Hypothesis for Shared Central Processing of Canal and Otolith Signals

ANDREA M. GREEN AND HENRIETTA L. GALIANA
Department of Biomedical Engineering, McGill University, Montreal, Quebec H3A 2B4, Canada

Green, Andrea M. and Henrietta L. Galiana. Hypothesis for shared central processing of canal and otolith signals. J. Neurophysiol. 80: 2222–2228, 1998. A common goal of the translational vestibulocular reflex (TVOR) and the rotational vestibulocular reflex (RVOR) is to stabilize visual targets on the retinae during head movement. However, these reflexes differ significantly in their dynamic characteristics at both sensory and motor levels, implying a requirement for different central processing of canal and otolith signals. Semicircular canal afferents carry a signal proportional to angular head velocity, whereas primary otolith afferents modulate approximately in phase with linear head acceleration. Behaviorally, the RVOR exhibits a robust response down to ~0.01 Hz, yet the TVOR is only significant above ~0.5 Hz. Several hypotheses were proposed to address central processing in the TVOR pathways. All rely on a central filtering process that precedes a “neural integrator” shared with the RVOR. We propose an alternative hypothesis for the convergence of canal and otolith signals that does not impose the requirement for additional low-pass filters for the TVOR. The approach is demonstrated using an anatomically based, simple model structure that reproduces the general dynamic characteristics of the RVOR and TVOR at both ocular and central levels. Differential dynamic processing of otolith and canal signals is achieved by virtue of the location at which sensory information enters a shared but distributed neural integrator. As a result, only the RVOR is provided with compensation for the eye plant. Hence canal and otolith signals share a common central integrator, as in previous hypotheses. However, we propose that the required additional filtering of otolith signals is provided by the eye plant.

INTRODUCTION

Numerous types of ocular responses may be elicited by linear acceleration stimuli, but it is perhaps the translational vestibulocular reflex (TVOR) whose role is best understood. Like the rotatory vestibulocular reflex (RVOR) driven by the semicircular canals, the otolith-driven TVOR functions to stabilize visual targets during head movement. Nevertheless, the TVOR differs markedly from the RVOR in certain key respects. First, at the sensory level, the canal acts as a low-pass filter to angular head acceleration such that signals on primary canal afferents encode head velocity over the frequency range relevant for locomotion (<10 Hz). By contrast, primary otolith afferents carry a signal that remains approximately in phase with, or even leads, linear head acceleration in the same frequency range (Fernandez and Goldberg 1976). Second, although the high-pass properties of the RVOR exhibit a robust response down to typically 0.01 Hz, those of the TVOR are only significant at frequen-

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.
stages (Telford et al. 1997). Alternatively, it was proposed that a head jerk signal (derivative of head acceleration) could be used in place of a low-pass filter in the first processing stage (Angelaki et al. 1993; Angelaki and Hess 1996; Hain 1986) because a differentiation would contribute the same phase shift as an integration with sign reversal, but the gain would have high-pass characteristics. This strategy, in isolation, gives the correct response only for pure sinusoidal inputs, although a system with jerk-like response properties cascaded with an appropriate low-pass filter could be used to introduce additional high-pass filtering. Regardless of the approach, all current hypotheses for otolith processing agree that a preliminary central filtering stage precedes an integration performed by the so-called neural integrator (Robinson 1981), which is shared with the rotational system.

An alternative hypothesis is proposed here for combined canal and otolith dynamic compensation that does not require an additional central low-pass filter to process otolith signals. The approach will be demonstrated by using an anatomically based, simple model structure that can reproduce the general dynamic characteristics of the RVOR and TVOR at both the ocular and premotor levels. Differential dynamic processing of otolith and canal sensory information is achieved by virtue of their unique projection sites in a shared but distributed central neural integrator.

PROPOSED STRATEGY FOR SHARED CANAL-OTOLITH PROCESSING

Model description

The proposed hypothesis will be investigated with the simple unilateral model structure shown in Fig. 1. Although the same dynamic processing strategy is applicable for compensatory reflexive responses in both the horizontal and vertical planes, the strategy will be described here in the context of rotations and interaural translations in the horizontal plane. For illustration purposes, only conjugate eye deviations (E) about an average ocular set point, which may correspond to a converged state, will be considered. Sensory drive for the RVOR and TVOR is provided by angular velocity, \( H_{\text{ang}} \), sensed by the horizontal semicircular canals, \( C(s) \), and interaural translational acceleration, \( H_{\text{lin}} \), from the utricles, \( O(s) \), respectively. The node labeled PVN is a lumped representation of premotor medial vestibular neurons (PVN), including PVPs, EHV and burst-tonic (BT) neurons (Scudder and Fuchs 1992). As previously suggested, the prepositus hypoglossi (PH) is presumed to contain a neural filter, \( F(s) \), which is a scaled internal model of the eye plant \( P(s) \) (Galiana and Outerbridge 1984). PH neurons at the output of \( F(s) \) modulate in phase with eye position under most circumstances and may be considered internal estimates or efference copies (E*) of eye position (Delgado-Garcia et al. 1989; McFarland and Fuchs 1992). Reciprocal connections between PVN and PH neurons (Belknap and McCrea 1988; McCrea and Baker 1985) form a positive feedback loop that acts as a distributed neural integrator and provides gaze holding in the absence of visual feedback. Visuomotor (VM) areas (e.g., cerebellum) are represented by a lumped controller, which provides brain stem areas with a combination of retinal slip and position errors during pursuit (Barnes 1993; Lisberger et al. 1987). Although a simplified representation of visual pathways, this formulation is sufficient to explore the effects of visual loops around a brain stem circuit.

Of key relevance are the sites at which primary afferent signals enter the PH–PVN feedback loop. Canal afferents make monosynaptic projections onto the PVN cells (Broussard and Lisberger 1992; McCrea et al. 1987), whereas otol...
Otolith signals are proposed to reach the lumped PVN cell type indirectly via the PH. Utricular afferents project monosynaptically to the VN and the abducens nucleus but not directly to the PH (Carleton and Carpenter 1984; Uchino et al. 1996). Hence it is proposed that some proportion of otolith signals are conveyed to PH via nonprenmotor, linear acceleration-sensitive cells located in the lateral or descending VN (e.g., Xerri et al. 1987); both areas are known to project to PH (Belknap and McCrea 1988; McCrea and Baker 1985). Otolith inputs to PH are weighted by vergence to account for the required modulation in TVOR gain with target distance. Parametric modulation is performed at this site for illustrative purposes only; evaluating sites of gain modulation would require a more complex model. The goal here is to demonstrate an approach for appropriate convergence of canal and otolith signals using a shared circuit.

**Model analysis**

To gain insight into how a single distributed integrator circuit can reproduce appropriate RVOR and TVOR behaviors, the ocular and central transfer functions during vestibular stimulation in the dark will be briefly outlined. Responses in the light are similar but reflect the addition of visual loops that were implemented to simulate a pursuit system with a bandwidth of 1.3 Hz. Visual feedback serves to enhance compensatory reflex responses at low frequencies (Barnes 1993). In the expressions below, the letter \( s \) will be used to refer to the Laplace operator. All other parameters are scalars. For ease of exposition, only deviations in activity from resting rates will be considered at the central level.

Because the goal is to illustrate a putative processing strategy for the convergence of different sensory signals rather than to reproduce detailed frequency response characteristics, models for the sensors and eye plant were reduced to their simplest forms (see Fig. 1 legend). Hence first-order low-pass models were chosen for the eye plant (Robinson 1981) and PH filter. Canal dynamics relative to head velocity are approximated by a first-order, high-pass filter (Fernandez and Goldberg 1971). Currently, little is known about the relative importance of different otolith afferent types in driving the TVOR. For simplicity, only regular otolith units with response gains and phases that are relatively flat up to at least 2 Hz in primate (Fernandez and Goldberg 1976) are considered; the otoliths are therefore treated as simple linear accelerometers.

During angular rotation or linear translation in the dark, VM projections (dashed pathways) are inactive, and the central structure simplifies to a single feedback loop interconnecting the PVN cell and the PH. Responses to angular rotation and linear translation at the PVN, PH output, and ocular levels are given by

\[
PVN(s) = \frac{pG}{T_s + 1} \frac{T_s}{T_s + 1} H_{\text{mn}}(s) + \frac{qbGK}{(T_o + 1)} H_{\text{lm}}(s) \tag{1}
\]

\[
PH(s) = \frac{pagGK}{(T_o + 1)} \frac{T_s}{T_s + 1} H_{\text{mn}}(s) + \frac{qGK}{(T_o + 1)} H_{\text{lm}}(s) \tag{2}
\]

\[
E(s) = -aPVN(s) \frac{K_s}{T_s + 1}
\]

\[
= -\frac{pagGK}{(T_o + 1)} \frac{T_s}{T_s + 1} H_{\text{mn}}(s) - \frac{qbGK}{(T_o + 1)} \frac{K_s}{(T_s + 1)H_{\text{lm}}(s)} \tag{3}
\]

when \( T = T_p \) and \( G = 1/(1 - abK) \). The time constant \( T = T_p/(1 - abK) \) may be much larger than the eye plant time constant, \( T_p \), (e.g., \( T_p \approx 17 \) s for parameter set in Fig. 1 legend) and provides a central integration of sensory signals. Response components related to canal stimulation were presented previously (Galiana 1991) and will not be described in detail here. Notice, however, that the PVN cell response to rotation has a zero (in numerator) given by the pole (in denominator) of the neural filter \( F(s) \). Hence, if \( F(s) \) is an internal model of the eye plant \( (T = T_p) \), then the zero of the PVN response cancels the eye plant pole at the ocular level, as required. By contrast, the PVN cell response to otolith stimulation exhibits no zero. Because its response reflects the long integrator time constant, \( T = T_p/(1 - abK) \) can be fixed to any desired value by suitable choice of \( abK \).

**RESULTS**

**Frequency response**

The dynamic behaviors of the RVOR and TVOR in the model were calculated analytically with the parameters in the Fig. 1 legend. Figure 2 provides gain and phase plots for the reflexes during VOR in the dark and in the light while viewing either an earth- or head-fixed target. The ideal TVOR gain varies as a function of fixation distance and therefore is shown normalized with respect to vergence, expressed here in meter–angles (MA, the reciprocal of fixation distance). The ideal TVOR gain in these units has an approximately constant value of 0.57°/cm/MA (Telford et al. 1997).

In the dark, the predicted RVOR (Fig. 2A) exhibits a flat gain \((\approx 0.87)\) in phase with angular head velocity over most of the frequency range (Paige 1983). Because velocity storage was not incorporated in this simple model, RVOR responses in the dark below 0.1 Hz are of lower gain and larger phase lead relative to head velocity than observed experimentally. In the presence of visual feedback, close to unity gain and zero phase are observed across the entire bandwidth, as expected. VOR cancellation in the model relies only on visual feedback, and therefore both the ability to track a moving target and to suppress the reflex diminish with increasing frequency, reflecting the model pursuit bandwidth of 1.3 Hz (Barnes 1993).
Predicted TVOR responses in the dark (Fig. 2B) are negligible at low frequencies but demonstrate an increasing gain and decreasing phase lead over the range of 0.2–4 Hz. Gain and phase values are comparable with those reported in humans (Paige et al. 1996) and primates (Telford et al. 1997). During earth- (Fig. 2B, solid line) and head-fixed (dotted line) target viewing, responses are nearly ideal at low frequencies. However, performance in both cases declines with frequency above the pursuit bandwidth so that gains in the dark and in the light are similar at 4 Hz, as observed (Paige et al. 1996).

Simulated performance

The model was implemented in SIMULINK (Mathworks, MA) at a sampling rate of 100 Hz. Model simulations during either pure angular rotation while viewing a far target or interaural linear translation while viewing a target 20 cm away are illustrated in Fig. 3. Results at 0.2 and 4 Hz are provided to contrast performance with frequency. As expected from Fig. 2, the RVOR (Fig. 3A) exhibits a gain of 0.87 in the dark at both frequencies, which increases to near unity gain at 0.2 Hz in the presence of visual feedback. The PVN cell modulates in phase with ipsilaterally directed head velocity at 4 Hz but lags considerably at 0.2 Hz, reflecting the cell’s lumped premotor nature. During pure head rotation, PH cells at the output of \( F(s) \) always code for contralaterally directed eye position in the model.

In contrast, the TVOR (Fig. 3B) response in the dark changes dramatically between 0.2 and 4 Hz. The ocular response is low at 0.2 Hz with a large phase lead (≈70°) relative to the ideal compensatory response but rises to a gain of 0.31°/cm/MA at 4 Hz with modulation in phase with translational head velocity (Paige et al. 1996; Telford et al. 1997). As expected, performance is close to ideal at 0.2 Hz in the presence of visual feedback. PVN cell activity modulates in phase with translational velocity rather than acceleration at both frequencies in the dark and at 4 Hz in the light, in agreement with experimental observations (Chen-Huang and McCrea 1997; McConville et al. 1996; McCrea et al. 1996). Note that this result stems from the overall dynamics of the circuit (see Eq. 2) and is unrelated to the additional lag on the lumped PVN cell during rotation; using our approach the same observation would be made even in a more detailed model that represents individual premotor cell types. The predicted response of the PH neuron at the output of \( F(s) \) is of particular interest. At 0.2 Hz, the cell modulates in phase with translational head velocity in the dark but more closely in phase with head position in the light. Ocular responses at this frequency are compensatory in the presence of visual feedback but lead ideal eye velocity by nearly 90° in the dark; hence, when considered relative to the motor response, the PH neuron provides a good estimate of eye position at low frequencies in keeping with its postulated role in providing an efference copy signal. At 4 Hz, the PH cell again modulates in phase with translational head velocity. However, because ocular responses at this frequency are indeed compensatory, the PH cell now modulates in phase with eye velocity in both the light and dark conditions. Hence the simulations predict a marked change in this cell’s response relative to motor output at higher frequencies during pure translation.

DISCUSSION

We demonstrated that the required differential dynamic processing of canal and otolith-related sensory signals may be achieved in a single shared central processor simply by virtue of the location at which each sensory signal enters the circuit. In agreement with previous hypotheses, a common neural integrator for otolith and canal signals is envisioned. However, our proposal differs in that a second central low-
pass filter is not required for the otolith signal. Canal signals enter a central feedback loop so as to achieve both a single integration and compensation for the eye plant. By contrast, otolith signals enter the loop such that a single integration but no eye plant compensation is performed. Hence, the eye plant provides the second filtering of otolith signals at frequencies above \( \sim 0.5 \) Hz. This scheme is consistent with behavioral observations of a robust, compensatory TVOR only at frequencies above the bandwidth of the eye plant (Paige and Tomko 1991a; Paige et al. 1996; Telford et al. 1997; Tokita et al. 1981). Furthermore, we demonstrated that the general characteristics of both the RVOR and TVOR may be reproduced even when only the dominant dynamic properties of the sensors and eye plant are taken into account. More detailed models of sensor and plant dynamics may be incorporated to improve the overall fit of our responses when the characteristics of the TVOR are available over a larger frequency range and the types of

**FIG. 3.** Model simulations during (A) angular rotation while viewing a far target or (B) interaural linear translation while viewing a target 20 cm away (\( \sim 17^\circ \) vergence for an interocular distance of 6 cm). Head rotations or translations are illustrated at 0.2 and 4 Hz in each case. Translations and rotations to the right are positive. Dotted lines represent ideal compensatory responses. Shaded portions of the simulations indicate dark conditions.
otolith afferents important in driving the reflex are identified.

The model here represents only one potential realization of our proposed strategy. For example, equivalent results could be reproduced with a classical feed-forward style RVOR model with two parallel pathways: a lumped oculomotor integrator pathway and a direct pathway (Robinson 1981). Using this approach, eye plant compensation during the RVOR relies on the appropriate weighting of projections to the eye plant from these two pathways. The appropriate TVOR response could be achieved if otolith signals were passed selectively only through the integrator pathway before being filtered a second time by the uncompensated eye plant. Central results could be reproduced by assuming that the PVN cell sums signals from both the direct pathway (i.e., canal primary afferent signals) and the output of the neural integrator. Inputs to the neural integrator, in this case, would be vestibular-only cells carrying angular head velocity and/or linear head acceleration signals but no eye position signal. Regardless of the implementation of the central filtering process (i.e., lumped feed-forward vs. a feedback approach), the basic strategy with respect to combined canal/otolith processing is the same; a shared neural integrator for both canal and otolith signals followed by a second integration of otolith signals by the eye plant.

Previous work proposed that central and behavioral observations could be reproduced by preliminary filtering with combinations of otolith afferents with different dynamic or spatiotemporal properties (Angelaki and Hess 1996; Angelaki et al. 1993; Raphan et al. 1996). However, these proposals may be difficult to confirm experimentally. An advantage of our hypothesis is that it makes testable predictions at behavioral, anatomic, and physiological levels, which may help to distinguish between a multistage central filtering process for otolith signals versus a single integration followed by filtering by the eye plant. First, because a basic premise of our strategy is that the eye plant itself is used to filter otolith signals, TVOR behavior should reflect the dynamics of the eye plant at high frequencies. Hence, the frequency associated with a second filtering of the otolith signal should correspond well with the dominant pole of the eye plant, and evidence of higher-order eye plant dynamics (not incorporated in the model here) would be expected in the TVOR responses. Recent investigations of high-frequency TVOR responses do indeed appear to reflect these higher-order plant dynamics (Angelaki, personal communication). Second, from an anatomic perspective, although PVN neurons (e.g., PVP and EHV) receive monosynaptic inputs from the semicircular canals, we predict that the majority of otolith afferents make only indirect (di- or trisynaptic) projections onto these cells.

Although both of the above observations would lend support to our proposal, neither could conclusively distinguish it from current hypotheses. For instance, compensation might be provided centrally for the dominant eye plant pole so that the eye plant does not in fact provide the second integration of the otolith signal, yet evidence for higher-order plant dynamics might still be observed in the TVOR responses. Similarly, a tendency for otolith afferents to make polysynaptic projections onto premotor VN cells would be equally consistent with either our strategy or a set of cascaded central filters. However, a third prediction, testable at the neuronal level, is specific to our approach. In particular, PH neurons at the output of $F(s)$ in the model provide an accurate internal estimate of eye position ($E^*$) during pure head rotation (see Eqs. 2 and 3 and Fig. 3A) or visual tracking across all frequencies. However, during linear translation, the quality of this efference copy is predicted to degrade at frequencies above the dominant eye plant time constant such that the same PH neurons would modulate more closely in phase with eye velocity. This condition would be true regardless of the model implementation (e.g., feedback vs. feed-forward parallel pathway model) because at most a single integration of the otolith signal is provided centrally; the second filtering is provided by the eye plant. Hence, our proposal could be easily tested by observing the responses of position-sensitive PH neurons at high frequencies ($>1-2\ Hz$) during linear translation.

The model presented here was clearly oversimplified to focus on a new strategy for combined canal and otolith dynamic processing. Although, for illustration purposes, the strategy was described in the general context of conjugate horizontal eye movements, the proposed scheme could be implemented for any direction of head rotation and translation in the horizontal or vertical planes. However, because ocular compensation for translation is a function of target distance, a bilateral model capable of binocular control is required to fully explore the issues of RVOR and TVOR interaction and their modulation in performance with target location. A step in this direction was to model the RVOR and the central behavior of individual premotor cell types during viewing-context-dependent gain modulation (Green and Galiana 1996). An extension of this model incorporating the strategy proposed here to examine viewing distance effects on the TVOR and its interaction with the RVOR should contribute to a better understanding of the central processing underlying the dynamic and spatial characteristics of compensatory vestibulooculor reflexes.

The authors express gratitude for the helpful comments of Drs. R. Baker and D. E. Angelaki in the preparation of the manuscript.

This research was supported by the Medical Research Council of Canada. Address for reprint requests: H. L. Galiana, Dept. of Biomedical Engineering, McGill University, 3775 University St., Montreal, Quebec H3A 2B4, Canada.

Received 12 May 1998; accepted in final form 1 July 1998.

REFERENCES


Busettini, C., Miles, F. A., Schwarz, U., and Carl, J. R. Human ocular


