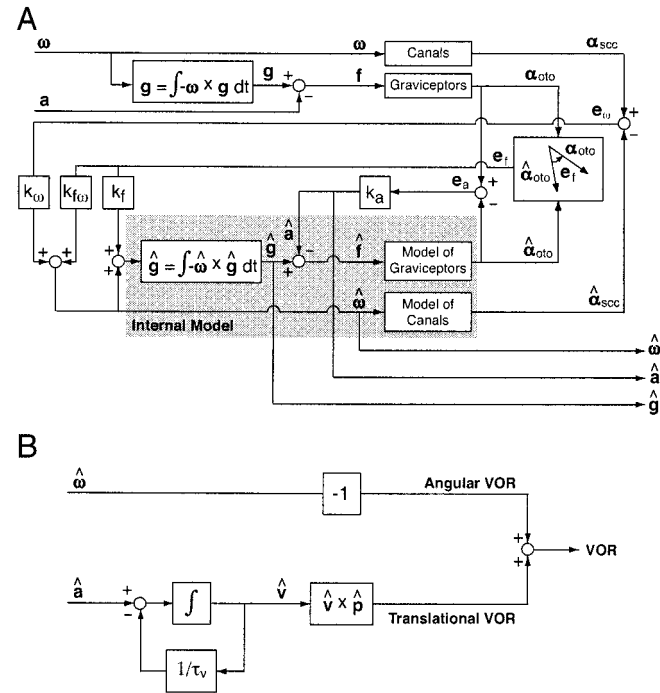


FIG. 1. A: the inputs to the model are angular velocity (ω), linear acceleration (\mathbf{a}), and gravity (\mathbf{g}). The model outputs are the neural estimates of angular velocity ($\hat{\omega}$), linear acceleration ($\hat{\mathbf{a}}$), and gravity ($\hat{\mathbf{g}}$). Physical effects and sensory transduction associated with these inputs are represented at the top of the block diagram ($\mathbf{g} = \int -\omega \times \mathbf{g} dt$, $\mathbf{f} = \mathbf{g} - \mathbf{a}$, Canals, Graviceptors). These components represent known effects and influences. The internal model (neural representation) of these components is included within the gray box ($\hat{\mathbf{g}} = \int -\hat{\omega} \times \hat{\mathbf{g}} dt$, $\hat{\mathbf{f}} = \hat{\mathbf{g}} - \hat{\mathbf{a}}$, Model of Canals, Model of Graviceptors). These internal model components represent hypothesized neural calculations performed by the nervous system. B: the VOR is modeled as the sum of the angular VOR and the translational VOR. The angular VOR is modeled as the negative of the estimated angular velocity. The translational VOR is derived from the estimate of linear acceleration ($\hat{\mathbf{a}}$) by leaky integration followed by a cross product with an estimated target proximity vector ($\hat{\mathbf{p}}$), which accounts for distance and gaze direction influences.

SIMULATIONS

In this section, we present simulated human responses to several types of motion stimuli that have been used to investigate tilt and translation responses. We start by showing simulated responses induced by motion paradigms used in the earlier reports in this series, postrotational tilt (Zupan et al. 2000) and centrifugation (Merfeld et al. 2001). We then show responses during rapid tilts, both steps (Stockwell and Guedry 1970) and sinusoids. We then use the model to make general predictions about human responses to combined roll tilt and interaural linear acceleration stimuli, as used in previous monkey studies (Angelaki et al. 1999, 2001).

Postrotational tilt ("dumping")

Postrotational tilt has been used to investigate how the human nervous system processes sensory interactions between

the canals and otoliths (e.g., Benson 1966a,b; Benson and Bodin 1966; Fetter et al. 1992; Merfeld et al. 1999; Zupan et al. 2000). Findings consistently show that the static otolith cues reduce the time constant of the postrotational VOR and that the VOR remains primarily horizontal with little or no "axis shift." More recently, this paradigm has shown how humans process tilt versus translation (Merfeld et al. 1999; Zupan et al. 2000). Findings show that an illusion of tilt is induced by the sensory interaction of the canal and otolith cues, and that a small neural representation of linear acceleration is induced, leading to a measurable translational VOR.

Model predictions for nose-down dumping following a 100°/s counter-clockwise (CCW) rotation are shown (Fig. 2). The simulations show that the postrotational neural representation of angular velocity decays more rapidly than the per-rotatory response (Fig. 2*B*). The model also predicts illusory

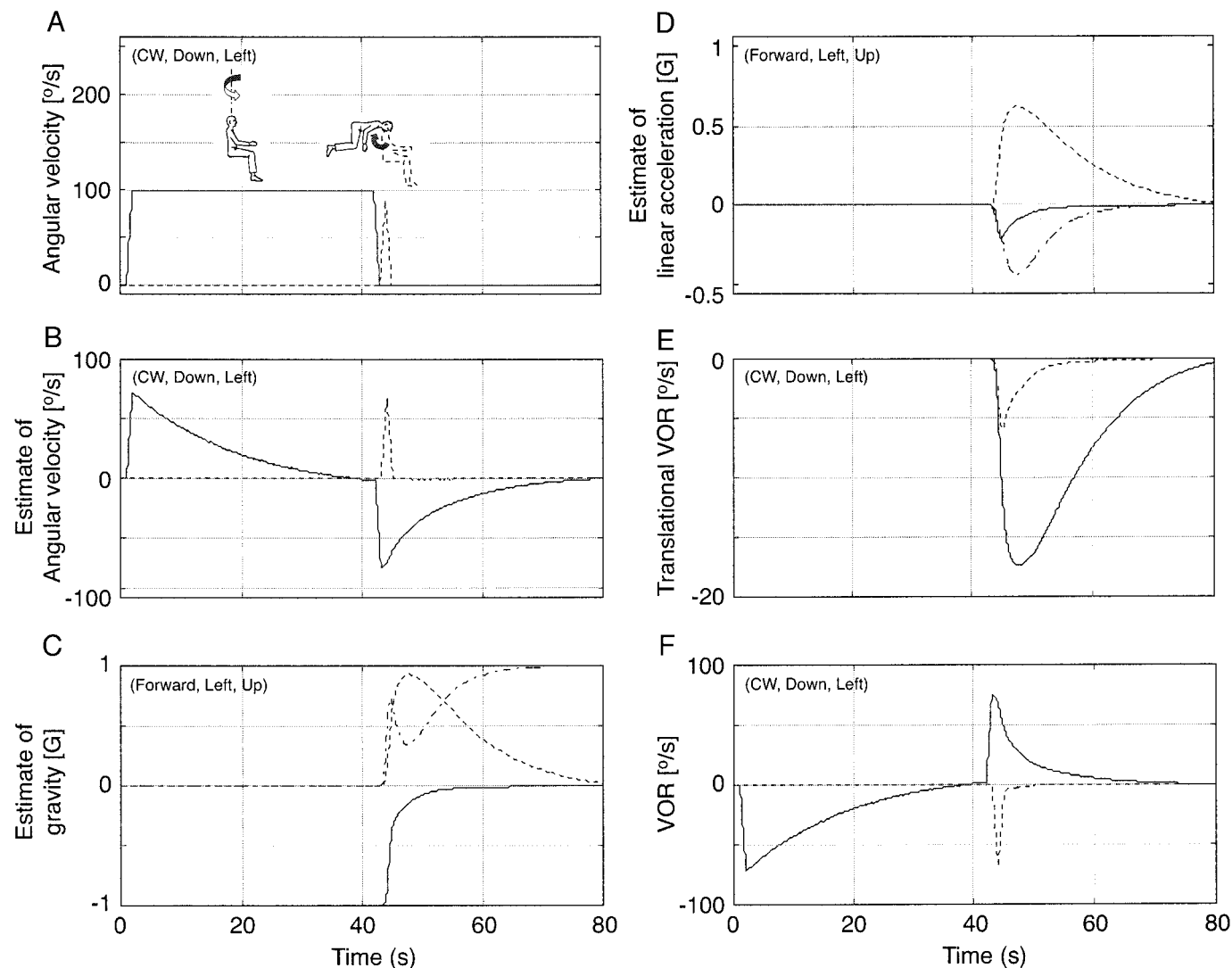


FIG. 2. Predicted responses induced by a postrotational 90° tilt ("dumping") to a nose-down orientation. *A*: the yaw angular velocity (100°/s trapezoid) and the pitch angular velocity (spike) yielding a 90° tilt are shown. Modeling predictions of the neural representations of angular velocity (*B*), gravity (*C*), and linear acceleration (*D*) are shown. Also shown are modeling predictions of the translational VOR (*E*) and the total VOR (*F*). (The angular VOR component is not shown since it is simply equal and opposite the neural representation of angular velocity shown in *B*.) For all plots, the *y*- and *z*-components are represented by dash and solid lines, respectively. For the gravity and linear acceleration plots, the *x*-component is also shown and is represented by a dash-dot line. To allow direct comparison to published data (Zupan et al. 2000), the simulated conditions precisely match the 100°/s postrotary tilt trials.

yaw tilt, indicated by the neural representation of gravity (Fig. 2C) having a component along the interaural axis (y-axis). The difference between the otolith measure and neural estimate of gravity elicits a neural representation of linear acceleration (Fig. 2D), with a component along the interaural axis.

A transient horizontal translational VOR (Fig. 2E) is predicted to be elicited by the estimated interaural (y-axis) linear acceleration (Fig. 2D). This horizontal VOR combines with the *angular* VOR to yield the total VOR (Fig. 2F). The model predicts that the angular VOR is independent of subject orientation. This is consistent with perceptual studies that do not demonstrate a significant orientation dependency of subjective rotation sensations (Benson and Bodin 1966). On the other hand, the model predicts that a horizontal translational VOR component varies sinusoidally with subject orientation. If the angular VOR and translational VOR sum in a mostly linear manner, this yields a total VOR that varies sinusoidally with subject orientation as observed (Merfeld et al. 1999). Although not shown, the model also demonstrates the observed dependency of the horizontal translational VOR and total VOR responses on per-rotatory angular velocity (Zupan et al. 2000). It also predicts that the time constant of the *angular* VOR is smaller following a tilt in any direction than that for the upright orientation.

The mechanisms used to predict these effects are briefly described. Following the 90° postrotatory tilt, the postrotational yaw canal cue is orthogonal to gravity. As presented in the APPENDIX, the model includes a “neural” mechanism that uses rotational cues to predict the relative orientation of gravity. Following postrotatory tilt, this mechanism rotates the neural representation of gravity away from the otolith measurement of gravity when the yaw canal cue is misaligned with gravity. Since the neural representation of gravity and the otolith measurement of gravity become different, the nervous system interprets this difference as linear acceleration, eliciting a translational VOR.

It is worth noting that, in the absence of other influences, the strong yaw postrotational cue might act to rotate the neural representation of gravity around the subject's head in yaw. In the model, this is prohibited by the feedback loops that tend to pull the neural representation of gravity toward alignment with the measurement of gravity (k_f and $k_{f\omega}$). This effect seems confirmed by findings obtained when subjects were stimulated with visual rotational cues (Dichgans et al. 1972). The study reported an illusory roll tilt that built up after dynamic roll vection cues were applied. But the amount of tilt saturated, even though the dynamic roll vection cue indicated continuous rotation, with subjects reporting the paradoxical sensations of rotating without getting anywhere.

Fixed-radius centrifugation

Fixed-radius centrifugation has been widely used to investigate how the human nervous system processes tilt versus translation as well as to investigate sensory interactions between the semicircular canals and otolith organs (Clark and Graybiel 1963, 1966; Curthoys 1996; Curthoys et al. 1998; Graybiel and Brown 1951; Haslwanter et al. 1996; Lansberg et al. 1965; Merfeld et al. 2001; Seidman et al. 1998). The data show the following: 1) an illusory tilt that lags well behind the actual GIF tilt during acceleration with little or no lag during deceleration, 2) a horizontal VOR that is much greater with the

subjects “facing the motion” than with “back to motion,” and 3) a small vertical nystagmus that builds up gradually after the steady-state velocity is reached.

Model simulations match these findings (Fig. 3). The neural representation of gravity gradually tilts in roll during angular acceleration, as shown by the gradual increase in the interaural (y-axis) component of gravity that lags behind the increase in the y-axis gravito-inertial force (Fig. 3C). Little or no lag is evident during deceleration. A significant neural representation of interaural linear acceleration is elicited (Fig. 3D) during angular acceleration that leads to a substantial horizontal translational VOR (Fig. 3E). This horizontal translational VOR maintains a substantial steady-state component, due to a constant difference between the measurement of GIF (magnitude >1 G) and the central estimate of gravity with a fixed magnitude of 1 G. A similar constant horizontal VOR has been measured (Merfeld et al. 2001). This combines with the horizontal angular VOR to yield the total measured horizontal VOR (Fig. 3F), which for the back-to-motion simulation shown is smaller than the facing-motion horizontal VOR (not shown). A relatively small orientation-dependent vertical VOR is also predicted (Fig. 3F). This vertical VOR consists of an angular VOR, which shifts the axis of eye rotation toward alignment with GIF, and a linear VOR, which compensates for a “z-axis” estimate of linear acceleration.

The yaw cues from the semicircular canals explain the perceived tilt lag during acceleration. In this case, the yaw canal cues are incongruent with the tilt of gravity, because if gravity were truly tilted in roll while the subjects were rotated in yaw, the force of gravity would swing about the subject as in off-vertical-axis rotations (OVAR). (In fact if the subject were tilted in roll and rotated in yaw, this *would be* OVAR.) During steady-state stimulation, the yaw rotation measured by the canals is not confirmed by the otoliths, which measure the constant unchanging gravito-inertial force. One way to resolve this discrepancy is to delay the illusory tilt until the canal cues have decayed.

The lag in the neural representation of tilt relative to the actual GIF stimulation results in a difference between the GIF measured by the otolith organs and the estimated orientation of gravity (Merfeld et al. 2001). As discussed above and measured experimentally (Merfeld et al. 2001), this difference is estimated as linear acceleration, leading to a horizontal translational VOR. This translational VOR combines with the angular VOR to yield a total VOR that is substantially greater when humans face the direction of motion than with back to motion. The difference between facing-motion and back-to-motion VORs is simply the difference between addition of angular and linear VORs versus their subtraction. It is worth noting that these human responses and model predictions are different from monkey responses (Merfeld and Young 1995; Wearne et al. 1999) and model predictions (Merfeld 1995b). We return to this topic later (see DISCUSSION).

Variable-radius centrifugation

When rotated at a constant velocity about an earth-vertical axis, the response of the canals decays to zero in about 1 min. When the subject is subsequently moved radially outward, a variable centrifugal force, proportional to the radius multiplied by the angular velocity squared, is experienced. Since the canal responses have decayed to zero (or very near zero), this para-

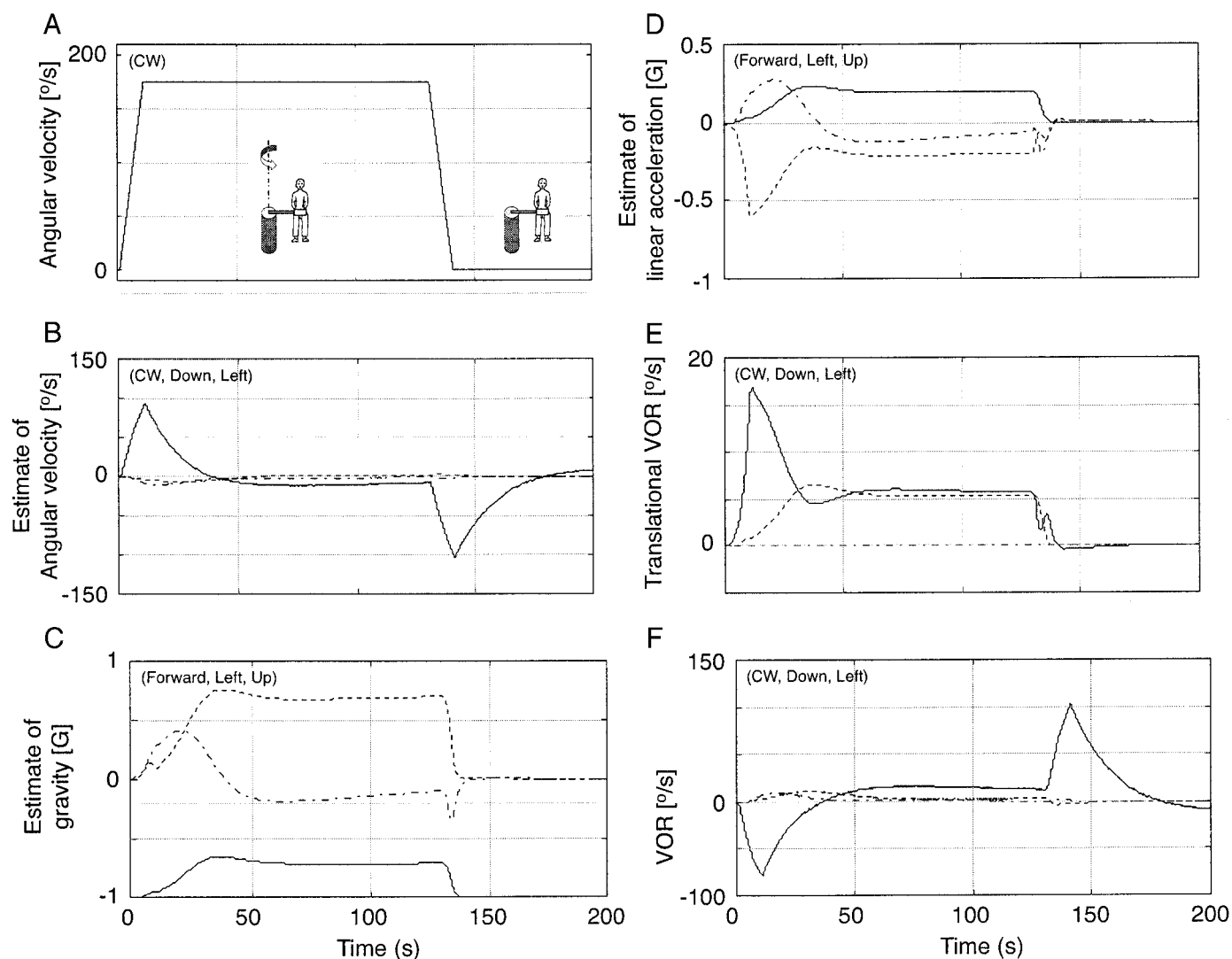


FIG. 3. Predicted responses induced by fixed-radius ($r = 1$ m) centrifugation with subject oriented back to motion. A: the yaw angular velocity ($175^\circ/\text{s}$ trapezoid) is shown. Modeling predictions of the neural representations of angular velocity (B), gravity (C), and linear acceleration (D) are shown. Also shown are modeling predictions of the translational VOR (E) and the total VOR (F). (The angular VOR component is not shown since, in this simple representation, it is equal and opposite the neural representation of angular velocity shown in B.) For all plots, the x-, y-, and z-components are represented by dash-dot, dash, and solid lines, respectively. To allow direct comparison to published data (Merfeld et al. 2001), the simulated conditions precisely match the $175^\circ/\text{s}$ fixed-radius centrifugation trials.

digm allows the presentation of low-frequency inertial cues in the absence of canal cues (Seidman et al. 1998). To allow direct comparison to the fixed-radius simulations (Fig. 3) and to the previously published data (Merfeld et al. 2001), we have precisely matched the centrifugal force cues present during fixed-radius centrifugation in this variable-radius simulation by varying the radius quadratically (Fig. 4A), as we did in the experimental investigation (Merfeld et al. 2001). Model predictions show a neural representation of gravity (Fig. 4B) that tilts more rapidly toward alignment with GIF than for fixed-radius centrifugation, though it is still slightly delayed relative to the actual GIF tilt. The difference between the fixed-radius and variable-radius model predictions (where the only difference is the presence or absence of transient yaw canal cues) confirms the experimental finding (Merfeld et al. 2001) that yaw rotational cues from the canals substantially influence perceived roll tilt.

The small difference between the otolith measure of GIF and the estimate of gravity elicits a small transient neural representation of interaural linear acceleration (Fig. 4C) that decays to a steady-state level of slightly <0.2 G and a similar steady-state “z-component” of predicted linear acceleration. The small interaural neural representation of linear acceleration elicits a predicted horizontal translational VOR (Fig. 4D), which includes a brief transient response (peak of $\sim 7^\circ/\text{s}$) followed by a steady-state response of roughly $5^\circ/\text{s}$. The small z-axis component of estimated linear acceleration elicits a predicted vertical translational VOR, which builds to a steady-state level of roughly $5^\circ/\text{s}$. Because the yaw rotational cue decays prior to the radial movement, the model predicts little or no estimated angular velocity and, therefore little or no angular VOR. These model predictions mimic the human responses that have been reported, though the steady-state translational VOR responses are larger than those measured experimentally (Merfeld et al.

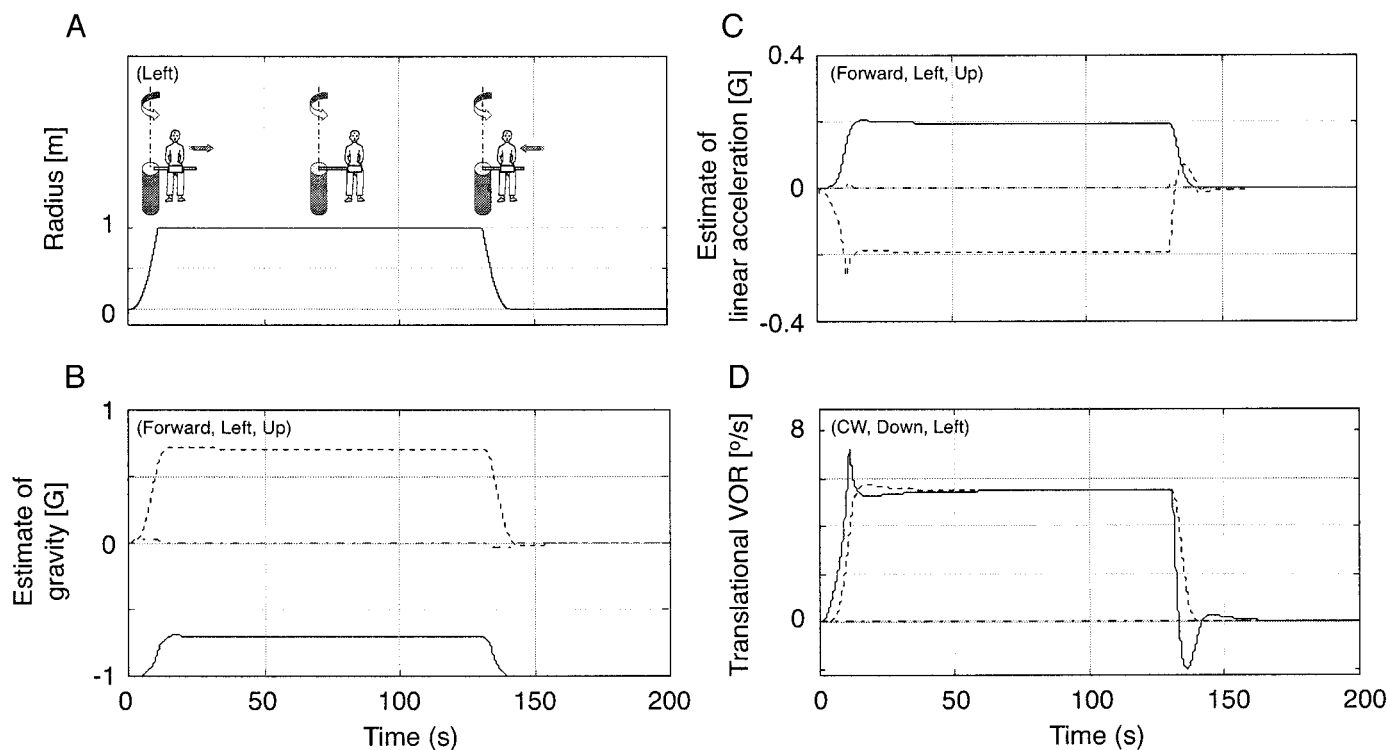


FIG. 4. Predicted responses induced by variable-radius centrifugation ($175^\circ/\text{s}$). A: the parabolic radius change to 1 m is shown. Modeling predictions of the neural representations of gravity (B) and linear acceleration (C) are shown. Also shown are modeling predictions of the translational VOR component (D). (There is little or no angular VOR response during this paradigm, so the total VOR is simply the VOR component that is compensatory for translation.) For all plots, the x -, y -, and z -components are represented by dash-dot, dash, and solid lines, respectively. To allow direct comparison to published data (Merfeld et al. 2001), the simulated conditions precisely match the $175^\circ/\text{s}$ variable-radius centrifugation trials.

2001). In the model, these large steady-state components result from the fact that the actual GIF has a magnitude of roughly 1.4 G, while the neural representation of gravity in the model has a fixed amplitude of 1 G.

Roll tilt and interaural translation

It has been shown that canal cues indicating roll rotation can be used to help correctly estimate the relative orientation of gravity (Stockwell and Guedry 1970) during rapid roll tilt steps. It has also been shown that squirrel monkeys have little or no horizontal VOR during or immediately following rapid roll tilts (Merfeld 1995b), despite the presence of an interaural force measured by the otolith organs. Model simulations match these findings. Figure 5, A–C, shows simulated human roll tilt responses induced by a rapid trapezoidal tilt of 11.3° , yielding an interaural force of 0.2 G. The tilt occurs over a very short interval (20 ms), so that the stimulation includes high-frequency components. For comparison to high-pass and low-pass filters, we also show the output of low-pass ($\tau = 2$ s) and high-pass ($\tau = 50$ ms) filters (Fig. 5A). Parameter values were chosen to match those previously published (Telford et al. 1997). The estimate for the component of gravity aligned with the interaural axis increases almost immediately to near the steady-state value of 0.2 G (Fig. 5C). A very small estimate of linear acceleration (peak ~ 0.025 G) is elicited that decays back toward zero (Fig. 5B). Figure 5, D–F, shows roll tilt responses induced by a sinusoidal roll tilt of 11.3° , yielding an interaural force of 0.2 G, at a frequency of 1.0 Hz. The responses show

a relatively small (0.04 G), sinusoidal, neural representation of linear acceleration and a relatively large (0.15 G) neural representation of interaural gravitational force (i.e., estimated roll tilt).

The gain of the modeled tilt (Fig. 6A) and translation (Fig. 6B) responses were calculated and plotted for frequencies between 0.001 and 10 Hz (Fig. 6, A and B). The tilt gain is mostly flat, ranging from a nearly perfect gain of 1.0 at low frequencies to a gain of 0.75 at high frequencies, with the transition occurring around 0.2 Hz. Concomitantly, the linear acceleration gain is always small, starting out at zero at low frequencies, where the estimate of gravity nearly matches actual gravity, and increasing to about 0.2 at high frequencies, where the estimate of gravity no longer perfectly matches actual gravity. These responses can be compared and contrasted to the predicted responses elicited by sinusoidal interaural linear translation (Fig. 6, C and D) with the acceleration chosen to match the interaural shear force obtained during roll tilts. These responses show low-pass (tilt) and high-pass (translation) filtering characteristics. These low-pass and high-pass characteristics were obtained *without explicit high-pass or low-pass filtering* of otolith cues. This demonstrates that one does not need to have explicit low-pass and high-pass filters (e.g., Mayne 1974; Paige 1983) to achieve the filtering that has been hypothesized to explain the tilt/translation processing of otolith cues.

The model mechanism by which the canal cues influence the processing of otolith cues is straightforward. As a first step, the neural representation of rotation is used to help keep track of the relative orientation of gravity due to rotation; this is cap-

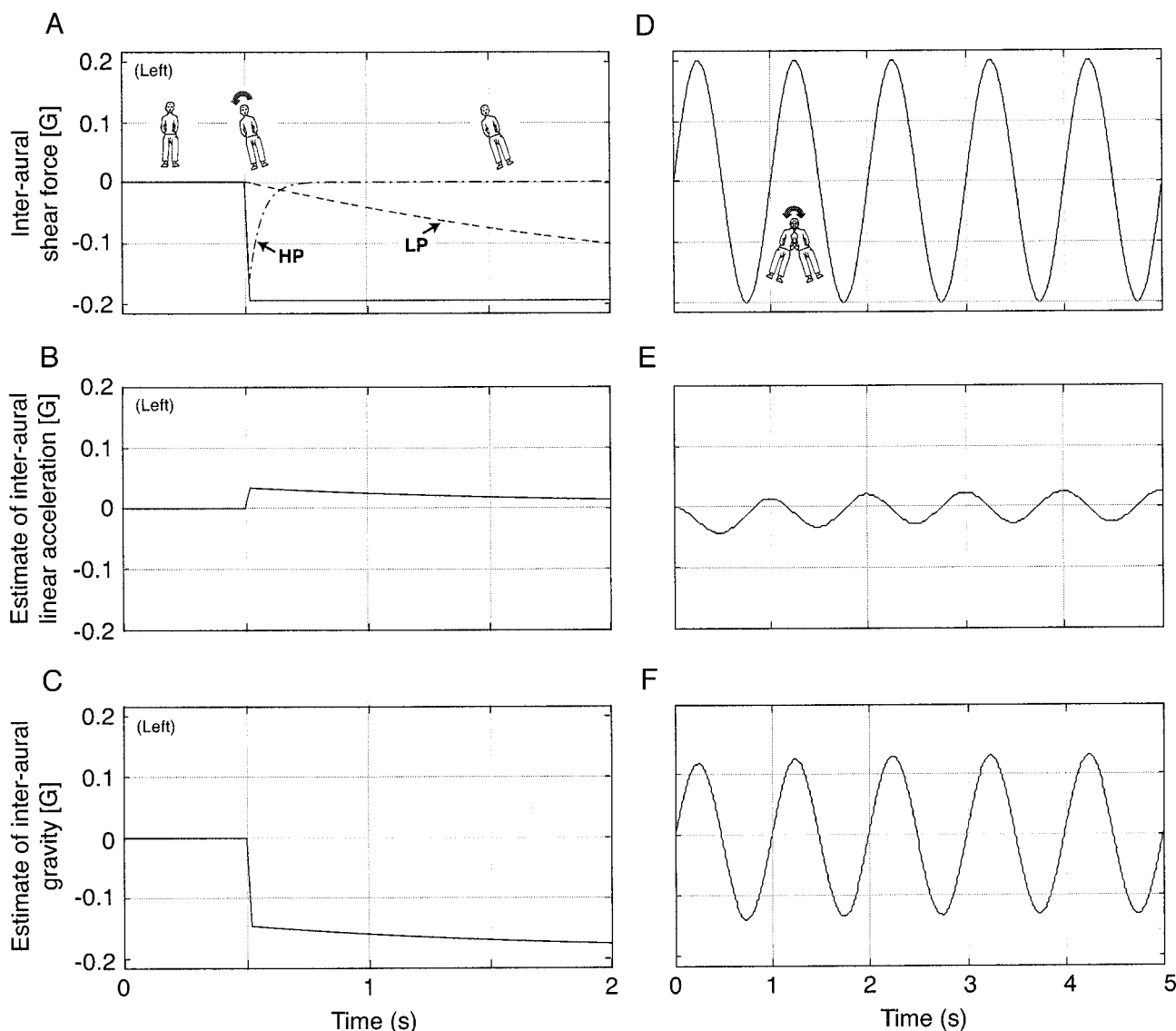


FIG. 5. Predicted responses induced by roll tilt alone. *A*: interaural gravitational shear force due to a step roll tilt (11.3° in 20 ms). Dash and dash-dot curves correspond to low-pass (LP, $t = 2$ s) and high-pass (HP, $t = 50$ ms) filtering of the interaural shear force. The low-pass filter does not include a rapid change in tilt. The response of the high-pass filter is much greater than that shown by our model and decays very rapidly back to zero. *B*: predicted neural representation of interaural linear acceleration during a step tilt. *C*: predicted neural representation of interaural gravity (tilt) during a step tilt. *D*: sinusoidal tilt stimuli (1.0 Hz, 11.3°). The peak interaural force caused by the tilt is 0.2 G. *E*: predicted neural representation of interaural linear acceleration during sinusoidal stimuli. *F*: predicted neural representation of interaural gravity (tilt) during sinusoidal stimuli.

tured² by the differential equation $d\hat{\mathbf{g}}/dt = -\hat{\boldsymbol{\omega}} \times \hat{\mathbf{g}}$ (e.g., Droulez and Darlot 1989; Merfeld 1995b; Merfeld et al. 1993a). The influence of canal cues causes the dramatic difference between the responses to roll tilt (Fig. 6, *A* and *B*) and interaural translation (Fig. 6, *C* and *D*) at high frequencies, with the canal cues used to help calculate the relative tilt of gravity during roll tilt. However, these canal influences are not perfect, as can be observed by the tilt gain of 0.75 for roll tilts at frequencies above roughly 0.1 Hz. This tilt gain is below 1.0 because the estimated roll angular velocity has a gain of only

0.75 (not shown). [The angular velocity gain was derived and discussed in great detail in an earlier publication (Merfeld et al. 1993a).] If the estimate of angular velocity ($\hat{\boldsymbol{\omega}}$) is 75% of the actual angular velocity, it is easy to see, by the differential equation $d\hat{\mathbf{g}}/dt = -\hat{\boldsymbol{\omega}} \times \hat{\mathbf{g}}$, that the estimate of gravitational tilt will be underestimated proportionally. If the calculation of changes in gravity fall short of the actual changes in the orientation of gravity by roughly 25% , this will further lead to incorrect estimates of linear acceleration during roll tilt, as demonstrated by our modeling predictions. It is interesting to note that the model predicts that there might be a transient and very small neural representation of interaural linear acceleration during rapid roll tilts. Since this neural representation is very small, the average response may rise above noise only after many trials.

² It seems prudent to point out that we do not think that the nervous system "implements" this differential equation. Rather, we hypothesize that the nervous system uses rotational cues to help predict the relative orientation of gravity. The differential equation simply shows the mathematical technique we used to implement this influence of rotational cues.

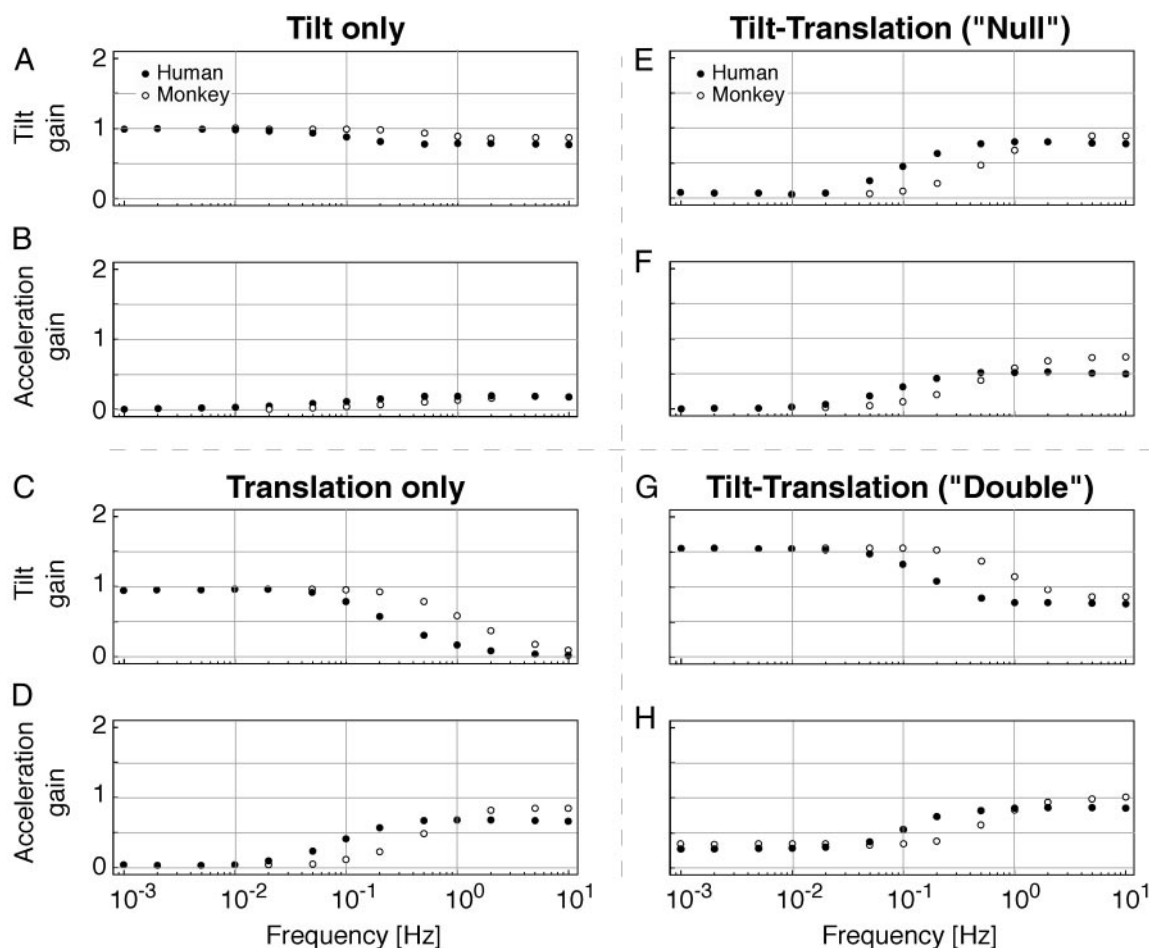


FIG. 6. Predicted frequency response induced by tilt and translation stimulation. Solid symbols (●) show human predictions; open symbols (○) show predictions from monkey model. Predicted tilt (A) and translation (B) gain during roll tilt only. During roll tilt, the only interaural force is due to gravity. Therefore the tilt gain is defined as the peak interaural estimate of gravity divided by the peak interaural gravitational force; the translation gain is defined as the peak interaural estimate of linear acceleration divided by the peak interaural gravitational force. Predicted tilt (C) and translation (D) gain during translation only. During translation, the only interaural force is due to linear acceleration. Therefore the tilt gain is defined as the peak interaural estimate of gravity divided by the peak interaural linear acceleration; the translation gain is defined as the peak interaural estimate of linear acceleration divided by the peak interaural linear acceleration. Predicted tilt (E) and translation (F) gain during combined translation and roll tilt stimulation when the inertial stimuli "nulls" interaural gravitational force. Predicted tilt (G) and translation (H) gain during combined translation and roll tilt stimulation when the inertial stimuli "doubles" the interaural gravitational force. During combined tilt/translation stimulation (E–H), the tilt gain is defined as the peak interaural estimate of gravity divided by the peak interaural gravitational force; the translation gain is defined as the peak interaural estimate of linear acceleration divided by the peak interaural linear acceleration.

Combined roll tilt and interaural translation

When sinusoidal linear acceleration is combined with sinusoidal roll tilt, the phase between linear acceleration and tilt can be set such that the interaural gravitational force approximately cancels the interaural inertial force due to linear acceleration (Fig. 7, A–D); or, the phase can be set so that the interaural gravitational force adds to the inertial force caused by the interaural linear acceleration, yielding an approximate doubling of the net interaural force measured by the otolith organs (Fig. 7, E–H). Humans have not yet been tested using this paradigm, but data show that rhesus monkeys are able to correctly separate tilt and translation during such combined stimulation (Angelaki et al. 1999).

The predicted neural representation of interaural linear acceleration for humans for both paradigms is much greater than that shown for roll tilt alone (Fig. 5), and the neural represen-

tation of interaural gravitational force is much greater than that shown for linear acceleration alone (see Fig. 6). In addition, the acceleration response was smaller when the gravitational and inertial forces canceled one another (Fig. 7C) than when these forces added (Fig. 7G). Finally, a small vertical response at twice the frequency of the stimulation was predicted, matching the actual linear acceleration, which includes a significant z-axis component at twice the frequency of stimulation. The model predictions for humans appear mostly consistent with published monkey data (Angelaki et al. 1999). As for roll tilts alone, the model predicts these responses by using the canal cue to help estimate the relative orientation of gravity. As before, the difference between the otolith measurement of force and the neural representation of gravity is processed as linear acceleration. However, during combined tilt and translation stimulation, this difference includes the true sinusoidal

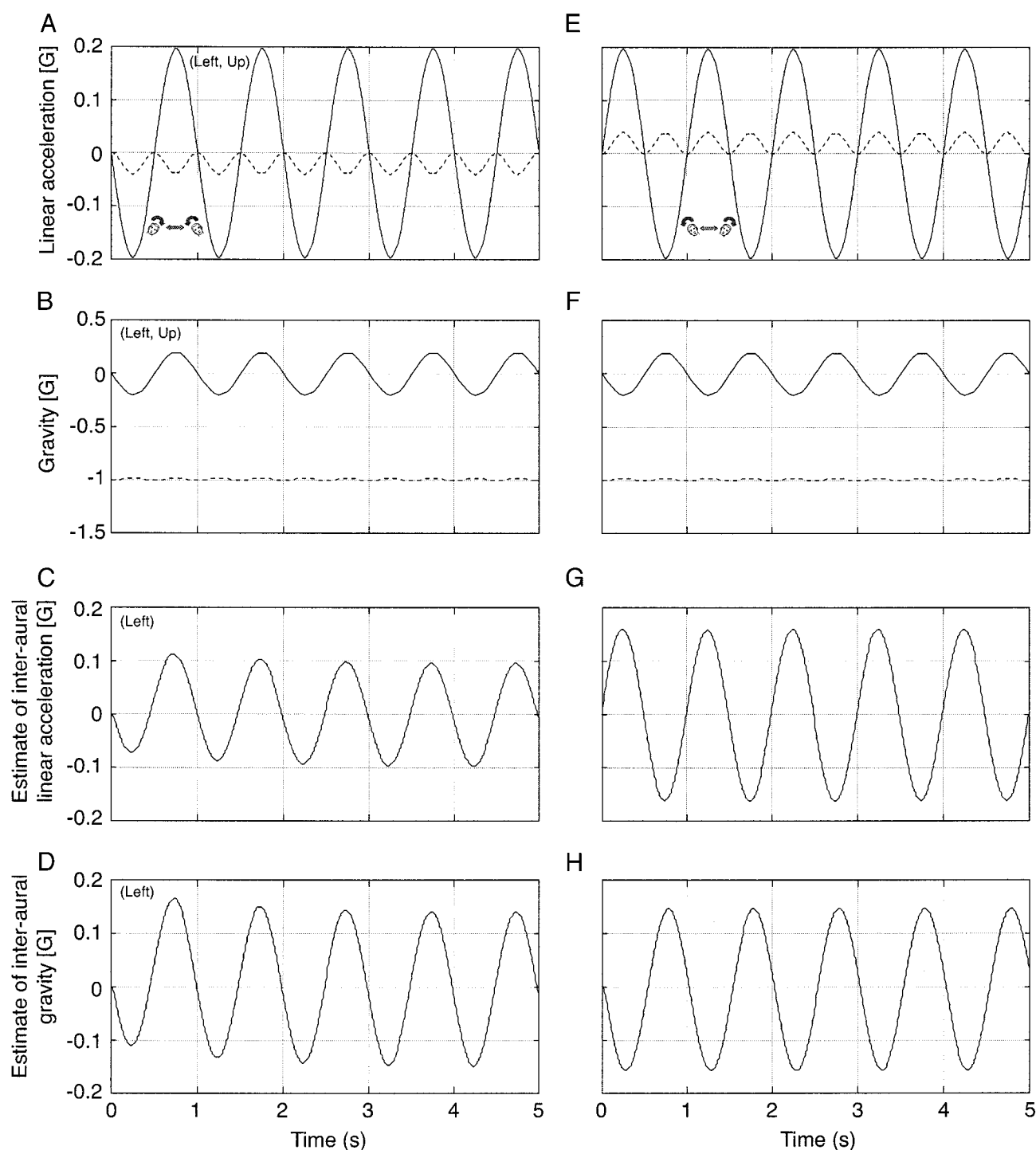


FIG. 7. Predicted responses induced by combining sinusoidal roll tilt with sinusoidal interaural linear acceleration. **A:** sinusoidal linear acceleration stimuli (1.0 Hz, 0.2 G). The solid line is the component of linear acceleration aligned with the y-axis (interaural axis). The dash line is the component aligned with the z-axis due to roll tilt during translation. **B:** sinusoidal gravitational stimuli (1.0 Hz, 0.2 G). The solid line shows changes in the gravitational component aligned with the y-axis (interaural axis). The dash line shows tiny changes in the gravitational component aligned with the z-axis. The phase between the linear acceleration and gravitational changes is such that little or no interaural (y-axis) force is measured by the otolith organs. **C:** predicted neural representation of interaural linear acceleration. **D:** predicted interaural neural representation of gravity ("roll tilt"). **E:** sinusoidal linear acceleration stimuli (1.0 Hz, 11.3°). The solid line is the component of linear acceleration aligned with the y-axis (interaural axis). The dash line is the component aligned with the z-axis due to roll tilt during translation. **F:** sinusoidal gravitational stimuli (1.0 Hz, 11.3°). The solid line shows changes in the gravitational component aligned with the y-axis (interaural axis). The dash line shows tiny changes in the gravitational component aligned with the z-axis. The phase between the linear acceleration and gravitational changes is such that the peak interaural force measured by the otolith organs is approximately 0.4 G. **G:** predicted neural representation of interaural linear acceleration. **H:** predicted interaural neural representation of gravity ("roll tilt").

linear acceleration. Hence, identical mechanisms as those described above explain these combined responses as well.

It is worth noting that reports (Angelaki et al. 1999) indicate that the amplitude of the horizontal response is the same, whether acceleration is in phase or out of phase with tilt. This appears inconsistent with our modeling prediction that the amplitude of the neural representation of linear acceleration and, hence, the horizontal translational VOR depends on whether the forces add (Fig. 7G) or cancel (Fig. 7C). This difference primarily arises because the neural rotation calculations in the model are not perfect. This small discrepancy between the model and available data can be resolved only with additional data. It is possible that this effect is smaller in monkeys than that in humans, such that it becomes evident in monkeys only with numerous repeat trials. (Recall that the version of the model reported in this study is for human responses, which have been shown to be somewhat different from monkey responses for various motion paradigms.) Similarly, the model predicts a small neural representation of linear acceleration (peak-to-peak amplitude of approximately 0.021 and 0.035 G for when the forces canceled or added, respectively) at twice the frequency of the applied translations along the subject's z -axis (not shown). This, in turn, elicits a vertical VOR at twice the frequency of stimulation. Such responses were not reported in monkeys.

For comparison to the earlier frequency responses, the gain of the modeled tilt and translation responses were calculated and plotted for frequencies between 0.001 and 10 Hz for combined tilt and translation (Fig. 6, *E-H*). The tilt gain is fairly accurate (gain ~ 0.75) at high frequencies, when the canals provide useful rotation information, for both the "null" force (Fig. 6E) and "double" force (Fig. 6G) conditions. The linear acceleration gain is also fairly accurate at high frequencies, although the gain is somewhat higher for the "double" force condition (Fig. 6H) than that for the "null" force condition (Fig. 6F). At low frequencies, where accurate canal information is no longer available, there is little or no tilt or linear acceleration response for the "null" condition, even though both should have a gain of about 1. Similarly, the tilt gain is very large (~ 1.6) for the "double" force condition and the linear acceleration gain is small (~ 0.25), even though both should have a gain of about 1. These deficits suggest that, in the absence of accurate rotational cues at low frequencies, the nervous system is no longer able to accurately separate tilt from translation. To our knowledge, human (or even monkey) responses to such stimulation across a broad frequency band have not yet been measured; these model predictions await refutation or verification by such data sets when available.

DISCUSSION

Internal models

We define internal models as neural systems that mimic physical principles associated with sensory transduction or movement. For our modeling investigations, we choose an even more conservative definition, limiting internal models to neural systems that mimic physical principles that we can represent mathematically. Our model includes three primary internal model components: 1) the influence of rotational cues on the neural processing of gravity, 2) the resolution of mea-

sures of GIF into neural representations of gravity and linear acceleration, and 3) the neural representation of the dynamics of the semicircular canals. We briefly discuss the evidence for each component.

INFLUENCE OF ROTATIONAL CUES ON THE NEURAL REPRESENTATION OF GRAVITY. One internal model hypothesis predicts that a neural representation of rotation influences the neural representation of gravity ($d\hat{\mathbf{g}}/dt = -\hat{\boldsymbol{\omega}} \times \hat{\mathbf{g}}$) in a manner consistent with the physics of the real world ($d\mathbf{g}/dt = -\boldsymbol{\omega} \times \mathbf{g}$). (See APPENDIX for details.) In principle these rotational cues can come from the semicircular canals, vision, or any other system that might provide rotational cues, but only the influence of the canals is presently implemented. The earliest direct evidence supporting this hypothesis comes from a study in which subjects were rotated about an earth-horizontal axis and then brought to a stop. In the postrotary period, the subjects reported illusory tilt that was in the direction consistent with the postrotational canal cues (von Holst and Grisebach 1951). Because the subjects were rotated at a relatively slow speed and for a relatively short duration, the measured effects were small. We have confirmed these findings using verbal reports following rotation at much higher speeds and longer rotation duration (Merfeld et al. 1999). Another study used actual roll tilt stimulation to show that subjects utilized the dynamic roll cues from the semicircular canals to help accurately detect roll tilt with little or no lag (Stockwell and Guedry 1970). Neurons in the vestibular nuclei show characteristics similar to the perceptual findings of Stockwell and Guedry, with canal cues converging to influence the neural responses (Zhou et al. 1998, 2000). In addition, rotational visual cues can induce similar effects; illusory roll tilt has been reported when upright subjects are provided with a rollvection cue (Dichgans et al. 1972). The illusory tilt is again in the direction that the subject would tilt if the rotational cues indicated a real rotation.

Several other very recent findings also support the notion that rotational cues influence the neural representation of gravity. We found that the time course of perceived roll tilt during centrifugation depends on the presence or absence of yaw canal cues (Merfeld et al. 2001); this confirms an earlier report showing that yaw canal cues influence perceived pitch tilt (Seidman et al. 1998). In another recent study (Hess and Angelaki 1999), primary eye position varied during off-vertical-axis rotation but not during pure translation, yielding similar otolith cues, with the modulation enhanced at the beginning of rotation when the rotational cues from the semicircular canals were veridical. Since a primary difference between the incoming sensory information during these motion conditions was the contribution of the semicircular canals, the authors concluded that the contributions of the semicircular canals helped discriminate between gravity and linear acceleration.

GIF RESOLUTION. A second "internal model" predicts that the neural representation of gravity minus the neural representation of linear acceleration equals the neural representation of GIF ($\hat{\mathbf{g}} - \hat{\mathbf{a}} = \hat{\mathbf{f}}$), consistent with real-world physics ($\mathbf{g} - \mathbf{a} = \mathbf{f}$). (See APPENDIX for details.) This hypothesis was first developed to explain centrifugation responses (Merfeld 1990). It had been shown that illusory tilt developed much more gradually during acceleration on a fixed-radius centrifuge than the tilt sensation dissipated during deceleration (Clark and Graybiel 1963, 1966; Graybiel and Brown 1951). The gradual build up of the illusion

of tilt, much slower than the actual GIF tilt, meant that a substantial difference between the measured GIF and the neural representation of gravity existed during acceleration. The GIF resolution hypothesis suggested that this difference should be interpreted as linear acceleration ($\hat{\mathbf{a}} = \hat{\mathbf{g}} - \hat{\mathbf{f}}$). Since a horizontal translational VOR is elicited by inter-aural linear acceleration, the hypothesis suggested that a horizontal translational VOR should be present transiently during centrifuge acceleration, with little or no translational VOR during deceleration. [Recall that the estimate of gravity ($\hat{\mathbf{g}}$) and the measurement of GIF ($\hat{\mathbf{f}}$) were nearly equal during deceleration, but not acceleration, of the centrifuge. Hence the estimate of linear acceleration, the difference between measured GIF and estimated gravity, would be about zero during angular deceleration and larger during angular acceleration.] Furthermore, the time course of the horizontal VOR should match the time course with which estimated tilt aligns with GIF.

These predictions were consistent with earlier studies showing that the horizontal VOR, including both translational and angular components, was dramatically different with humans facing motion than that with back to motion (Lansberg et al. 1965; Young 1967). We recently confirmed these findings in a comprehensive centrifugation study with human subjects (Merfeld et al. 2001) and, also consistent with model predictions, found that the time course of the translational VOR component was approximately equal to the time course with which the illusory tilt aligns with GIF.

While monkey responses during centrifugation are quantitatively different from the human responses, we had previously reported compatible results in squirrel monkeys (Merfeld and Young 1995). We found a facing-motion and back-to-motion asymmetry in the horizontal VOR response, similar to though smaller than that in humans. Furthermore, the axis of eye rotation lagged (slightly) behind the actual GIF tilt. This provides evidence for a small lag in the alignment of the neural representation of gravity with GIF in squirrel monkeys.³ The lag in alignment of the axis of eye rotation with the stimulus was approximately the same as the time course over which the translational VOR component decayed to zero, again consistent with the GIF resolution hypothesis. Furthermore, we tilted the monkeys in roll and showed that there was little or no translational VOR response (Merfeld and Young 1995), even though there was a substantial interaural force and even though the introduction of the interaural force included substantial high-frequency components. The explanation we provided (Merfeld and Young 1995) and modeled (Merfeld 1995b) is similar to that presented herein for humans.

Two other recent studies have confirmed the hypothesized neural mechanisms and have substantially augmented these earlier studies. One study (Angelaki et al. 1999) showed that a horizontal translational VOR response could still be elicited when dynamic tilt and translation stimuli were combined. Calculations indistinguishable from those modeled herein explained the observed responses (Angelaki et al. 1999). Another study used a 90° postrotatory tilt following a yaw rotation about an earth-vertical axis ("dumping") and measured a hor-

izontal translational VOR component, even in the absence of physical linear acceleration (Merfeld et al. 1999; Zupan et al. 2000).

NEURAL REPRESENTATION OF CANAL DYNAMICS. While not as direct or influential as the other two principal internal models, the model also includes an internal model that mimics the dynamics of the semicircular canals. Some support for this hypothesis exists. First, as shown previously (Merfeld et al. 1993b), the internal model hypothesis predicts "velocity storage," the prolongation of rotational responses beyond the canal afferent responses, as a result of the neural process of multi-sensory integration. This is accomplished by the internal model of canal dynamics. The fact that velocity storage is an emergent property of the model, without any explicit attempt to include velocity storage, supports the existence of an internal model of the semicircular canal dynamics.

This implementation contrasts with the most familiar model of velocity storage (Raphan and Sturm 1991; Raphan et al. 1977, 1979; Wearne et al. 1999), which uses low-pass filters (i.e., leaky integrators) to accomplish the same effect. The leaky integrator model successfully matches many responses by using a time-varying feedback matrix to control the eigenvalues and eigenvectors of the three-dimensional angular VOR. This "leaky-integrator" model does not include the influence of rotational responses on the processing of ambiguous GIF cues.

Sensory dynamics are very difficult to manipulate experimentally, except by drastic surgical alterations like those provided by canal plugging or labyrinthectomy. Therefore the veracity of this internal model of the canal dynamics is less established than the other internal model components. Experimental manipulation of canal dynamics will allow a more direct evaluation of this hypothesis.

Other models of sensory integration

This model was derived from a series of models (e.g., Oman 1991, 1998; Sperry 1950; Von Holst and Mittelstaedt 1950). Similar to our approach, models describing three-dimensional, sensory interactions between visual and vestibular cues were developed by two other groups, in parallel with our efforts. One of these models is based on the concept of "Coherence Constraints" (Droulez and Darlot 1989). This model includes internal models of sensory dynamics, body dynamics, and physical relationships, differing only in its implementation of these internal models. The Coherence Constraint model of visual/vestibular interactions simulates reflexive eye movements induced by three-dimensional motion stimuli in darkness and in light (Zupan 1995; Zupan et al. 1994) and has also been used to model motor control (Darlot et al. 1996). The second family of these models (Glasauer 1992) was based on optimal estimation and was shown to simulate human tilt perception during fixed-radius centrifugation. This model was shown to be very similar to the internal model approach presented herein (Glasauer and Merfeld 1997). Another very recent model (Holly 2000) includes internal models like our own, in which the primary difference in this new model is that it uses the physical stimulation (e.g., angular velocity, linear acceleration, etc.), while we include mathematical representations of the sensory systems (e.g., semicircular canals, otolith organs, etc.).

One of the earliest sensori-integration models was developed by Mayne (1974). This two-dimensional model relied primar-

³ The axis of eye rotation was previously shown to rapidly align with gravity following postrotational tilt (Angelaki and Hess 1994; Merfeld and Young 1992; Merfeld et al. 1993b). Therefore the axis of eye rotation provides an indirect measure of "tilt" in the monkey (analogous to the perceptual measure of tilt in humans).

ily on low-pass and high-pass filtering of the cues from the otolith organs, to elicit tilt and translation responses, but also included two-dimensional influences of the cues from the semicircular canals on the processing of cues from the otolith organs. Another early model of the angular vestibuloocular (Robinson 1977) used a single positive feedback loop to prolong the VOR compared with the activity of the semicircular canal first-order afferent. This model was later modified to implement the influence of the otolithic information on visual/vestibular interactions (Hain 1986). Hain's model implemented the influence of otolith information on rotational cues but did not implement the influence of canal cues on self-orientation. [Several other models (Galiana and Outerbridge 1984; Green and Galiana 1998) successfully match characteristics of the angular VOR but do not include sensory interactions between two or more sensory systems.]

Other models utilized techniques borrowed from optimal estimation (Borah et al. 1988; Ormsby and Young 1977). Ormsby's model included the influence of rotational cues on the orientation of gravity using a mechanism resembling an internal model of a physical relationship. However, the primary estimation processes were carried out for each sensory system individually. This differs from the internal model approach in which the primary estimation processes are carried out by the internal models. Borah's model, based on Kalman filtering, did not include explicit internal models.

Differences between human and monkey responses

There are substantial differences between human and monkey responses. In brief, the human horizontal VOR demonstrates a large orientation dependency during fixed-radius centrifugation (e.g., Lansberg et al. 1965; Merfeld et al. 2001) and following postrotational tilt (Merfeld et al. 1999; Zupan et al. 2000). The monkey horizontal VOR shows little orientation dependency during centrifugation (Merfeld and Young 1995; Wearne et al. 1999) or following postrotational tilt (Angelaki and Hess 1994; Merfeld et al. 1993b). Furthermore, for monkeys the axis of eye rotation shifts nearly into alignment with GIF during fixed-radius centrifugation (Merfeld and Young 1995; Wearne et al. 1999) and following postrotational tilt (Angelaki and Hess 1994; Merfeld et al. 1993b); humans show little or no axis shift (vertical and/or torsional responses) during centrifugation (Merfeld et al. 2001) or following "dumping" (Fetter 1996; Fetter et al. 1992; Zupan et al. 2000).

To investigate these species differences further, we changed the human model reported herein back to a monkey model, by altering just four parameters⁴ (Table 1). While the overall "repertoire" of the model is limited, with changes in just these four free parameters, the model still successfully predicts monkey responses. For example, the model successfully predicts a large axis shift during fixed-radius centrifugation and following postrotary tilt. The predicted axis shifts are similar to those published in previous versions of the monkey model (Merfeld 1995b; Merfeld et al. 1993a) and quite unlike the small axis shift observed in humans (Merfeld et al. 2001) or for the human simulations (Fig. 3). Furthermore, the model also suc-

cessfully predicts that the horizontal VOR depends on subject orientation during centrifugation. This small, predicted orientation dependency is similar to that presented in published versions of the monkey model (Merfeld 1995b) and, more important, is similar to the small orientation dependency that has been measured experimentally (Merfeld and Young 1995). This present version of the model also predicted the ability of the monkey to separate tilt from translation accurately during combined tilt/translation stimuli, as has been shown experimentally (Angelaki et al. 1999). These model predictions (not shown) match those published in a recent study that included a monkey version of this model (Angelaki et al. 2001).

The differences between the human and monkey model predictions during combined tilt and translation are shown in Fig. 6. Qualitatively, the predicted monkey responses are similar to the predicted human responses, although there are some quantitative differences. The magnitude of the human and monkey responses is slightly different, and the transition frequency is shifted toward a slightly higher frequency in the monkey. This represents the somewhat greater tendency of the monkey to interpret GIF as gravity. In the model, this is primarily due to the increase in the GIF feedback parameter $k_{f\omega}$. To our knowledge, experimental investigations across such a broad frequency range have yet to be performed. Such data will provide a test of this model.

The model can match the different responses of both human and monkeys⁵ while maintaining identical internal models; this shows that we do not need to find different neural mechanisms to explain the large interspecies differences that have been measured. The same neural calculations can explain both human and monkey responses, although the weighting provided these calculations might differ.

By combining a few simple hypotheses within the internal model framework, the model presented herein qualitatively matches responses to a number of different paradigms. This is true for both human and monkey responses, despite large differences between the species. It is interesting that the exact same mechanisms used to explain eye movement responses to simple movements like those observed during rapid roll tilts (Angelaki et al. 1999; Merfeld 1995b; Merfeld and Young 1995) can also explain eye movement responses during more complex paradigms like centrifugation (Merfeld 1995b; Merfeld and Young 1995; Merfeld et al. 2001), combined tilt and translation (Angelaki et al. 1999, 2001), and postrotational tilt (Zupan et al. 2000). The demonstrated presence of these neural mechanisms during each of the above passive motion paradigms adds credence for the presence of these mechanisms during all passive motion. These general characteristics, along with the fact that internal models have been reported across several scientific disciplines,⁶ add confidence

⁵ It is worth noting that with a third set of parameters, the model matched cynomolgus monkey responses (Wearne et al. 1999), with the horizontal VOR nearly the same when the monkeys were facing the motion or had their backs toward the motion. The model accomplishes this with a greater weighting of the otolith cues to indicate gravity, consistent with the rapid, large axis shift reported in these experiments.

⁶ For example, internal models have been invoked to help explain motor control (e.g., Bhushan and Shadmehr 1999; Darlot et al. 1996; Mussa-Ivaldi 1999; Wolpert et al. 1995; Yasui and Young 1975; Zupan 1995), sensorimotor integration (Bell et al. 1997; Kuo 1995; Paulin 1993), and sensory processing (Droulez and Darlot 1989; Glasauer 1992; Lewald and Ehrenstein 1998; Rao and Ballard 1997).

⁴ To allow direct comparison to this human model, the gravity rotation element for this new monkey model was the same as that for the human model reported herein. Hence, this monkey model is slightly different from the earlier monkey models.

to our conclusion that humans use internal models to process motion cues.

APPENDIX

The model includes three components that determine the afferent signals ("sensory inputs") from the semicircular canals and otolith organs. These components are briefly described below.

INFLUENCE OF ROTATIONAL CUES ON THE RELATIVE ORIENTATION OF GRAVITY. Rotation of an object influences the relative orientation of gravity with respect to that object. This simple effect is represented by the differential equation $d\mathbf{g}/dt = -\boldsymbol{\omega} \times \mathbf{g}$, where $\boldsymbol{\omega}$ is the angular velocity of the head and \mathbf{g} is gravity. In the model, this is implemented by integrating both sides of this equation to yield $\mathbf{g} = \int (-\boldsymbol{\omega} \times \mathbf{g})dt$. This influence of rotational cues on the relative orientation of gravity is discussed in depth in a companion study (Zupan et al. 2000).

GRAVITOINERTIAL FORCE. The otolith organs, and all other physiological linear accelerometers, measure gravitoinertial force, the vector difference of gravity minus linear acceleration. This physical law can be represented by the equation $\mathbf{f} = \mathbf{g} - \mathbf{a}$, where \mathbf{f} is gravitoinertial force per unit mass, \mathbf{g} is gravitational force per unit mass, and \mathbf{a} is linear acceleration. This issue is discussed in depth in a companion study (Merfeld et al. 2001).

SENSORY DYNAMICS. The dynamics of the neural responses from afferent units innervating the semicircular canals have been widely investigated. It has long been known that in the squirrel monkey the time constant of the regular units innervating the canals averages about 5.7 s (Fernandez and Goldberg 1971; Goldberg and Fernandez 1971). The same studies also demonstrated a response reversal (sometimes referred to as adaptation) during extended stimulation. The average neural adaptation response component was modeled using a time constant of 80 s (Fernandez and Goldberg 1971). Roughly matching these values for this human model, we included a scalar transfer function of the form:

$$\frac{\alpha_{\text{sc}}(s)}{\omega(s)} = \frac{s^2}{(s + 1/\tau_d)(s + 1/\tau_a)}$$

where s is the standard Laplace transform variable, ω is a scalar angular velocity along one of three axes, α_{sc} is a scalar semicircular canal afferent signal along the same axis, τ_d is the dominant time constant (5 s) of the semicircular canals, and τ_a is the adaptation time constant (80 s). The higher frequency components of modeled transfer functions (e.g., Fernandez and Goldberg 1971) were not included because these high-frequency characteristics would not have a large impact on the responses modeled herein and have not been quantified in humans (and may not exist in humans).

To model the three-dimensional responses of the semicircular canals we repeated this one-dimensional canal representation three times, once for each spatial dimension. This representation ignores any potential asymmetries in the afferent canal responses for the various semicircular canals. (Such asymmetries could be included in this model when relevant neural responses are known.) To keep the model as simple as possible, we included the canals as being aligned with the x -axis, y -axis, and z -axis of the head. The actual geometrical orientation of the canals is known (Curthoys et al. 1977) and could have been included in a two-eared version of this model. We chose not to include it in this one-eared sensori-integration model because inclusion has no effect on model predictions, as long as the identical geometrical orientation is included in the internal model of the semicircular canals.

For similar reasons the otolith organs were modeled using a diagonal transfer function matrix representing the three-dimensional responses of neurons innervating the two otolith organs. For simplicity, as in the earlier publications, the modeled afferent responses were

directly proportional to the gravitoinertial force measured by the otolith organs. This approximately represents the dynamics of regular afferent neurons innervating the otolith organs (Fernandez and Goldberg 1976a,b) but ignores the phasic responses of the irregular units as well as several high-frequency effects, which were mostly beyond the range of the dynamic simulations performed for this study.

Internal model

The nervous system does not know the angular velocity or linear acceleration of the head or the relative orientation of gravity; it can only measure and estimate these quantities based on the available information (vestibular, visual, tactile, etc.). In this model, this neural estimation process is accomplished by an internal model. There are three principal components that make up the internal model. These components, briefly described below, include: 1) the influence of rotational cues on the neural representation of gravity, 2) the resolution of gravitoinertial force into neural representations of gravity and linear acceleration, and 3) the neural representation of the dynamics of the semicircular canals.

INFLUENCE OF ROTATIONAL CUES ON THE NEURAL REPRESENTATION OF GRAVITY. We hypothesize that the nervous system utilizes a neural network to use rotational cues to help estimate the relative orientation of gravity. This is represented by the nonlinear integral equation $\hat{\mathbf{g}} = \int (-\hat{\boldsymbol{\omega}} \times \hat{\mathbf{g}})dt$, where $\hat{\mathbf{g}}$ is the neural representation of gravity and $\hat{\boldsymbol{\omega}}$ is the neural representation of angular velocity. This matches the real-world effect described earlier in the APPENDIX.

RESOLUTION OF GRAVITOINERTIAL FORCE. The second principal component of the internal model is the GIF resolution hypothesis, which mimics the fact that GIF per unit mass equals gravity minus linear acceleration ($\mathbf{f} = \mathbf{g} - \mathbf{a}$), described above. In the internal model, the neural representation of GIF equals the neural representation of gravity minus the neural representation of linear acceleration, $\hat{\mathbf{f}} = \hat{\mathbf{g}} - \hat{\mathbf{a}}$, where $\hat{\mathbf{f}}$ is the neural representation of GIF, $\hat{\mathbf{g}}$ is the neural representation of gravity, and $\hat{\mathbf{a}}$ is the neural representation of linear acceleration.

SENSORY DYNAMICS. The third of the principal components of the internal model is the models of sensory dynamics. The internal model of the semicircular canals is a diagonal three-dimensional transfer function, matching the diagonal representation of the semicircular canals described previously. The dynamics of the internal model of the canals are a simplified version of the canal dynamics:

$$\frac{\hat{\alpha}_{\text{sc}}(s)}{\hat{\omega}(s)} = \frac{s}{(s + 1/\hat{\tau}_d)}$$

where $\hat{\omega}$ is the scalar neural representation of angular velocity, $\hat{\alpha}_{\text{sc}}$ is a scalar semicircular canal afferent signal, and $\hat{\tau}_d$ is the dominant time constant of the internal model of the semicircular canals ($\hat{\tau}_d = \tau_d = 5$ s). The adaptation time constant was not included in the internal model of the semicircular canals, since previous modeling (Merfeld et al. 1993a) showed that the adaptation time constant of the internal model had little influence on modeled responses. The internal model of the otolith organ dynamics is an identity matrix, exactly matching the otolith organ representation discussed previously.

Error calculations

The model (Fig. 1A) includes three error calculations that define the inputs to the internal model. Two of these calculations are simple mathematical difference operations. The angular velocity error vector (\mathbf{e}_ω) is calculated by subtracting the predicted semicircular canal signal ($\hat{\alpha}_{\text{sc}}$) from the actual semicircular canal signal (α_{sc}). Similarly, one GIF error signal (\mathbf{e}_g), the linear acceleration error, is calculated by subtracting the predicted otolith signal ($\hat{\alpha}_{\text{oto}}$) from the actual otolith signal (α_{oto}). A second GIF error (\mathbf{e}_p), the GIF rotation

error, is simply the rotation vector representing the rotation that would align the predicted otolith measurement ($\hat{\alpha}_{oto}$) with the actual otolith measurement (α_{oto}). This GIF rotation error is calculated in two steps. The magnitude and sign of the error is calculated by finding the angle between the predicted and measured otolith cues, $\cos^{-1}[(\alpha_{oto}/|\alpha_{oto}|) \cdot (\hat{\alpha}_{oto}/|\hat{\alpha}_{oto}|)]$ where the "dot" represents the dot product, sometimes called the inner product. The dimensionless direction of the rotation is calculated as $(\alpha_{oto}/|\alpha_{oto}|) \cdot (\hat{\alpha}_{oto}/|\hat{\alpha}_{oto}|)$. This error calculation represents a structural change to the most recent publications of this monkey model (Angelaki et al. 2000, 2001; Merfeld 1995b). This is the same three-dimensional error used in the earliest versions of this model (Merfeld 1990; Merfeld et al. 1993a). Later versions of the model (Merfeld 1995a,b) used a vector cross product that was not normalized. For most simulations, these two different forms of this error calculation are nearly indistinguishable. Therefore the actual form of the error calculation does not seem crucial under most circumstances. However, the cross product reaches a maximum when the vectors are orthogonal (i.e., when the signals are separated by 90°). The two-step error vector presented above reaches a maximum when the signals are separated by almost 180°. This difference was not critical in our earlier models of monkey responses, since the angle between otolith vectors was always small. However, since this angle becomes large for humans, this difference becomes important for human models.

Four feedback parameters are used to convert these feedback errors into estimates of motion and orientation. The angular velocity feedback parameter (k_{ω}) converts the difference between the expected and actual semicircular canal signals to a neural representation of angular velocity ($\hat{\omega}$). The linear acceleration feedback parameter (k_a) converts the linear acceleration error (e_a) to a neural representation of linear acceleration (\hat{a}). (Both k_{ω} and k_a are dimensionless.) The other two feedback parameters, the GIF feedback parameter (k_f) and the remaining feedback parameter (k_{fo}) were used to feedback the nonlinear error term and have units of rad/s/rad. The parameter values are shown in Table 1.

This work was supported by National Institute on Deafness and Other Communication Disorders Grants DC-03066 and DC-04158 and also in part by a grant from the European Space Agency External Fellowship Program to L. H. Zupan.

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