INTRODUCTION

A common characteristic of all vertebrate vestibular systems is the existence of primary afferents with different response dynamics. At the two extremes, the most regularly firing primary otolith afferents are characterized by purely tonic response properties (i.e., they encode linear acceleration), whereas the most irregularly firing afferents have phasic or phasic- tonic response dynamics (i.e., they encode a signal related to a fractional derivative of linear acceleration) (Fernández and Goldberg 1976a,b; Goldberg et al. 1990). These vestibular afferents also differ in their excitability to electrical stimulation of the labyrinths. Irregular (phasic) afferents have a lower threshold and a higher sensitivity to electrical stimulation of the ear compared with regular (tonic) firing cells (Chen-Huang et al. 1997; Goldberg et al. 1984; Minor and Goldberg 1991). In fact, when anodal (inhibitory) labyrinthine currents are delivered, a selective, reversible ablation (silencing) of neural firing is produced in the most irregular afferents that lasts for the duration of the electrical stimulation. Regularly firing afferents, on the other hand, are little affected by even the largest current levels used (Dickman and Angelaki 1993; Goldberg et al. 1984). Even though constant anodal or cathodal currents elicit horizontal and torsional nystagmus in both eyes when only a single labyrinth is stimulated, bilateral anodal stimulation results in the selective silencing of the most irregularly firing neurons with no nystagmus being generated. Bilateral constant anodal stimulation has, thus, become a useful tool to study the contribution of irregular vestibular afferents to the production of the VORs.

Using this technique, it was demonstrated that irregular vestibular afferents do not contribute to the rotational VOR in the dark at frequencies between 0.5 and 4 Hz (Minor and Goldberg 1991). There has been some evidence, however, that irregular vestibular afferents might contribute to the VOR during long-duration rotations (Angelaki and Perachio 1993; Angelaki et al. 1992) and the viewing distance-dependent changes in the rotational VOR during near target fixation (Chen-Huang and McCrea 1998). Despite the modest effects of irregular vestibular afferent ablation on the rotational VOR, vestibular nuclei neurons have been shown to receive inputs from the whole continuum of afferents (Boyle et al. 1992; Chen-Huang et al. 1997; Goldberg et al. 1987; Highstein et al. 1987). The goal of the present study was to characterize the effects of bilateral labyrinthine currents on the translational VORs (trVORs). Several lines of evidence support the hypothesis that the most irregularly firing otolith afferents could contribute to the trVORs. First, trVORs are tuned to much higher frequencies compared with the rotational VOR and are characterized by response sensitivities that increase with frequency (Angelaki 1998; Angelaki et al. 2000; Paige and Tomko 1991; Telford et al. 1997). In essence, the high-pass filtered properties of the translational VORs could partly reflect the contribution from the high-pass filtered properties of irregular otolith afferents. Second, as mentioned in the preceding text, a contribution of irregular otolith afferents to the trVORs would explain, at least in part, the extensive irregular vestibular afferent inputs to second-order vestibuloocular neurons (e.g., Boyle et al. 1992). Preliminary results of this work have been presented elsewhere (Angelaki et al. 1998, 1999b).

METHODS

Animal preparation and eye movement recording

Five juvenile rhesus monkeys were chronically implanted with a circular molded, light-weight dental acrylic ring that was anchored by stainless steel screws, placed as inverted T-bolts under the skull and then secured to the ring. For single-unit recordings from the vestibular
nerve in three of the animals, a platform (3 cm × 3 cm, 5 mm height) constructed of machinable plastic-delin was secured stereotaxically to the skull and fitted inside the head ring (e.g., Correia et al. 1992). The platform had staggered rows of holes (spaced 0.8 mm apart) that extended from the midline to the area overlying the vestibular nerves bilaterally.

Subsequent to the eye coil surgeries and after animals had been trained sufficiently to fixate visual targets, labyrinthine stimulating electrodes were implanted in both ears. An incision was made on the rear side of the pinna and the temporal bone exposed. The soft tissue of the external ear canal was displaced gently and the bony meatus enlarged using a dental drill until the long process of the malleus and the chorda tympani (facial nerve) were visualized. A platinized Teflon-insulated silver wire (250 μm diam and insulated to within 1 mm of its tip) was then press fit into a small hole drilled into the promontorium between the round and oval windows. The electrode penetrated into the perilymphatic space but was sealed against perilymphatic leak by the Teflon insulation. A second, reference electrode was placed into a hole drilled close to the entrance of the bony meatus. The two wires were led under the skin to the top of the skull and mated to a connector. The incision in the temporal muscle and the skin was sutured closed. When animals were in their cages, the implanted delrin ring was covered with a cap to protect the recording platform and prohibit the animals from touching the leads of the eye coils and stimulating electrodes.

Binocular three-dimensional (3-D) eye movements were recorded in a 16-in side-length two-magnetic field system (CNC Engineering). For this, dual eye coils were implanted (Hess 1990) in each eye. Eye movements were calibrated in two stages. First, before implantation using a calibration jig. Second, daily calibrations were performed before experimental protocols by requiring the animals to perform a visual fixation task. Details for surgical procedures, eye movement calibration, and experimental testing have been reported in the preceding papers (Angelaki et al. 2000; McHenry and Angelaki 2000).

All surgical procedures were performed under sterile conditions in accordance to National Institutes of Health guidelines.

**Experimental setup and protocols**

During experimental testing, the monkeys were seated in a primate chair with their heads statically positioned such that the horizontal head plane was tilted 18° nose down. The animal’s body was secured with shoulder and lap belts, while the extremities were loosely tied to the chair. The primate chair then was secured inside the inner frame with shoulder and lap belts, while the extremities were loosely tied to the chair. The primate chair then was secured inside the inner frame with shoulder and lap belts, while the extremities were loosely tied to the chair. Experimental setup and protocols consisted of an array of translational and rotational stimulus profiles, as follows.

**FORE-AFT MOTION.** Three animals (C, P and G) were oscillated at 4 and 10 Hz (0.3–0.4 g peak acceleration) while fixing on two of the targets at a distance of 20 cm: ~6 cm to the left and to the right (relative to the right eye; eye positions of ~17°).

**LATERAL MOTION.** Three animals were sinusoidally laterally translated in complete darkness at several frequencies ranging between 0.3 and 12 Hz. At the lowest frequencies (0.3 and 0.37 Hz), the stimulus amplitude was 0.2 and 0.3 g, respectively. At higher frequencies, the amplitude was 0.3–0.4 g. To examine if the effects of the currents differed for different stimulus amplitudes, peak linear acceleration for 5-Hz oscillations was varied between 0.1 and 0.4 g in two animals.

2) Four animals were oscillated laterally at different frequencies between 4 and 12 Hz (0.3–0.4 g) while fixating on a centered (i.e., approximately zero horizontal eccentricity relative to a point midway between the two eyes) head-fixed target LED located 40, 30, 20, 15, or 10 cm from the eyes (in an otherwise dark laboratory room).

3) Four animals were translated laterally using a transient stimulus consisting of a step-like linear acceleration profile followed by a short period of constant velocity (peak linear acceleration: 0.5 g; peak linear velocity: ±22 cm/s; Fig. 8) while fixating on a centered space-fixed target LED located 87 and 10 cm (animals E, C, and P) or 15 cm (animal G) from the eyes.

**YAW ROTATION.** As a control, three animals also were tested during yaw oscillations (0.5–2 Hz). These same animals also were rotated at constant velocity (±60/°s) in complete darkness. The axis of rotation was either earth-vertical (yaw VOR) or tilted 23.6° from the earth-vertical (i.e., off-vertical axis or yaw OVAR).

For all behaviorally controlled experiments, each trial was initiated under computer control when the animal had satisfactorily fixated the target light in a dimly illuminated environment. After successful fixation had been satisfied, the sled (or rotator) was commanded to deliver either 3–25 cycles or the transient motion profile. During motion, the target remained illuminated but the background lights were turned off. For transient motion stimuli, labyrinthine stimulation started ~1 s before the execution of the motion. For sinusoidal motion stimuli, labyrinthine stimulation started ~20 ms before the execution of the motion. Because the transient portion of the sinusoidal response was discarded, analysis only focused on cycles ~500 ms after labyrinthine current onset. An attempt was made to repeat each sinusoidal protocol three times and each transient protocol a minimum of five times. Experimental sessions did not usually exceed 2–3 h and runs with no ear stimulation, anodal and cathodal currents always were intermingled. Other than the unilateral ear stimulations where currents as high as 200 μA were used to elicit eye movements in three of the animals, all other labyrinthine electrical stimulations never exceeded 100 μA. Between experimental sessions, a shorting plug was used for both ear electrodes.

Neither the surgical intervention nor the use of electrical stimulation interfered with labyrinthine function as demonstrated by normal rotational and trVOR responses (as compared with controls before electrode implantation). In addition, no increase in the threshold for evoking nystagmus was observed throughout the duration of these experiments (~2 wk in animals E, G, and H and ~2 mo in animals C and P). There was no sign of vestibular neuropathy (i.e., increased spontaneous nystagmus or head tilt) observed at any time during these experiments, in contrast to problems often encountered in previous studies (Angelaki and Perachio 1993; Angelaki et al. 1992; Chen-Huang and McCrea 1998). The regular use of both anodal and cathodal currents, shorting of the wires in-between experiments, as well as extreme care not to deliver higher or longer-duration currents are all thought to provide a more stable labyrinthine electrode use.

For each recording session, the eight voltage signals of the two eye-coil assemblies, the three output signals of a 3-D linear accelerometer (mounted on fiberglass members that firmly attach the animal’s head ring to the inner gimbal of the rotator), as well as velocity
and position feedback signals from the linear sled and/or rotator were low-pass filtered (200 Hz, 6-pole Bessel), digitized at a rate of 833.33 Hz (Cambridge Electronics Design, model 1401, 16-bit resolution) and stored on a PC for off-line analysis.

Once all behavioral experiments were completed, extracellular recordings from single fibers in the vestibular nerve were obtained in three animals (P, H, and G) with epoxy-coated, etched tungsten microelectrodes. Electrodes were inserted into guide tubes, then advanced through a predrilled hole in the recording platform and manipulated vertically with a remote control mechanical microdrive. Neural activity was amplified, filtered (300 Hz to 6 kHz) and passed through a BAK Instruments dual time-amplitude window discriminator the output of which was displayed on an oscilloscope. For each recorded cell, acceptance pulses from the BAK window discriminator were passed to the Cambridge Electronics Design signal processor (model 1401) and microcomputer where instantaneous firing rates were computed and displayed on-line (Spike 2) and subsequently stored for off-line analysis.

The vestibular nerve was localized stereotaxically (located laterally around AP-0) and by the following landmarks. 1) Once the recording electrode exited the guide tube, it usually encountered cells (including Purkinje cells) with both oculomotor and vestibular sensitivity, characteristic of neurons in the flocculus/ventral paraflocculus. 2) After a silent area of ~0.5–2 mm, the electrode picked up fiber action potentials with vestibular but not oculomotor sensitivity. Many of these cells were characterized by a regular firing rate and their overall discharge pattern was very different from neurons in the cerebellum. 3) To further verify that these cells were primary vestibular afferents, their input selectivity was characterized carefully through a combination of yaw/pitch/roll rotations and linear sled movements (e.g., Dickman 1996; Estes et al. 1975). Specifically, each afferent was tested with the following rotational stimuli (0.5 Hz, ±10°): yaw and pitch rotations, as well as rotations in the plane of the anterior and posterior semicircular canals (i.e., 45° away from the pitch and roll axes). In addition to the rotational stimuli, all units also were tested during translation along at least two different directions (0.5 Hz, ±0.2 g). All afferents tested with electrical stimulation were first characterized adequately in terms of their vestibular sensitivity. All cells received input from only one sensory organ, with spatial and dynamic properties consistent with those characterizing the vestibular nerve in squirrel monkeys (Fernández and Goldberg 1971, 1976a,b). To characterize the high-frequency dynamics or regularly and irregularly discharging otolith afferents under conditions similar to those used for the eye movement studies, a total of 21 otolith afferents was also tested at different frequencies between 0.16 and 10 Hz during lateral and/or fore-aft motion (Fig. 11).

Data analyses

All data analyses were performed off-line using a combination of computer software written to perform specific tasks. Calibrated 3-D eye positions were expressed as rotation vectors, E (Haustein 1989; van Opstal 1993) (the reference position was straight ahead). The eye angular velocity vector, Ω, was computed from 3-D eye position, as previously described (c.f., Angelaki and Hess 1996a,b). Both eye position and angular eye velocity vectors were expressed relative to a head-fixed right-handed coordinate system, as defined in the 18° nose-down position. Torsional, vertical, and horizontal eye position and velocity were the components of the eye position and eye velocity vectors along the nasoocipital, interaural, and vertical head axes, respectively. Positive directions were clockwise (as viewed from the animal, i.e., rotation of the upper pole of the eye toward the right ear), downward and leftward for the torsional, vertical, and horizontal components, respectively.

The horizontal, vertical, and torsional components of the calibrated eye position vectors were smoothed and differentiated with a Savitzky-Golay quadratic polynomial filter with a 15-point forward and backward window (Press et al. 1988; Savitzky and Golay 1964). For frequencies >6 Hz, response amplitudes have been corrected for the gain attenuation of the filter (Angelaki 1998; Angelaki et al. 2000). For steady-state sinusoidal responses in the dark, the fast phases of nystagmus were removed using a semiautomated procedure based on time and amplitude windows set for the second derivative of the eye velocity vector amplitude. For behaviorally controlled runs, no fast phase removal was usually necessary. Selected cycles during application of electrical currents were averaged and compared with the averaged cycles selected during interleaved periods without currents. Cycles that occurred during the onset and offset of current application were excluded from the analysis. As a general rule, responses within 500 ms from current onset were always excluded. Otherwise, average response cycles were computed from steady-state response components (i.e., horizontal, vertical, and torsional) for each eye. Sensitivity and phase were determined by fitting a sine function (and a DC offset) to both response and stimulus (output of the 3-D linear accelerometer or tachometer velocity for rotation) using a nonlinear least squares algorithm based on the Levenberg-Marquardt method. tVOR sensitivity was expressed as the ratio of peak eye velocity to peak linear velocity (computed as the integral of linear acceleration). Phase was expressed as the difference (in degrees) between peak eye velocity and peak stimulus velocity. On the basis of the sign definitions used, the phase of the compensatory horizontal response during lateral motion should be ~0°. Primary afferent activity was expressed as instantaneous frequency. Gain and phase of neural activity during translation were determined by fitting sinusoidal functions similarly as in eye velocity responses. Both gain and phase of primary otolith afferent responses have been expressed relative to linear acceleration (similarly as in Fernández and Goldberg 1976b).

For transient response analyses, the Savitzky-Golay quadratic polynomial filter was used with a 1 (rather than 15)-point forward and backward window. For each individual run, initial eye acceleration was estimated as the slope of a line fitted to the first 17 ms after response onset. Response latencies were computed as the onset of eye velocity relative to ideal velocity (3-SD method) (see Angelaki and McHenry 1999).

To quantitatively evaluate the effects of anodal and cathodal labyrinthine stimulation on yaw VOR during long-duration velocity steps, a straight line was fit to 2-s segments of horizontal slow phase velocity both immediately before and ~300 ms after onset of 3- or 5-s duration of bilateral anodal or cathodal currents. The effect of labyrinthine electrical stimulation to slow phase eye velocity then was computed as the percent change in the zero-intercept of the two regression lines for each current presentation (Table 4). Because there was no consistent change in the rate of decay of slow phase eye velocity (see also Angelaki and Perachio 1993), the slopes of the fitted lines are not reported here. For yaw OVAR, the same analysis was used to quantify the effects of the currents. Nevertheless, quantitative measurements were only possible in two of the three animals tested (animal E for ±60°/s and animal C for ±60°/s), when the relative magnitude of the sinusoidal modulation was small compared with the steady-state, “bias” horizontal component. Otherwise, when steady-state eye velocity was small and the sinusoidal modulations in eye velocity large, the effects of the currents (always lasting ≤5 s) could not be evaluated.

Because of the larger efficacy of the labyrinthine electrodes in animal E, stimulation effects were generally larger in this animal. However, all effects observed in animal E also were present (although often they were smaller) in all other tested animals. Not all protocols were tested in all animals. In general, testing a minimum of three animals was used as a goal for each of the specific questions addressed here. Statistical comparisons were based on analyses of variance (ANOVA) with repeated measures. For sinusoidal response gain and phase, independent variables were frequency, viewing distance, and labyrinthine stimulation. For transient analysis, independent variables were addition/abduction, viewing distance and labyrinthine stimulation. All F values reported are based on comparisons where the
labyrinthine stimulation factor had three levels: no stimulation, anodal stimulation (+100 μA), and cathodal stimulation (−100 μA). The effects of anodal or cathodal stimulation alone also were tested separately (2-level comparisons). Unless otherwise stated, when the three-level labyrinthine stimulation factor was significant, the same significance levels also held for the separate comparisons of anodal or cathodal stimulation with control values.

RESULTS

3-D eye movements evoked by unilateral anodal and cathodal labyrinthine stimulation

Unilateral anodal or cathodal stimulation elicited conjugate eye movements with slow phase velocity that increased sharply to a peak. Nystagmus persisted throughout the duration of stimulation, although some decay in slow phase velocity was occasionally observed (Fig. 1). For all five animals, the nystagmus was primarily horizontal and torsional with small, inconsistent vertical components (primarily with upward slow phase). Slow phases were contralaterally directed for cathodal (excitatory) currents. Left ear cathodal stimulation, for example, rotated both eyes clockwise (i.e., extorsion of the right eye and intorsion of the left eye) and rightward (Fig. 1, left; positive torsional and negative horizontal components, respectively). Opposite-directed eye movements were observed during anodal (inhibitory) stimulation (Fig. 1). Peak responses in all five animals are illustrated in Fig. 2. Despite consistent horizontal and torsional responses, vertical eye movements were highly variable. In four of the animals, the direction of vertical slow phase velocity was upward (negative) and independent of the polarity of the stimulus. In the fifth animal, left cathodal stimulation and right anodal stimulation elicited downward (positive) slow phase eye movements (Fig. 2, bottom).

The peak amplitudes of the horizontal and torsional components were similar, although a strong asymmetry between anodal and cathodal stimulation was always observed, particularly for large current amplitudes. The peak amplitude of slow phase eye velocity increased for larger current amplitudes and exhibited a clear saturation for anodal stimulation of similar magnitude (Fig. 2). This behavior was quantified through second-order linear regression fits (Table 1). Anodal currents of 100 μA resulted in a slow phase velocity of ~15–30°/s in four of the animals and ~40–50°/s in the fifth animal (E). For this reason, animal E was tested with 50 and 100 μA (the remaining animals were tested primarily with 100 μA currents).

Bilateral labyrinthine currents resulted in negligible horizontal nystagmus. Torsional nystagmus, however, was sometimes not completely cancelled (e.g., Fig. 3 and 9). We have used such bilateral anodal labyrinthine electrical stimulation during

![FIG. 1. Binocular torsional, vertical, and horizontal components of eye position (E_tor, E_ver, and E_hor) and eye velocity (Ω_tor, Ω_ver, Ω_hor) during unilateral cathodal (negative) and anodal (positive) stimulation (100 μA, 1 s). Left: data during left ear stimulation; right: data during right ear stimulation. ⋯⋯⋯ız position (straight-ahead gaze) and 0 eye velocity. Data from animal C. Even though not as prominent as in squirrel monkeys (Minor et al. 1996), torsional slow phases were generally curved.](http://jn.physiology.org/)

Downloaded from http://jn.physiology.org/ by 10.220.33.2 on October 8, 2016
The effects of viewing distance depended on current stimulation (Fig. 4A, ▲, △, ■, and □; see also Table 2). In the presence of cathodal labyrinth stimulation, both the zero intercept and the regression line slope increased in amplitude. The opposite was generally true for anodal currents. These differences were statistically significant [slope: F(2,18) = 11.5, P < 0.01, 0-intercept: F(2,18) = 9.97, P < 0.01]. The same significance levels also were obtained when anodal or cathodal effects were considered alone (and compared with control data).

The effects of labyrinthine stimulation were observed in all eye velocity components, not just the horizontal. Specifically, labyrinthine stimulation affected the viewing distance-dependence of the torsional and vertical eye velocity components of the trVOR (e.g., Fig. 3). As shown in Fig. 4B, for example, the magnitude of the torsional response component increased in a viewing distance-dependent manner in the presence of cathodal labyrinthine currents.

**Effects of labyrinthine currents on the dynamics of the trVOR during lateral motion**

In addition to the large effects on the sensitivity amplitude and viewing distance dependence of eye velocity, cathodal and anodal stimulation consistently altered the high-frequency dynamics of the trVOR during near target fixation (Fig. 5). The most profound effect was the observed changes in response phase [F(2,26) = 19.4, P < 0.01]. Compared with control responses, anodal currents increased the phase lags, whereas cathodal currents decreased the phase lags (or equivalently, increased the phase leads). Response sensitivity was also significantly affected by the currents [F(2,26) = 29.8, P < 0.01].

To examine the effects of labyrinthine electrical stimulation on the trVOR dynamics in a broader frequency range, three animals also were tested in complete darkness (verbatim). The opposite was generally true for anodal currents. These differences were statistically significant [slope: F(2,18) = 11.5, P < 0.01, 0-intercept: F(2,18) = 9.97, P < 0.01]. The same significance levels also were obtained when anodal or cathodal effects were considered alone (and compared with control data).

**Effects of labyrinthine currents on the viewing distance-dependent properties of the trVOR during steady-state lateral oscillations**

Both anodal and cathodal stimulation had a profound effect on the sensitivity of trVORs during near target fixation. As shown in Fig. 3 for a viewing distance of 10 cm, anodal stimuli resulted in decreased trVOR responses. In contrast, cathodal stimuli increased trVOR responses. In the absence of labyrinthine electrical stimulation and as expected based on the kinematic requirements of the reflex, the elicited horizontal eye movements depended on target distance, as it was varied between 10 and 40 cm (Fig. 4A, ◆). Horizontal response sensitivity increased approximately proportional to the inverse of viewing distance, although the regression line slope was never as steep as that required for ideal gaze stabilization (see also Telford et al. 1997). In addition to a less than ideal slope, regression lines did not pass through zero, suggesting that there is a nonzero response during viewing at infinity (see also Telford et al. 1997).

**TABLE 1.** Eye velocity (Ω) as a function of current amplitude (I): second-order regression parameters

<table>
<thead>
<tr>
<th>Animal</th>
<th>Left Ear</th>
<th>Right Ear</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Horizontal component</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>Ω = 0.67 (I) − 1.7 e⁻³ (I²)</td>
<td>Ω = −0.57 (I) + 1.1 e⁻³ (I²)</td>
</tr>
<tr>
<td>C</td>
<td>Ω = 0.22 (I) − 4.6 e⁻⁴ (I²)</td>
<td>Ω = −0.13 (I) − 0.8 e⁻³ (I²)</td>
</tr>
<tr>
<td>P</td>
<td>Ω = 0.23 (I) + 1.7 e⁻⁴ (I²)</td>
<td>Ω = −0.26 (I) + 5.1 e⁻³ (I²)</td>
</tr>
<tr>
<td>H</td>
<td>Ω = 0.26 (I) − 6.0 e⁻⁴ (I²)</td>
<td>Ω = −0.38 (I) + 3.1 e⁻³ (I²)</td>
</tr>
<tr>
<td>G</td>
<td>Ω = 0.17 (I) − 2.5 e⁻⁴ (I²)</td>
<td>Ω = −0.15 (I) + 1.3 e⁻³ (I²)</td>
</tr>
<tr>
<td><strong>Torsional component</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>Ω = −0.83 (I) + 2.1 e⁻³ (I²)</td>
<td>Ω = 0.60 (I) − 1.3 e⁻³ (I²)</td>
</tr>
<tr>
<td>C</td>
<td>Ω = −0.30 (I) + 8.3 e⁻⁴ (I²)</td>
<td>Ω = 0.19 (I) − 1.3 e⁻³ (I²)</td>
</tr>
<tr>
<td>P</td>
<td>Ω = −0.31 (I) + 3.2 e⁻⁴ (I²)</td>
<td>Ω = 0.31 (I) − 3.4 e⁻³ (I²)</td>
</tr>
<tr>
<td>H</td>
<td>Ω = −0.40 (I) + 1.1 e⁻³ (I²)</td>
<td>Ω = 0.46 (I) − 3.4 e⁻³ (I²)</td>
</tr>
<tr>
<td>G</td>
<td>Ω = −0.13 (I) + 6.6 e⁻⁵ (I²)</td>
<td>Ω = 0.14 (I) − 6.1 e⁻³ (I²)</td>
</tr>
<tr>
<td><strong>Vertical component</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>Ω = 0.06 (I) − 9.0 e⁻⁴ (I²)</td>
<td>Ω = 0.03 (I) − 8.0 e⁻⁴ (I²)</td>
</tr>
<tr>
<td>C</td>
<td>Ω = −0.0003 (I) − 7.3 e⁻³ (I²)</td>
<td>Ω = 0.0008 (I) − 5.7 e⁻³ (I²)</td>
</tr>
<tr>
<td>P</td>
<td>Ω = −0.08 (I) + 8.2 e⁻³ (I²)</td>
<td>Ω = 0.08 (I) − 9.2 e⁻³ (I²)</td>
</tr>
<tr>
<td>H</td>
<td>Ω = 0.14 (I) − 1.9 e⁻³ (I²)</td>
<td>Ω = −0.05 (I) − 8.8 e⁻³ (I²)</td>
</tr>
<tr>
<td>G</td>
<td>Ω = 0.01 (I) − 5.6 e⁻³ (I²)</td>
<td>Ω = 0.05 (I) − 7.0 e⁻³ (I²)</td>
</tr>
</tbody>
</table>
gence angles of ~1 MA) (Angelaki 1998). Both anodal and cathodal stimulation significantly altered the sensitivity $[F(2,36) = 12.2, P < 0.01]$ and phase $[F(2,36) = 39.2, P < 0.01]$ of the horizontal trVOR response, as tested at 0.3–12 Hz (Fig. 6). Labyrinthine stimulation also significantly altered the frequency dependence of the reflex [sensitivity: $F(28,36) = 4.0, P < 0.01$; phase: $F(28,36) = 3.1, P < 0.01$]; anodal currents decreased the slope of the sensitivity curves and increased the phase lags. Cathodal stimulation had effects that were opposite and usually larger. As a result of the change in slope, trVOR sensitivity during cathodal labyrinthine stimulation was larger than control data at high frequencies but smaller than control data at low frequencies. Between ~1 and 4 Hz, little effect of the current on trVOR sensitivity actually was observed.

The observed effects of labyrinthine currents were independent of peak acceleration (and consequently, velocity) amplitude. This was tested in two animals where the effects of the currents were studied for four different peak acceleration magnitudes at 5 Hz (Fig. 7). In both animals, the effects of the currents were independent of peak stimulus amplitude.

**Effects of labyrinthine currents on transient trVOR responses during lateral motion**

The changes in the dynamics and sensitivity of the trVOR with anodal and cathodal labyrinthine currents that were observed during steady-state lateral oscillations were also apparent in the eye movements elicited during transient head displacements. Responses from four animals during fixation of a space-fixed target at a distance of 87 cm have been illustrated in Fig. 8. Similar to the data during sinusoidal oscillations (Fig. 6), current effects were largest in *animal E* (Fig. 8, *top left*). Despite variability in the magnitude of the changes (which reflected the different effectiveness of electrodes in the 4 animals; e.g., Fig. 2), anodal currents during transient motion elicited trVORs that had more sluggish dynamics as compared with control responses (Fig. 8, compare blue with green lines). Moreover, cathodal stimulation usually resulted in larger and

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**Fig. 3.** Binocular torsional, vertical, and horizontal components of eye position ($E_{tor}$, $E_{ver}$, and $E_{hor}$) and eye velocity ($\Omega_{tor}$, $\Omega_{ver}$, $\Omega_{hor}$) during lateral translation at 8 Hz, ~0.4 g in the absence (*A*) and presence of anodal and cathodal labyrinthine currents (*B* and *C*) while fixating a target approximately straight ahead at a distance of 10 cm. ---, 0 position (straight ahead gaze) and 0 eye velocity. Stimulus (*bottom*) traces show the labyrinthine currents (Cur) and the output of a linear accelerometer mounted on the animal’s head (Hacc). Data from *animal C*. 

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**A** No labyrinthine stimulation  
**B** Anodal stimulation  
**C** Cathodal stimulation
more dynamic responses for the first ~60 ms following lateral motion onset (Fig. 8, red lines).

Results from all four animals at both viewing distances (10 and 87 cm) have been summarized in Table 3. Labyrinthine stimulation had a significant effect on initial eye acceleration and 87 cm) have been summarized in Table 3. Labyrinthine motion onset (Fig. 8, red lines).

Effects of labyrinthine currents on fore-aft VOR

The effects of anodal and cathodal labyrinthine stimulation on the dynamics and sensitivity of the trVORs during fore-aft motion were tested in three animals (C, P and G) during 4 and 10 Hz oscillations while fixating targets to the left and to the right at a distance of 20 cm (vergence of ~10°). Results were similar to those during lateral oscillations. Accordingly, anodal stimulation had a significant effect on initial eye acceleration and during lateral stimulation [F(1,229) = 23.0, P < 0.01] (see also Angelaki and McHenry 1999). These asymmetries were affected by the currents [F(2,229) = 6.4, P < 0.01]. More specifically, no significant asymmetry was observed in the presence of anodal (+100 µA, ■) and cathodal (−100 µA, ▲) stimulation. Data from animal E.

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TABLE 2. Dependence of trVOR sensitivity on the inverse of viewing distance: linear regression parameters

<table>
<thead>
<tr>
<th>Frequency, Hz</th>
<th>Animal</th>
<th>No Stimulation</th>
<th>Anodal Stimulation (+100 µA)</th>
<th>Cathodal Stimulation (−100 µA)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Regression equation</td>
<td>R²</td>
<td>Regression equation</td>
</tr>
<tr>
<td>5</td>
<td>E</td>
<td>y = 0.18 (1/D) + 0.52</td>
<td>0.91</td>
<td>y = 0.12 (1/D) + 0.39</td>
</tr>
<tr>
<td>5</td>
<td>P</td>
<td>y = 0.15 (1/D) + 0.33</td>
<td>0.98</td>
<td>y = 0.21 (1/D) + 0.16</td>
</tr>
<tr>
<td>5</td>
<td>G</td>
<td>y = 0.21 (1/D) + 0.35</td>
<td>0.95</td>
<td>y = 0.14 (1/D) + 0.30</td>
</tr>
<tr>
<td>10</td>
<td>E</td>
<td>y = 0.16 (1/D) + 0.70</td>
<td>0.75</td>
<td>y = 0.08 (1/D) + 0.57</td>
</tr>
<tr>
<td>10</td>
<td>C</td>
<td>y = 0.10 (1/D) + 0.52</td>
<td>0.88</td>
<td>y = 0.05 (1/D) + 0.50</td>
</tr>
<tr>
<td>10</td>
<td>P</td>
<td>y = 0.20 (1/D) + 0.53</td>
<td>0.99</td>
<td>y = 0.18 (1/D) + 0.43</td>
</tr>
<tr>
<td>10</td>
<td>H</td>
<td>y = 0.08 (1/D) + 0.11</td>
<td>0.97</td>
<td>y = 0.02 (1/D) + 0.13</td>
</tr>
<tr>
<td>10</td>
<td>G</td>
<td>y = 0.26 (1/D) + 0.07</td>
<td>0.99</td>
<td>y = 0.16 (1/D) + 0.18</td>
</tr>
</tbody>
</table>

Data from 5 animals at 10 Hz and 3 animals at 5 Hz. Ideal equation for maintaining fixation on the target is y = 0.57 (1/D). Animal E (squares in Fig. 2) exhibited the largest changes with anodal and cathodal stimulation. Smallest changes were observed in animals P and G (circles and up triangles in Fig. 2). trVOR, translational vestibuloocular reflex.
labyrinthine stimulation decreased the sensitivity and the phase lags of the fore-aft VORs. Cathodal stimulation, on the other hand, increased the sensitivity and introduced larger phase leads. The current effects on both sensitivity and phase were statistically significant $F(2,64) = 35.6, P < 0.01$ and $F(2,64) = 6.63, P < 0.01$, respectively. The observed differences were similar for both 4 and 10 Hz.

Effects of labyrinthine currents on the rotational VOR

In contrast to the lack of any prominent changes in the rotational VOR during 0.5–2 Hz sinusoidal oscillations, bilateral labyrinthine stimulation resulted in changes in the rotational VOR during long-duration velocity steps (see also Angelaki and Perachio 1993). In 2/3 animals tested, anodal currents consistently decreased slow phase eye velocity throughout the duration of per- or postrotatory nystagmus (Fig. 9). In the third animal ($P$), the effects were rather asymmetric for the two directions of rotation. Percent changes in slow phase eye velocity for all three animals have been included in Table 4A. Even though cathodal currents tended to have the opposite effect and increase slow phase velocity, results were more variable among animals. The effects of current stimulation on the steady-state velocity during off-vertical axis rotations (OVAR) could be evaluated using the 2-s straight line fit only when the relative magnitude of the horizontal slow phase velocity modulation was small compared with the steady-state (“bias”) component. In the cases where the effects could be assessed quantitatively, anodal currents decreased and cathodal currents increased the steady-state horizontal eye velocity (Table 4B).

Single-unit recordings from primary vestibular afferents

Because all previous studies of the effects of labyrinthine electrical stimulation on primary vestibular afferent activity have been conducted in other species, the efficacy of this technique in rhesus monkeys was verified by examining the effects of 1–2 s ipsilateral labyrinthine electrical stimulation on the firing rate of vestibular afferent fibers. Examples from four afferent fibers, two of which are characterized by regular firing rates and two of which are characterized by irregular firing rates, have been illustrated in Fig. 10. Results in 15 cells recorded from the vestibular nerve of two rhesus monkeys were similar to what has been reported previously in squirrel monkey (Minor and Goldberg 1991), gerbil (Kaufman and Perachio 1994; Marshburn et al. 1997), and pigeon afferents (Dickman and Angelaki 1993). The most irregularly firing cells were silenced completely by positive 100–μA currents, whereas regularly firing cells were affected only slightly.

Because the dynamics of primate otolith afferents have only been examined at frequencies $\leq$ 2 Hz and to be able to simulate the effects of labyrinthine currents on the dynamics of the trVOR, we recorded the gain and phase from 21 primary otolith afferents during sinusoidal oscillations similar to those used for the eye movement studies. Of these 21 afferents tested, 6 were regularly discharging ($CV^* < 0.1$) ($CV^*$ computed as in Goldberg et al. 1984) and 15 were irregularly discharging ($CV^* > 0.1$). Average data for each population are compared with those reported in squirrel monkeys in Fig. 11 ($\bigcirc$ and $\bigcirc$: present study; $\square$ and $\bigcirc$: Fernández and Goldberg 1976b). Both sets of data were fitted with the following transfer functions

$$H_{REGaff}(s) = \frac{0.91e^{0.07(1 + 0.022s)^{1.61}}}{(1 + 0.05s)} \quad (1a)$$

![Fig. 6. Effects of labyrinthine electrical stimulation (100 μA) on the trVOR dynamics in complete darkness (vergence angles of $\approx$ 1 MA). Horizontal trVOR sensitivity and phase without electrical stimulation (○) are compared with those in the presence of anodal (●) and cathodal (▲) stimulation. Data from animal E.](http://jn.physiology.org/)

![Fig. 7. Effects of labyrinthine electrical stimulation (100 μA) on trVOR sensitivity at different peak linear acceleration amplitudes. Average (± SD) horizontal trVOR sensitivity at 5 Hz without electrical stimulation (○) is compared with those in the presence of anodal (●) and cathodal (▲) stimulation. Data from animals G and P in complete darkness.](http://jn.physiology.org/)
FIG. 8. Horizontal eye velocity during transient lateral motion while fixating a space-fixed target at a distance of 87 cm that remained on throughout motion. Green lines: average (± SD) right eye velocity without ear stimulation. Blue (red) lines: average eye velocity (~5–20 runs) in the presence of bilateral anodal (cathodal) electrical stimulation that started ~1 s before the initiation of the movement. Because of a small nystagmus that was present in animal P due to incomplete cancelling of eye movements during bilateral anodal stimulation, there is a nonzero eye velocity baseline prior to stimulus onset (blue lines in bottom left traces). Black lines illustrate linear head velocity.
TABLE 3. Transient response parameters

<table>
<thead>
<tr>
<th></th>
<th>No Stimulation</th>
<th>Anodal (+100 μA)</th>
<th>Cathodal (−100 μA)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial eye acceleration (°/s²)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Animal E (10 cm-AB)</td>
<td>1.53 ± 0.42 (25)</td>
<td>0.58 ± 0.45 (16)</td>
<td></td>
</tr>
<tr>
<td>(10 cm-AD)</td>
<td>1.23 ± 0.21</td>
<td>0.73 ± 0.34</td>
<td></td>
</tr>
<tr>
<td>Animal C (10 cm-AB)</td>
<td>1.02 ± 0.20 (16)</td>
<td>0.58 ± 0.30 (17)</td>
<td>1.11 ± 0.60 (8)</td>
</tr>
<tr>
<td>(10 cm-AD)</td>
<td>0.87 ± 0.26</td>
<td>0.61 ± 0.32</td>
<td>0.88 ± 0.47</td>
</tr>
<tr>
<td>Animal P (10 cm-AB)</td>
<td>1.36 ± 0.22 (16)</td>
<td>1.02 ± 0.43 (13)</td>
<td>1.32 ± 0.37 (16)</td>
</tr>
<tr>
<td>(10 cm-AD)</td>
<td>1.34 ± 0.35</td>
<td>0.89 ± 0.53</td>
<td>1.35 ± 0.40</td>
</tr>
<tr>
<td>Animal G (15 cm-AB)</td>
<td>0.99 ± 0.22 (23)</td>
<td>0.60 ± 0.16 (42)</td>
<td>1.20 ± 0.20 (38)</td>
</tr>
<tr>
<td>(15 cm-AD)</td>
<td>0.78 ± 0.13</td>
<td>0.57 ± 0.19</td>
<td>0.90 ± 0.42</td>
</tr>
<tr>
<td>All animals (87 cm-AB)</td>
<td>0.17 ± 0.12 (78)</td>
<td>0.16 ± 0.20 (80)</td>
<td>0.18 ± 0.13 (52)</td>
</tr>
<tr>
<td>(87 cm-AD)</td>
<td>0.23 ± 0.13</td>
<td>0.16 ± 0.15</td>
<td>0.20 ± 0.11</td>
</tr>
<tr>
<td>Latency (ms) AB</td>
<td>8.6 ± 3.5 (80)</td>
<td>9.6 ± 2.7 (88)</td>
<td>11.3 ± 3.9 (64)</td>
</tr>
<tr>
<td>AD</td>
<td>7.9 ± 2.4</td>
<td>9.8 ± 1.5</td>
<td>10.9 ± 4.4</td>
</tr>
</tbody>
</table>

Data from four animals. Because of asymmetric initial eye acceleration (Angelaki and McHenry 1999), abduction (AB, i.e., left eye during rightward motion and right eye during leftward motion) and adduction (AD) response parameters have been computed separately. Response latencies have been estimated only for a viewing distance of 10 or 15 cm. The slightly shorter latencies measured here compared with our previous report (Angelaki and McHenry 1999) could be due to the higher resolution provided with the newest 16-bit analog to digital converter (some of the data in the previous study were collected with a 12-bit system). n values are in parentheses. Means values are ±SD.

Irregular afferents: $H_{IRaff}(s) = \frac{0.71s^{0.39}(1 + 0.030s)^{1.32}}{(1 + 0.05s)} \quad (1b)$

Equations 1a and 1b are the simplest functions that would satisfactorily describe the dynamics of primary otolith afferents in the whole frequency range. The 50-ms pole probably represents the peripheral mechanics (Fernández and Goldberg 1976b; Grant and Cotton 1990), $s^k$ is a frequency-independent adaptation operator and $(1 + \tau s)^k$ is responsible for the high-frequency (>2 Hz) phase leads.

Yaw rotation

TABLE 4. Percent (%) changes in horizontal slow phase eye velocity during constant velocity yaw rotations

<table>
<thead>
<tr>
<th></th>
<th>Anodal Stimulation (+100 μA)</th>
<th>Cathodal Stimulation (−100 μA)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Animal E</td>
<td>60°/s</td>
<td>60°/s</td>
</tr>
<tr>
<td>E</td>
<td>−22 ± 5</td>
<td>0.2 ± 5</td>
</tr>
<tr>
<td>C</td>
<td>−20 ± 10</td>
<td>−1 ± 15</td>
</tr>
<tr>
<td>P(***）</td>
<td>−42 ± 14</td>
<td>−19 ± 6</td>
</tr>
</tbody>
</table>

Negative numbers indicate percent decreases in eye velocity. Positive numbers indicate percent increases in eye velocity. For animal P (**), results were asymmetric possibly because bilateral labyrinthine stimulation did not totally cancel each other. Also, because of small steady-state and large sinusoidal modulation responses, data from animal P could not be evaluated for off-vertical axis rotations.

DISCUSSION

We have examined the effects of bilateral labyrinthine electrical stimulation on the sensitivity, phase and viewing distance-dependent properties of the trVORs by delivering 100 μA of anodal (inhibitory) and cathodal (excitatory) currents during translational motion. Functional ablation (anodal currents), as well as potential recruitment (cathodal currents), have been both shown to alter the sensitivity, dynamics and viewing distance-dependence of the trVORs.

FIG. 9. Effects of labyrinthine stimulation on yaw VOR during long-duration velocity steps. Torsional, vertical, and horizontal components of right eye position ($E_{tor}$, $E_{ver}$, and $E_{hor}$) and velocity ($\Omega_{tor}$, $\Omega_{ver}$, $\Omega_{hor}$) during rotation at 60°/s in darkness. Bilateral cathodal (negative) and anodal (positive) current steps (100 μA, 5 s) were delivered several times throughout the per- and postrotatory responses. ---, 0 position (straight-ahead gaze) and 0 velocity. Stimulus (bottom) traces show the labyrinthine currents (Cur) and head velocity (Vel). Data from animal E.
Use of labyrinthine currents as a means to investigate the functional role of irregular vestibular afferents

The sensitivity of primary vestibular afferents to labyrinthine electrical stimulation has been shown to be a function of discharge regularity. The more irregularly firing an afferent, the higher its sensitivity to electrical stimulation (Goldberg et al. 1984). This property has been demonstrated to be true in several species, including squirrel monkeys (Goldberg et al. 1984; Lysakowski et al. 1995; Minor and Goldberg 1991), rhesus monkeys (present study), chinchillas (Goldberg et al. 1990), and pigeons (Dickman and Angelaki 1993). Even though unilateral ear stimulation results in significant nystagmus, bilateral labyrinthine stimulation largely cancels most nystagmus while concurrently decreasing the spontaneous activity of many vestibular afferents. The technique of bilateral, constant labyrinthine stimulation often has been used as a means of addressing the role of irregularly firing vestibular afferents to the VOR (Angelaki and Perachio 1993; Angelaki et al. 1992; Chen-Huang and McCrea 1998; Minor and Goldberg 1991) and central vestibular processing (Chen-Huang et al. 1997; Dickman and Angelaki 1993).

Even though bilateral labyrinthine electrical stimulation is still the sole way of addressing the role of different afferent types, it presents several limitations that can be both practical and functional. Repeated electrical stimulation often has been a problem in previous studies. In the present experiments, special care was taken to avoid electrode polarization. First, the two electrodes in each ear remained shorted in between experimental sessions. Second, both anodal and cathodal stimuli were alternated during each experimental session. Third, the labyrinthine electrodes were platinized rather than silver-chlorided before implantation. These three measures were sufficient to eliminate any observable effects due to electrode polarization throughout these experiments.

The functional effectiveness of the labyrinthine electrical stimulation technique is more difficult to quantify. There are at least two problems in interpreting results from these ablation studies. First, there is the possibility that the decrease in primary afferent discharge during anodal stimulation (including both regular and irregular afferents) results in a global silencing or lowering of spontaneous activity of central neurons such that large peak-to-peak sinusoidal stimuli drive the cells into inhibitory saturation. Such a central mechanism would result in decreased VOR responses without necessarily a direct involvement of irregular vestibular afferents to reflex properties. The following results argue against such an interpretation. 1) The largest effects of the currents on trVOR dynamics were observed in response phase. The global inhibitory saturation mechanism would predict changes in sensitivity but not response phase. 2) The effects of the currents were present not only during steady-state sinusoidal oscillations but also very early in the response during transient head displacements. And 3) if the observed results were primarily due to central inhibitory saturation, the effects of the currents should increase as a function of peak stimulus acceleration amplitude. When we varied peak linear acceleration, there was no evidence of such a dependence (Fig. 7).

The second problem in the interpretation of results from ablation studies is related to the fact that primary vestibular afferents are known to constitute a continuum, such that absolute segregation into regular and irregular afferents is problematic. Electrical stimulation of the labyrinth results in changes in the mean firing rates of both regularly and irregularly firing

![Fig. 10. Primary afferent discharge (spikes/s or Hz) during cathodal (negative) and anodal (positive) ipsilateral labyrinthine stimulation (100 μA). Data from 4 afferents with different discharge regularities. A: posterior canal afferent (CV* = 0.05). B: horizontal canal afferent (CV* = 0.07). C: anterior canal afferent (CV* = 0.45). D: otolith afferent (CV* = 0.46). CV* has been computed after Goldberg et al. (1984).](http://jn.physiology.org/)

![Fig. 11. Primary otolith afferent dynamics. Average gain and phase (re linear acceleration) from primary otolith afferents in rhesus and squirrel monkeys (● and ○ and □ and ▪, respectively). Before averages were computed, gains were normalized to unity (1 spike·s⁻¹·g⁻¹) at 0.5 Hz. Regular afferents (CV* < 0.1): ● and ■, irregular afferents (CV* > 0.1): ○ and ▪, fits of transfer functions (1).](http://jn.physiology.org/)
vestibular afferents (e.g., Fig. 10), although irregularly firing afferents are much more sensitive. In fact, our experience in both rhesus monkeys and pigeons suggests that it is essentially impossible to silence regularly firing afferents even with very large currents (≤500 μA) that we were able to deliver in acute bird preparations (Dickman and Angelaki 1993). Significant changes in a VOR response parameter in the presence of anodal labyrinthine stimulation could suggest that irregularly firing afferents contribute to the normal function of the reflex. Quantitative conclusions regarding more specific afferent contributions are, however, difficult. Keeping these functional limitations in mind, the following paragraphs summarize the main experimental results in the context of previous knowledge as well as attempt to speculate on the functional implications of the present findings by simulating a simple model for the trVOR.

Effects of labyrinthine electrical stimulation on the dynamics and viewing distance dependence of the trVORs

Significant effects of anodal and cathodal labyrinthine stimulation on the dynamics of the translational VORs were observed in the present studies. Anodal stimulation decreased trVOR sensitivity and increased phase lags. Cathodal stimulation had the opposite effects and resulted in more high-pass filter properties (i.e., it increased both the phase leads and the slope of the sensitivity changes as a function of frequency). Changes in reflex sensitivity and phase were common to both fore-aft and lateral responses.

The effects of the currents on the trVOR dynamics were also significant during transient head displacements. Anodal stimulation significantly decreased initial eye acceleration compared with control values. As also shown in our previous study (Angelaki and McHenry 1999), initial eye acceleration during near target viewing was larger for abduction compared with adduction responses. Anodal stimulation eliminated this asymmetry, suggesting that there might be a differential irregular afferent input to the otolith-abducens compared with the otolith-medial rectus pathways.

The significant effects of labyrinthine stimulation on the dynamics of the trVORs observed here might seem in contrast to recent results during eccentric rotation in squirrel monkeys (Chen-Huang and McCrea 1998). Using comparisons between the VOR elicited during centered and eccentric rotations, the authors concluded that there was no effect of the currents on the translational VOR. The difference in the two sets of observations could be due to the different stimuli used in the two studies. Chen-Huang and McCrea (1998) used relatively low frequencies (0.5–4 Hz). As shown here, labyrinthine stimulation alters the slope of the sensitivity increase over frequency such that the largest changes are seen for frequencies >5 Hz (Figs. 5 and 6). Coactivation of both semicircular canal and otolith-ocular pathways during eccentric rotation might also constitute another difference. For example, nonlinear interactions between semicircular canal and otolith signals have been shown recently to be fundamental in the detection of head translation (Angelaki et al. 1999a).

Irregularly firing vestibular afferents are characterized by more phasic response properties compared with regularly firing cells (Fig. 11) (see also Fernández and Goldberg 1976b; Goldberg et al. 1990). Thus the reduced initial eye acceleration, the increase in phase lag and the decrease in the high-pass filtered properties of the reflex in the presence of anodal stimulation could then be a direct consequence of the functional ablation of the most phasic afferents. This hypothesis has been investigated further here by simulating a simple model considering both regular and irregular otolith afferents (see following text). The opposite effects of cathodal stimulation in the dynamics of the trVORs are more puzzling. To explain these results, one would have to consider a “functional recruitment” during cathodal stimulation that operates in a similar fashion as the postulated “functional ablation” due to silencing of the background discharge of a population of vestibular afferents during anodal stimulation. For example, cathodal currents could increase the background discharge of low-firing irregular vestibular afferents that normally would rectify during high-frequency stimuli. By increasing the peak-to-peak modulation of these units, their contribution to the central pathways mediating the reflex also increases. Hence addition of the dynamics from a larger number of phasic, higher-lead afferents could augment the high-pass filtered properties and increase the phase leads of the trVORs (see following text).

Anodal and cathodal labyrinthine stimulation also resulted in significant but opposite changes in the reflex sensitivity as a function of viewing distance. Anodal stimulation did not simply induce a parallel-shift in the linear regression lines describing response sensitivity as a function of the inverse of viewing distance, but also decreased their slopes (Fig. 4; Table 2). In fact, it was both the zero crossing (viewing distance-independent component) and the regression line slope (viewing distance-dependent component) (see Angelaki et al. 2000) that decreased with anodal stimulation. The opposite effects of cathodal labyrinthine stimulation whereby both the zero crossing and slope of the lines increased might represent an effect of functional recruitment, as outlined in the preceding text.

Response dynamics-model simulations

The dynamic properties of the translational VORs have been simulated here using the following transfer function (Fig. 12A)

\[
H(s) = \frac{\text{eye velocity}}{\text{linear velocity}} = sH_v(s)H_{\text{int}}(s)[G_{\text{reg}}H_{\text{REGaff}}(s) + G_{\text{irreg}}H_{\text{IRRaff}}(s)]e^{-t_d/s}
\]

Where \(t_d = 9\) ms is the time delay and \(H_{\text{int}}(s) = s(\tau_\text{int}s + 1)\) (\(\tau_\text{int} = 20\) s) is the neural integrator, whereas \(H_{\text{REGaff}}(s)\) and \(H_{\text{IRRaff}}(s)\) are given in Eq. 1. For the high-frequency data fitted here, the exact value of \(\tau_\text{int}\) is irrelevant and \(H_{\text{int}}(s)\) is only considered for completeness. The \(s\) in the numerator of \(H_{\text{int}}(s)\) is due to the fact that eye velocity rather than eye position has been simulated here. The \(s\) in Eq. 2 relates to the fact that the sensitivity and phase of the data have been expressed as eye velocity/linear velocity and the afferent transfer functions have been expressed relative to linear acceleration.

The following simulations were performed with \(H_v(s) = s(\tau_v + 1), \tau_v = 0.318\) s (corresponding to a frequency of 0.5 Hz), \(G_{\text{reg}} = 0.148\) and \(G_{\text{irreg}} = 0.0148\) (Fig. 12B, C). Anodal

1 Function \(H_v(s)\) consists of an integrator (which can be either neural or contributed by the eye plant) (e.g., Green and Galiana 1998) and a high-pass filter. Even though this simple function cannot accurately describe the phase of the reflex, it has been used here for simplicity (see also Telford et al. 1997). To
and cathodal stimulation was assumed to decrease and increase the irregular afferent contribution by $\frac{1}{2}$ (Fig. 12B, ■ and ▲, respectively). Within the constraints related to the fact that Fig. 12A is only a very rough approximation of the trVOR processing, simulations agree qualitatively with experimental results. Anodal stimulation that is assumed to decrease the contribution of irregular afferents decreases trVOR sensitivity and increases the phase lags. Cathodal stimulation that is assumed to increase the contribution from irregular afferents increases trVOR sensitivity and decreases the phase lags. The simple block diagram summarized in Fig. 12A could predict the viewing distance effects of the currents only if it is assumed that the irregular afferent signals are selectively scaled by the inverse of viewing distance (Fig. 12C). When this scaling was applied to all afferent signals, the simulated effects of the currents were to change the trVOR sensitivity without affecting the slope of the dependence on $1/D$. Because of the crudity of the simplified model of Fig. 12A, no attempt was made to simulate quantitative aspects of the trVORs (e.g., the nonzero sensitivity during viewing at infinity).

It should be added that multiple computational schemes could be implemented to account for the effects of the currents in the viewing distance dependence of the trVORs. The exact details of each plausible scheme would depend fundamentally on how the viewing distance-dependent properties are implemented in the VORs. In the simplified block diagram of Fig. 12A (proposed by Paige and colleagues, e.g., Telford et al. 1997), vergence has been assumed to directly modulate trVOR interneurons based on simple multiplicative interactions. Alternatively the viewing distance-dependent properties could be implemented through distributed networks where the linear scaling of response sensitivity as a function of the inverse of viewing distance emerges as a network property and the neuronal implementation of this scaling is more complex than the simple multiplication scheme. For example, one

---

**FIG. 12.** Simulations of a simplified block diagram for the trVOR. A: layout of the diagram. B: sensitivity and phase simulations as a function of frequency at a viewing distance of 10 cm. C: dependence of sensitivity on the inverse of viewing distance (5 Hz). Parameters are as follows: $r_a = 9 \text{ ms}, G_{\text{reg}} = 0.1485, G_{\text{irreg}} = 0.01485$ (no stm), $H_{\text{in}}(s) = s(0.318s + 1)$ and $H_{\text{out}}(s) = s/(20s + 1)$. For anodal and cathodal current simulations, the gain of the irregular afferent pathway was assumed to change to $0.5G_{\text{irreg}}$ and $2G_{\text{irreg}}$, respectively.
such network could be postulated to modulate the background (mean) firing rates of the constituent neurons as a function of vergence angle. That is, the closer the target and the higher the vergence angle, the larger the firing rates and the larger the number of neurons that are recruited to participate in the tVORs. In fact, such a mechanism could easily be made to account for the nonzero sensitivity during viewing at infinity. According to such a hypothetical scheme, labyrinthine currents would “mimic” larger or lower vergence angles by affecting the background firing rates of the network neurons.

Effects of labyrinthine electrical stimulation on the rotational VOR

Even though there is universal agreement that labyrinthine electrical stimulation has no effect on the midfrequency (~0.5–4 Hz) rotational VOR in darkness, this is not the case for other aspects of the VOR during head rotation. Chen-Huang and McCrea (1998), for example, reported that the small viewing distance dependent increases in the gain of the rotational VOR were abolished during anodal labyrinth stimulation. In addition, Angelaki and Perachio (1993) reported that anodal labyrinthine stimulation seemed to decrease slow phase eye velocity during long duration rotation steps in squirrel monkeys. Similar results to those previously reported in squirrel monkeys also were made here (Fig. 9; Table 4).

It should be noted also that the effects of bilateral labyrinthine electrical stimulation on the rotational VOR have not yet been tested at high frequencies (i.e., >4 Hz). It is possible that the current effects on the rotational VOR parallel those seen in the translational VOR at a corresponding frequency and viewing distance range. Taken together, the present and previous results suggest that labyrinthine electrical stimulation seems to alter specific aspects of the VORs, primarily at low and high frequencies. Even though the details of such a processing await investigation, these behavioral observations do provide some preliminary conclusions regarding the differential role of the vestibular afferent continuum in the sensorimotor transformations of the vestibuloocular system.

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