Canal and Otolith Contributions to Compensatory Tilt Responses in Pigeons

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McArthur KL, Dickman JD. Canal and otolith contributions to compensatory tilt responses in pigeons. J Neurophysiol 100: 1488–1497, 2008. First published July 16, 2008; doi:10.1152/jn.90257.2008. Gaze-stabilizing eye and head responses compensate more effectively for low-frequency rotational motion when such motion stimulates the otolith organs, as during earth-horizontal axis rotations. However, the nature of the otolith signal responsible for this improvement in performance has not been previously determined. In this study, we used combinations of earth-horizontal axis rotational and translational motion to manipulate the magnitude of net linear acceleration experienced by pigeons, under both head-fixed and head-free conditions. We show that phase enhancement of eye and head responses to low-frequency rotational motion was causally related to the magnitude of dynamic net linear acceleration and not the gravitational acceleration component. We also show that canal-driven and otolith-driven eye responses were both spatially and temporally appropriate to combine linearly, and that a simple linear model combining canal- and otolith-driven components predicted eye responses to complex motion that were consistent with our experimental observations. However, the same model did not predict the observed head responses, which were spatially but not temporally appropriate to combine according to the same linear scheme. These results suggest that distinct vestibular processing substrates exist for eye and head responses in pigeons and that these are likely different from the vestibular processing substrates observed in primates.

INTRODUCTION

Vestibular signals from the semicircular canals and otolith organs generate compensatory eye movements during self-motion (reviewed in Raphan and Cohen 2002). Eye responses to angular acceleration are generated by signals from the semicircular canals and help to maintain visual image stability during rotations. These are collectively referred to as the angular vestibuloocular responses (aVOR) and have been studied in several animal classes including fish (Pastor et al. 1992), amphibians (Straka and Dieringer 2004), reptiles (Gioanni et al. 1993), birds (Dickman et al. 2000), and mammals (Angelaki and Hess 1996a,b; Baarsma and Collewijn 1975; Baloh et al. 1983; Barmack 1981; Bilotto et al. 1982; Brettler et al. 2000; Harrod and Baker 2003; rabbit: Barmack 1981; cat: Rude and Baker 1988; nonhuman primate: Angelaki and Hess 1996b; human: Bockisch et al. 2005; Groen et al. 1999; Schmid-Prisoveanu et al. 2000). Eye responses to linear acceleration are of two types. The translational vestibuloocular reflexes (tVORs) generally consist of conjugate eye movements that function to maintain binocular foveal image stability during linear motion. The tVOR has been studied extensively in frontal-eyed animals such as primates, where it is known to depend on target viewing distance and eccentricity (Angelaki 1998; Angelaki et al. 2003; Merfeld et al. 2005; Paige and Tomko 1991; Telford et al. 1997). A second category of linear acceleration responses are the orienting responses, which compensate for actual or apparent head tilt relative to gravity (Angelaki and Hess 1996a; Cohen et al. 2001; Maruta et al. 2001, 2005). Although primates exhibit both tVOR and orienting responses to linear acceleration, lateral-eyed species exhibit mainly orienting responses (Baarsma and Collewijn 1975; Dickman and Angelaki 1999; Hess and Dieringer 1991).

Because natural motion generally includes a combination of angular and linear accelerations, it is important to understand how canal and otolith signals interact in the generation of compensatory eye responses. For example, natural activities, like walking, typically evoke a combination of aVOR and tVOR responses (squirrel monkey: Paige and Tomko 1991; Sargent and Paige 1991; Snyder and King 1992; Telford et al. 1996, 1998; rhesus monkey: Viirre et al. 1986; human: Crane et al. 1997; Seidman et al. 2002), as well as eye and head orienting responses that serve to maintain gaze orientation relative to gravity (Oommen and Stahl 2008). Another example of canal-otolith co-stimulation occurs when the head rotates around an earth-horizontal axis (EHA). Previous studies across species have shown that the eye response compensates more effectively during EHA rotation than during earth-vertical axis (EVA) rotation. This effect is most pronounced for low-frequency motion (pigeon: Dickman et al. 2000; mouse: Harrod and Baker 2003; rat: Brettler et al. 2000; rabbit: Barmack 1981; cat: Rude and Baker 1988; nonhuman primate: Angelaki and Hess 1996b; human: Bockisch et al. 2005; Groen et al. 1999; Schmid-Prisoveanu et al. 2000). The enhanced eye response during EHA rotation has been attributed to augmentation of the canal-driven aVOR by the additional presence of a dynamic otolith signal generated by reorientation of the head relative to gravity. However, otolith afferents respond to net linear acceleration, the result of gravitational and translational acceleration (Angelaki and Dickman 2000; Fernández and Goldberg 1976). Thus the aVOR enhancement could be driven by an otolith afferent-like net linear acceleration signal or by a central representation of gravitational acceleration (Green and Angelaki 2007; Merfeld et al. 1999). Previous studies have not discriminated between these two possibilities, so the nature of the aVOR-enhancing otolith signal remains unclear. The way in which this otolith signal is integrated with the canal signal to produce eye and head responses is also unknown.

In this study, we used combinations of tilt and translation to test whether the aVOR improvement during EHA rotation correlates best with gravitational or net linear acceleration. In addition, we compared eye and head orienting responses to linear acceleration when the animals were free to move their

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heads. Finally, we tested whether pigeon eye and head responses could be modeled as a linear combination of canal- and otolith-driven responses. We conclude that, whereas a linear model combining canal- and otolith-driven responses can account for pigeon eye movements, the interaction seems to be more complex for head movements.

METHODS

Five adult pigeons (Columba livia), ranging in weight from 400 to 700 g, were used in accordance with the guidelines set forth by the National Institutes of Health Guide for the Care and Use of Animals in Research, as well as those approved by the Institutional Animal Care and Use Committee. The animals were housed and cared for in the Laboratory Animal Facilities under veterinary supervision.

Animal preparation

Each bird was surgically implanted with a head stud and a dual eye coil. General anesthesia was achieved using isoflurane gas (3–5% in O2) via endotracheal intubation. Heart rate was monitored, and core temperature was maintained using a heating pad. First, each bird was chronically implanted with a Delrin head stud. An incision was made along the midline of the skull, and the underlying periosteum was removed from the bone. The head stud was attached to the skull via titanium self-tapping screws and secured with dental acrylic mixed with ampicillin powder (5%). The head was positioned stereotaxically such that the upright orientation of the head stud corresponded to alignment between an earth-horizontal plane and the horizontal semicircular canals. After surgery, the head wound margin was kept clean with betadine washes and antibiotic ointment.

Following a 5- to 7-day recovery period, a dual eye coil was implanted in one eye. The coil assembly consisted of a large diameter (12 mm) direction coil and a small diameter (2 mm) torsion coil. The direction coil was constructed using three turns of multi-stranded, Teflon-coated, 41-gauge stainless steel wire (A-M Systems), and the torsion coil consisted of a 100-turn copper wire watchmaker coil (Imetra) attached perpendicularly to the direction coil. The three-dimensional (3D) coil assembly was coated in a thin layer of Araldite (Huntsman). For implantation, the animal was anesthetized using isoflurane gas (3–5% in O2) via endotracheal intubation. A circumferential incision was made in the conjunctiva to allow visualization of the sclera. In pigeons, the sclera is calcified near the cornea, so the 3D coil assembly was attached to the posterior margin of the scleral globe with 8-0 prolene sutures. Coil leads were threaded through the bone of the posterior orbit and passed underneath the skin to exit near the head stud. Next, the conjunctiva was approximated and closed with 8-0 vicryl sutures. Lead wires were soldered to a connector (Onmetics), which was secured next to the head stud with dental acrylic. To monitor head movements, a separate 3D coil assembly was attached to the posterior margin of the scleral globe with 8-0 prolene sutures. Coil leads were threaded through the 3D coil assembly, which was secured next to the head stud with dental acrylic. To monitor head movements, a separate 3D coil assembly was attached to the posterior margin of the scleral globe with 8-0 prolene sutures. Coil leads were threaded through the 3D coil assembly, which was secured next to the head stud with dental acrylic. To monitor head movements, a separate 3D coil assembly was attached to the posterior margin of the scleral globe with 8-0 prolene sutures. Coil leads were threaded through the 3D coil assembly, which was secured next to the head stud with dental acrylic. To monitor head movements, a separate 3D coil assembly was attached to the posterior margin of the scleral globe with 8-0 prolene sutures. Coil leads were threaded through the 3D coil assembly, which was secured next to the head stud with dental acrylic. To monitor head movements, a separate 3D coil assembly was attached to the posterior margin of the scleral globe with 8-0 prolene sutures. Coil leads were threaded through the 3D coil assembly, which was secured next to the head stud with dental acrylic. To monitor head movements, a separate 3D coil assembly was attached to the posterior margin of the scleral globe with 8-0 prolene sutures. Coil leads were threaded through the 3D coil assembly, which was secured next to the head stud with dental acrylic. To monitor head movements, a separate 3D coil assembly was attached to the posterior margin of the scleral globe with 8-0 prolene sutures. Coil leads were threaded through the 3D coil assembly, which was secured next to the head stud with dental acrylic.

Experimental protocols

A three-field AC magnetic coil system (CNC Engineering) was used to monitor rotational eye and head movements. The coil system provided a 5-in homogeneous magnetic field cube centered about the pigeon’s head. The field coils were mounted to a servo-controlled rotator/sled system (Neurokinetics) driven by a PC and programmable interface (CED Model 1401plus, Cambridge Electronic Design). Stimulus control and data acquisition were performed using custom scripts written for the interface environment (Spike2, Cambridge Electronic Design). Stimulus deliveries were monitored using a rate sensor and a three-axis linear accelerometer mounted near the animal’s head. For each experiment, the pigeon was placed in a padded body holder and secured in the motion system. Eye and head movement responses were obtained under both head-fixed and head-free conditions. All experiments were performed in total darkness. All motion profiles were delivered along axes that passed through the center of the head. A right-handed field coil-fixed coordinate system was used to describe eye and head movements and stimulus orientations. With the head fixed, the x-, y-, and z-axes corresponded to the pigeon’s nasooccipital, interaural, and dorsoventral axes, respectively. Positive rotations were right-ear down, nose down, and leftward. Positive translations were forward, leftward, and upward.

To determine the effect of dynamic otolith stimulation on eye and head responses during rotational motion relative to gravity, the net linear acceleration experienced during EHA tilt was manipulated. The otolith organs act as inertial sensors and therefore detect inertial acceleration or deviation from free-fall on the Earth’s surface. The effect of gravity is sensed by the otolith organs as an upward 1g linear acceleration (see Hixson et al. 1966). When additional sources of linear acceleration are applied (e.g., translational motion), the otolith organs will respond to the net linear acceleration, according to the equivalence principle (Einstein 1907). For a given stimulus condition, we can represent the individual sources of linear acceleration as acceleration vectors relative to the head, and the resultant vector corresponds to the net linear acceleration detected by the otolith organs (Fig. 1). Across stimuli, the effect of gravity corresponds to a constant 1g linear acceleration along an EVA (green arrows). During steady-state sinusoidal rotation about an EHA (Fig. 1A, Tilt-only), the head rotates relative to gravity, creating a sinusoidal modulation in the head-horizontal component of gravitational acceleration (red arrows) at the fundamental rotation frequency. An additional sinusoidal variation in the head-vertical component is also present; however, this component is relatively small and modulates at the second harmonic (see Angelaki et al. 1999). Therefore future references to net linear acceleration refer only to head-horizontal linear acceleration unless otherwise specified. Steady-state sinusoidal translational motion along an EHA (Fig. 1B, Translation-only) produces a sinusoidally varying earth-horizontal linear acceleration (cyan arrows; head-horizontal component indicated by blue arrows). During combined rotational and translational motion, the net linear acceleration sensed by the otolith organs depends on the spatial and temporal relationship between the sinusoidal variations in gravitational and translational components. For example, when backward translational acceleration is paired in time with nose-upward tilt (Fig. 1C, Tilt-Translation), gravitational and translational components of head-horizontal linear acceleration are in opposite directions and work to cancel each other. Thus the magnitude of net linear acceleration is decreased relative to that experienced during the Tilt-only condition. When backward translational acceleration is paired in time with nose-downward tilt (Fig. 1D, Tilt+Translation), gravitational and translational components of head-horizontal linear acceleration are in the same direction and add with each other, increasing the magnitude of net linear acceleration.

In this study, steady-state sinusoidal oscillations were delivered at 0.25, 0.5, and 1 Hz. For each frequency, four combinations of tilt and translation were tested. The Tilt-only stimulus consisted of EHA rotations with peak angular velocity equal to 5 (0.25 Hz), 17.1 (0.5 Hz), and 31.3°/s (1 Hz). As the head reoriented relative to gravity, peak net linear accelerations of 0.06 (0.25 Hz) and 0.1g (0.5 and 1 Hz) were produced. The Translation-only stimulus consisted of translational displacements along an axis perpendicular to the axis of rotation used in the corresponding Tilt-only trial. Peak net linear acceleration during Translation-only was equal to 0.06 (0.25 Hz) and 0.1g (0.5 and 1 Hz), equivalent to that delivered in the Tilt-only trials. The Tilt-Translation and Tilt+Translation stimuli consisted of simultaneous rotational and translational motion, using the same parameters as the Tilt-only and Translation-only stimuli. During Tilt-Translation, linear
accelerations caused by tilt (rotation) and translation were opposite in phase (relative phase $\approx 180^\circ$), such that the net linear acceleration equaled zero (Fig. 1). During Tilt+Translation, the components of linear acceleration caused by tilt and translation were in phase with each other (relative phase $= 0^\circ$), such that the net linear acceleration was doubled, equal to 0.12 (0.25 Hz) or 0.2g (0.5 and 1 Hz). For combinations of $x$-axis translation and $y$-axis rotation, net linear acceleration (when present) was directed along the nasooccipital axis. For combinations of $y$-axis translation and $z$-axis rotation, net linear acceleration (when present) was directed along the interaural axis.

In addition to the primary experimental paradigm, some animals were also tested with an extended tilt/translation protocol at 0.25 Hz only, where the relative phase of rotational and translational components was varied in 45° increments (relative phase $= \pm 45, \pm 90$, and $\pm 135^\circ$). As a result, the peak net linear acceleration varied from 0 to 0.06g, and the phase of the modulation in net linear acceleration relative to tilt angular velocity varied from 0 to 180° (see Fig. 6). (Note that during Tilt-only, the net linear acceleration led tilt angular velocity by 90°.) These additional motion profiles varied the relationship between angular velocity and linear acceleration, providing the opportunity to test the ability of a simple linear canal-otolith integration model to predict eye and head movement responses.

**Data analysis**

The recorded eye and head movement signals were first converted to rotation vectors in Cartesian coordinates (expressed relative to the field coil-fixed coordinate), using the first sample from each trial as the reference position. Note that the animal’s nasooccipital axis was directed collinear to the positive $x$-axis and that the pigeon’s primary visual axis was located $\approx 66^\circ$ away from the bill tip (Martin and Young 1983). The rotation vectors were desaccaded using custom scripts written in Matlab (MathWorks). The desaccaded rotation vectors were differentiated to produce rotation velocity vectors. From the rotation vectors, angular velocity vectors with components about the $x$, $y$, and $z$ axes were calculated (Haustein 1989; Hess et al. 1992; van Opstal 1993). The eye rotation velocity vectors corresponded to the net movement of the eye in space. During head-fixed trials, no head movement relative to the motion system and field coils occurred, so only eye movements were obtained in response to the motion profile [head-fixed eye (VOR)]. During head-free trials, both eye and head movements combined to produce gaze responses, or eye-in-space. The eye movement component of gaze (eye-in-head) was computed by vectorially subtracting the head coil rotation velocity vectors from the eye coil rotation velocity vectors.

For each trial, the rate sensor and accelerometer signals, as well as the eye and head movement responses, were averaged over several cycles, and fit with sine curves at the fundamental frequency using a least-squares algorithm. The fitted curves were used to calculate gain and phase values for response components about the three cardinal stimulus axes. Only desaccaded (slow-phase) angular velocity responses were analyzed in this paper. Rotational gain values were expressed as eye/head/gaze angular velocity ($\circ$/s) per stimulus angular velocity ($\circ$/s), and phase values were expressed relative to peak positive angular velocity of the motion profile. Translational gain values were initially expressed as eye/head/gaze angular velocity ($\circ$/s) per net linear acceleration (g), and phase values were expressed relative to peak positive net linear acceleration. To facilitate comparison with responses to rotational stimulus measures, translation responses were also expressed relatively to apparent tilt (defined as the rotation stimulus that would produce equivalent linear accelerations). Apparent tilt gains and phases were calculated using the following formula

$$G_{\text{app tilt}} = \frac{R}{2\pi f \tan^{-1}(a)}$$

$$\theta_{\text{app tilt}} = \theta_a + 90^\circ$$

where, $R$ is the magnitude of response, $f$ is the stimulus frequency, $a$ is the linear acceleration caused by translation, and $\theta_a$ is the response phase (re peak linear acceleration). Here, $\tan^{-1}(a)$ is equal to the peak amplitude of head rotational displacement (deg) that would produce an equivalent head-horizontal linear acceleration of peak amplitude $a$ (g). For sinusoidal motion, multiplication by $2\pi f$ is used to convert peak displacement to peak velocity. Therefore the denominator in this equation represents the head tilt rotational velocity ($\circ$/s) that would produce an identical modulation in head-horizontal linear acceleration to that observed during a given translational stimulus.

Gain and phase values throughout are expressed as mean $\pm$ SD. Gain values represent response peak slow-phase velocity ($\circ$/s) divided by stimulus peak rotational velocity ($\circ$/s) unless otherwise specified.
All statistical analyses were performed using repeated measures or
one-way ANOVA (Statistica, Statsoft).

**Canal-otolith combination model**

A simple linear combination model was proposed to predict eye and
head responses during combinations of 0.25-Hz EHA tilt and transla-
tion motion profiles. For each animal tested (n = 3), the “canal-
only” response for each response component (head-fixed eye, head-
free eye/head/gaze) was defined as the mean response gain (G_c) and
phase (θ_c) during 0.25-Hz Tilt-Translation stimuli (where only the
canal afferents were activated). The “otolith-only” response was
defined as the mean response gain (G_o) and phase (θ_o) during
0.25-Hz Translation-only stimuli. These responses were used to pre-
dict responses during Tilt-only, Tilt+Translation, and the extended
paradigm: stimuli that dynamically activate both canal and otolith
afferents. The tilt stimulus was identical across these stimuli, whereas
the net linear acceleration varied in magnitude and in its temporal
relationship to tilt velocity. Predicted response gain and phase values
were computed in the following way. First, the canal-only component
was expressed relative to tilt velocity and converted into its polar
form (C)

\[ C = A_c + B_c \theta \]

\[ A_c = G_c \cos(\theta_c) \quad \text{and} \quad B_c = G_c \sin(\theta_c) \]

where G_c and θ_c were the canal-only response gain and phase
contributions expressed relative to tilt velocity. Across the stimulus
set used in our model analysis, the tilt component of the stimulus
remained constant. Therefore the canal-only contribution to the total
observed response also remained constant. The otolith-only compo-
nent was also expressed relative to tilt velocity and converted to its
polar form (O). However, since net linear acceleration varied across
stimuli, the specific value of otolith-only gain and phase varied with
the magnitude and relative timing of net linear acceleration for a given
stimulus

\[ G_o = \frac{G_o \times a}{v} \]

\[ \theta_o = \theta_o + \varphi \]

\[ O = A_o + B_o \theta \]

\[ A_o = G_o \cos(\theta_o) \quad \text{and} \quad B_o = G_o \sin(\theta_o) \]

where, G_o and θ_o were expressed relative to net linear acceleration,
and G_o and θ_o were the otolith-only response gain and phase
contribution expressed relative to tilt velocity when \( a = \) net linear
acceleration, \( v = \) tilt velocity, and \( \varphi = \) phase of net linear acceleration
relative to tilt velocity. Canal-only and otolith-only contributions were
added in the polar domain and converted to predicted gain (G_pred) and
phase (θ_pred) values for each stimulus

\[ A_{\text{pred}} = A_c + A_o \]

\[ B_{\text{pred}} = B_c + B_o \]

\[ G_{\text{pred}} = \sqrt{A_{\text{pred}}^2 + B_{\text{pred}}^2} \]

\[ \theta_{\text{pred}} = \tan^{-1}\left(\frac{B_{\text{pred}}}{A_{\text{pred}}}\right) \]

To evaluate the ability of the simple linear combination model to
predict actual responses, we performed linear regressions relating
predicted and actual responses (separately for gain and phase). Re-
gressions were performed for individual animals’ data, as well as
across animals for each response component (head-fixed eye, head-
free eye and head). The linear regression procedure was modified for
two dependent samples to minimize the sum square perpendicular
distance between data points and the best-fit linear relation. This
procedure yielded asymmetric confidence intervals on the slope and
intercept values. The strength of the linear relationship between actual
and predicted values was evaluated by computing the correlation
coefficients (R values) and associated P values. The slope of the linear
regression was used to determine whether strong linear relationships
were in fact one-to-one (indicating correspondence between actual
and predicted values).

In the linear regression analyses, the model used to predict re-
sponses assumed unity weights for canal-only and otolith-only con-
tributions to the total response. The best-fit weight for canal-only
and otolith-only response contributions was determined by fitting
responses to all stimulus conditions simultaneously with weights on
each contribution as free parameters (performed separately for head-
fixed eye and head-free eye/head/gaze). The fitting procedure was
done using an algorithm that minimized the sum square error with the
responses expressed in polar form (simultaneous minimization of gain
and phase errors). Goodness-of-fit was evaluated by computing cor-
relation coefficients (R values) and associated P values.

**RESULTS**

**Eye and head responses to combinations of EHA tilt and translation**

Eye and head responses to steady-state sinusoidal motion
stimuli in the dark were recorded from five alert pigeons using
the search coil technique. Consistent with previous studies, we
found that eye and head responses to EHA rotations were
compensatory for tilt direction (Dickman et al. 2000; Haque
and Dickman 2005). For example, as shown in Fig. 2, head-
fixed rotations (Tilt-only) about the y-axis elicited spatially
appropriate (E_y) slow-phase compensatory eye movements.
Orthogonal eye and head movement components directed
about the other two axes were negligible and were not analyzed
further. Similar compensatory eye and head responses to EHA
rotations were observed under head-free conditions, for all
spatial directions tested.

During EHA Tilt-only stimulation, reorientation of the head
relative to gravity produced a sinusoidal variation in the net
head-horizontal linear acceleration that led tilt angular velocity
by 90° (see METHODS). During combined tilt and translational
motion, the net head-horizontal linear acceleration was either
doubled (Tilt+Translation) or canceled (Tilt-Translation),
whereas the gravitational component of acceleration remained
constant (Fig. 2). Thus we examined the effect of manipulating
the magnitude of head-horizontal linear acceleration on eye
and head responses to tilt by comparing response gain and
phase values observed during the Tilt-Translation, Tilt-only,
and Tilt+Translation conditions. As shown in Fig. 3, net linear
acceleration magnitude had a significant main effect on eye
response phase (F(2,208) = 40.57, P < 0.001) but did not affect
eye response gain (ANOVA: P = 0.40). This is consistent with
the results of previous studies, where only at frequencies <0.1
Hz were both gain and phase values enhanced during EHA
rotation (Dickman et al. 2000; Haque and Dickman 2005). As
net linear acceleration increased from 0 (Tilt-Translation) to
0.12–0.2g (Tilt+Translation), the head-fixed eye response
phase decreased, approaching an ideal compensatory value
(i.e., −180°) for tilt velocity. The observed effect was inde-
dependent of stimulus orientation (ANOVA: $P = 0.11$) but interacted with stimulus frequency ($F(4,416) = 22.77, P < 0.001$), being largest for the lowest frequency tested (0.25 Hz). When the head was free to move, results were similar for the eye-in-head response, as shown in Fig. 4. In fact, eye-in-head response phase decreased with increasing net acceleration magnitude ($F(2,134) = 33.06, P < 0.001$) across all three frequencies tested ($P < 0.01$ for all frequencies). In contrast, head-free eye response gain was unaffected by the magnitude of net linear acceleration (ANOVA: $P = 0.29$).

The head response phase also decreased toward ideal as net linear acceleration magnitude increased, specifically for the lowest rotational frequency (0.25 Hz: $F(2,171) = 72.51, P < 0.001$; 0.5 Hz: $F(2,171) = 7.98, P < 0.001$).

**Canal- and otolith-driven responses: tilt-translation and translation-only responses revisited**

Our initial observations showed that eye and head response phase values were brought closer to ideal compensatory phase for tilt velocity by a dynamic net linear acceleration signal. How is this effect produced? One possibility is that independent otolith- and canal-driven responses are generated and combine linearly. If so, the otolith-driven response would by necessity be spatially appropriate to augment the canal-driven response during EHA rotations. Indeed, we observed such a response during Translation-only stimulation. For example, as shown in Fig. 5A (right), fore-aft ($x$-axis) translations elicited small slow-phase eye movements that would be compensatory to an apparent rotation about the $y$-axis. Similarly, head-fixed interaural ($y$-axis) translations elicited small eye movements that would be compensatory to an apparent rotation about the $x$-axis. These responses would be spatially appropriate to contribute to the aVOR when linear accelerations are produced by EHA tilt rather than by translation. These findings are
consistent with similar apparent tilt responses reported previously for pigeons (Dickman and Angelaki 1999) and other lateral-eyed species (Baarsma and Collewijn 1975; Hess and Dieringer 1991). Eye and head responses to translation were expressed relative to apparent tilt velocity, as shown in Fig. 5B (black symbols). Both eye and head response gains were quite small (<0.1; but similar to those observed in a previous study; Dickman and Angelaki 1999) and decreased significantly with increasing frequency (head-fixed eye: $F_{2,140} = 180.41, P < 0.001$; head-free eye: $F_{2,122} = 100.84, P < 0.001$; head-free head: $F_{2,110} = 41.73, P < 0.001$). The phase values observed at the different frequencies were consistent, even with low gains being present. In fact, the phase variance across trials and between individual animals was much less variable than would be expected if produced by random noise, as would occur if the response gains were zero. Instead, the observed variability in eye and head response phases during Translation-only was on the order of the variability in response phase overall. The Translation-only eye response exhibited phase lags relative to ideal (i.e., $-180^\circ$) that decreased significantly between 0.25 and 1 Hz (head-fixed: $F_{2,140} = 8.78, P < 0.001$; head-free: $F_{2,122} = 7.20, P < 0.001$) and were smaller overall during head-free stimulation. In contrast, the head response exhibited phase leads of $\sim 180^\circ$ that decreased with increasing frequency ($F_{2,122} = 12.57, P < 0.001$).

Having observed an otolith-driven apparent tilt response, we next examined the characteristics of the canal-driven response alone during Tilt-Translation (0g) stimulation, when the otolith-driven response to net linear acceleration was absent (Fig. 5, gray symbols). Relative to ideal compensatory phase for actual tilt velocity, eye and head responses exhibited phase leads that decreased with increasing frequency (head-fixed eye: $F_{2,140} = 198.55, P < 0.001$; head-free eye: $F_{2,92} = 11.82, P < 0.001$; head-free head: $F_{2,110} = 5.57, P < 0.005$), whereas response gains remained flat across frequencies (ANCOVA: $P > 0.15$ for all responses). We have already shown that both eye and head response phase values were closer to ideal when the otolith-driven response to net linear acceleration was also present. If this occurred by linear combination, we would expect the phase leads in the canal-driven response to be offset by phase lags in the otolith-driven response. Although the otolith-driven eye response exhibited the requisite phase lag, the otolith-driven head response actually exhibited a phase lead of $\sim 180^\circ$. A linear combination of canal- and otolith-driven head responses would thereby produce a response phase that was farther from ideal than the canal-driven response alone, contradicting our previous results. From these observations, we predicted that a linear combination model would be able to account for the eye response but not the head response to EHA rotations.

**Evaluating a simple linear combination model of canal-otolith response integration**

To study the utility of a linear combination model of eye and head responses for low-frequency (0.25 Hz) stimulation, dif-
Different tilt/translation combinations were used to manipulate the magnitude of net head-horizontal linear acceleration and its phase relative to tilt velocity (see METHODS). First, the predicted eye and head responses were calculated as a linear combination of the previously observed canal-driven (Tilt-Translation) and otolith-driven (Translation-only) responses, using the mean gain and phase values for each animal \( (n = 3) \). Next, linear regressions relating predicted and actual gains and phases were performed, as shown for the head-fixed eye responses in Fig. 6. There was a strong linear relationship between actual and predicted gain \( (R = 0.74, P < 0.001) \) and phase \( (R = 0.89, P < 0.001) \) values for the head-fixed eye response across animals. Regression slopes for both gain \( (0.91) \) and phase \( (1.3) \) were near unity, indicating a significant relationship between model predictions and actual response values. Results from linear regression analyses for eye and head responses across animals are summarized in Fig. 7. As shown, the actual and predicted values of eye response gain and phase were strongly linearly related across animals, under both head-fixed \( (R \geq 0.74, P < 0.01) \) and head-free \( (R \geq 0.76, P < 0.01) \) conditions. Moreover, the associated best-fit linear regression slopes were generally not significantly different from unity, as indicated by 95% CIs. In contrast, there was no significant correspondence between actual and predicted head responses for two of three animals tested \( (P > 0.35) \). In the third animal, head response gain and phase were linearly related to model predictions \( (gain: R = 0.91, P = 0.0018; phase: R = 0.90, P = 0.0026) \) with slopes not significantly different from unity. However, the overall relationship between actual and predicted head responses when all animals’ data points were considered was not strongly linear \( (gain: R = 0.50, P = 0.012; phase: R = 0.20, P = 0.36) \). Therefore we concluded that the linear combination model did provide a good approximation of the eye response but not the head response during combined canal-otolith stimulation.

It was possible that the model’s inability to account for the head response was caused by our initial assumption that the gains of the canal- and otolith-driven responses were constant across stimuli. An alternative possibility is that canal- and otolith-driven head responses combine linearly but that each response’s gain depends on the presence of the other. To investigate this possibility, we fit the response data with a modified version of the linear combination model, where each response component’s weight was a free parameter (see METHODS). Eye responses were once again fit well by the linear combination model, with best-fit weights near unity for
both the canal- and otolith-driven responses \((R > 0.9)\). However, head responses for two of three subjects were not fit well by the linear combination model \((R < 0.9)\). These results indicate that a linear combination model accounted for the eye response but did not account for the head response and that the model’s failure to predict the head response was not caused by nonunity response component weights.

**Discussion**

In this study, we showed that phase improvement of rotational eye and head responses was correlated with the magnitude of net linear acceleration rather than its gravitational component. Similar to previous studies (Angelaki and Hess 1996b; Barmack 1981; Bockisch et al. 2005; Brettler et al. 2000; Dickman et al. 2000; Groen et al. 1999; Haque and Dickman 2005; Rude and Baker 1988; Schmid-Priscoveanu et al. 2000), response improvement was only present at low rotational frequencies \((0.25 \text{ Hz in this study})\). We further showed that these observations can be modeled as a linear combination of canal- and otolith-driven response components in the case of the eye but not the head.

**Otolith-driven response: net linear acceleration or its components?**

We used tilt/translation combinations to manipulate the magnitude of net linear acceleration while gravitational acceleration remained constant. We showed that increasing net linear acceleration magnitude was sufficient to improve low-frequency \((0.25 \text{ Hz})\) eye and head response phase. Others have documented low-frequency aVOR enhancement when both the semicircular canals and otolith organs were stimulated (Angelaki and Hess 1996b; Barmack 1981; Bockisch et al. 2005; Brettler et al. 2000; Dickman et al. 2000; Groen et al. 1999; Haque and Dickman 2005; Rude and Baker 1988; Schmid-Priscoveanu et al. 2000). However, these findings represent the first direct demonstration that net linear acceleration is the stimulus component producing the enhancement.

Previous studies have provided evidence that changes in the gravitational component of linear acceleration are not necessary to generate otolith-driven tilt responses. During pure translational motion, small aVOR-like tilt responses with low-pass dynamics have been observed in both lateral-eyed (Baarsma and Collewijn 1975; Dickman and Angelaki 1999; Hess and Dieringer 1991) and frontal-eyed (Angelaki 1998; Paige and Tomko 1991) animals. In fact, otolith afferents respond to net linear acceleration (Angelaki and Dickman 2000; Fernández and Goldberg 1976), and we might expect otolith-driven responses to be generated by an afferent-like...
signal. However, there is considerable evidence that nonhuman primates decompose the otolith afferent signal into its gravitational (till) and translational components. For example, primate mid-frequency tVOR eye responses during till/translation stimuli depend on the translational component rather than net linear acceleration (Angelaki et al. 1999). Even when net linear acceleration equals zero, an appropriate tVOR is produced by nonzero translational acceleration. In contrast, pigeons not only lack a functional tVOR (Dickman and Angelaki 1999), but instead generate eye and head responses that do not discriminate between gravitational and translational acceleration.

**Canal-otolith interaction: species differences**

Pigeons also lack several key oculomotor behaviors that are observed consistently in primates and are thought to be related to the specialized canal-otolith integration required to discriminate between gravitational and translational acceleration (Green and Angelaki 2003, 2004). For example, primates exhibit velocity storage, a theoretical construct purported to lengthen the eye velocity time constant to improve low-frequency aVOR responses (Büttner and Waespe 1981; Raphan et al. 1979). In contrast, pigeons not only lack velocity storage but exhibit velocity leakage: their aVOR time constant is actually shorter than that of their canal afferents (Anastasio and Correia 1994; Dickman and Correia 1989). In addition, primates produce steady-state per-rotatory eye nystagmus during constant velocity off-vertical axis rotation, when canal afferents are no longer dynamically active (Angelaki and Hess 1996b), whereas pigeons produce no steady-state nystagmus (Dickman and Angelaki 1999).

Interestingly, canal plugging in primates results in oculomotor behavior qualitatively similar to that observed in normal pigeons. Canal plugging abolishes eye response selectivity for translational acceleration, generating a tVOR that depends on net linear acceleration (Angelaki et al. 1999). Furthermore, while the otolith-driven tilt response during pure translation is small and restricted to low frequencies in normal monkeys, this response increases over time after canal plugging, in parallel with recovery of the low-frequency aVOR to EHA rotations (Angelaki et al. 2002). In fact, both velocity storage and steady-state per-rotatory nystagmus to constant velocity rotation diminish in parallel over time after canal plugging (Angelaki et al. 2000). These observations raise the possibility that pigeons and primates share a fundamental oculomotor substrate but that primates have additionally developed specialized canal-otolith processing that dominates behavior as long as both canal and otolith organs are intact (Green and Angelaki 2003).

**Canal-otolith integration: linear or nonlinear?**

What distinguishes normal primate oculomotor processing from that observed in pigeons and other lateral-eyed animals? We have concluded that canal- and otolith-driven response components combine linearly to generate the pigeon aVOR. Previous studies in other lateral-eyed species have examined whether a linear model could account for the aVOR, with mixed results. However, these previous studies either used inverted EHA rotation as their primary test case (Barmack 1981; Brettler et al. 2000) or used observations from canal-plugged animals to calculate the otolith-driven response (Angelaki and Hess 1996b; Barmack and Pettorossi 1988). In this study, we constructed multiple discriminative test stimuli in normal animals and were able to determine conclusively that a linear model was sufficient to account for enhancement of the pigeon aVOR during EHA rotation.

Linear processing cannot account for observed primate eye movements, however, where responses are driven by specific linear acceleration components. To decompose net linear acceleration into gravitational and translational components, canal and otolith signals must interact in a nonlinear fashion that also generates an inertial representation of angular velocity (Green and Angelaki 2004, 2007). Moreover, these two processes are inextricably linked. Decomposition of linear acceleration into its gravitational and translational components necessarily involves decomposition of angular acceleration into earth-vertical and earth-horizontal components, and vice versa. In fact, studies of so-called tilt dumping indicate that primates represent eye movements in an inertial reference frame (Angelaki and Hess 1994), further evidence of nonlinear canal-otolith integration in these animals.

Although this study provides evidence that head responses to complex stimuli are nonlinear, we cannot conclude that the nature of this nonlinearity matches that observed in primate oculomotor behavior. It is possible that this nonlinearity arises from convergent vestibular and extravestibular cues produced during head-free motion. Most prominently, the presence of neck proprioceptive inputs from relative head-to-body rotation might influence the head response in a nonlinear fashion. However, it seems likely that pigeons, like primates, are able to discriminate between gravitational and translational sources of otolith afferent activity somewhere in their central vestibular pathways. Previous studies have shown that pigeons must be able to maintain a space-stable head orientation during flight to right themselves in the air and navigate efficiently around airborne obstacles (Warrick et al. 2002). An internal representation of inertial angular velocity or position could serve to maintain space-stable head orientation during flight. Whether such an internal representation exists in pigeons has yet to be determined and presents a fertile line of inquiry for future study.

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**References**


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