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# Dynamic Properties of the Human Vestibulo-ocular Reflex During Head Rotations in Roll

SCOTT H. SEIDMAN,*† R. JOHN LEIGH,*‡§¶ ROBERT L. TOMSAK,|| MICHAEL P. GRANT,§ LOUIS F. DELL'OSSO*‡

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**We investigated the dynamic properties of the human vestibulo-ocular reflex (VOR) during roll head rotations in three human subjects using the magnetic search coil technique. In the first of two experiments, we quantify the behavior of the ocular motor plant in the torsional plane. The subject's eye was mechanically displaced into intorsion, extorsion or abduction, and the dynamic course of return of the eye to its resting position was measured. The mean predominant time constants of return were 210 msec from intorsion, 83 msec from extorsion, and 217 msec from abduction, although there was considerable variability of results from different trials and subjects. In the second experiment, we quantify the efficacy of velocity-to-position integration of the vestibular signal. Position-step stimuli were used to test the torsional or horizontal VOR, being applied with subjects heads erect or supine. After a torsional position-step, the eye drifted back to its resting position, but after a horizontal position-step the eye held its new horizontal position. To interpret these responses we used a simple model of the VOR with parameters of the ocular motor plant set to values determined during Expt 1. The time constant of the velocity-to-position neural integrator was smaller (typically 2 sec) in the torsional plane than in the horizontal plane (>20 sec). No disconjugacy of torsional eye movements was observed. Thus, the dynamic properties of the VOR in roll differ significantly from those of the VOR in yaw, reflecting different visual demands placed on this reflex in these two planes.**

Torsional eye movements Neural integrator Vestibulo-ocular reflex

## INTRODUCTION

The vestibulo-ocular reflex (VOR) enables clear vision of the environment during head perturbations by generating eye rotations that largely compensate for head movements. The horizontal VOR has been widely investigated, and it has been possible to quantify the contributions to this reflex by the labyrinthine semicircular canals, the neural pathways, and the mechanical properties of the orbital tissues (reviewed by Robinson, 1981; Wilson & Melvill Jones, 1979). Thus, by studying the relationship between head rotation and the discharge characteristics of vestibular nerve afferents, Fernandez and Goldberg (1971) were able to determine the transfer function of the semicircular canals. Robinson (1964) studied the dynamic course of horizontal eye movements during saccades and isotonic movements, and proposed a transfer function to describe the mechanical properties of the ocular motor plant. Skavenski and Robinson (1973) measured the relationship between abducens motoneurons and vestibular eye movements and applied the aforementioned descriptions of the semicircular canals and ocular motor plant to deduce the contribution that the brain makes to the VOR. They determined that an integration of the head velocity signal emanating from the semicircular canals was necessary in order for the brain to generate the observed vestibular eye movements.

With the development of reliable methods to record torsional eye rotations (Collewijn, van der Steen, Ferman & Jansen, 1985), it has become possible to

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*Department of Biomedical Engineering, Department of Veterans Affairs Medical Center, and University Hospitals, Case Western Reserve University, Cleveland, Ohio, U.S.A.

†Present address: University of Rochester Medical Center, Rochester, NY 14642, U.S.A.

‡Department of Neurology, Department of Veterans Affairs Medical Center, and University Hospitals, Case Western Reserve University, Cleveland, Ohio, U.S.A.

§Department of Neuroscience, Department of Veterans Affairs Medical Center, and University Hospitals, Case Western Reserve University, Cleveland, Ohio, U.S.A.

¶To whom all correspondence should be addressed at: Department of Neurology, University Hospitals, 2074 Abington Road, Cleveland, OH 44106, U.S.A. [*Fax* 1 216 844 3160].

||Department of Ophthalmology, Mount Sinai Medical Center, and University Hospitals, Case Western Reserve University, Cleveland, Ohio, U.S.A.

measure the dynamic properties of the VOR during roll head rotations. Several studies have shown that the properties of the torsional VOR differ from those in the horizontal or vertical planes. For example, the gain of the torsional VOR is only about 50% of the corresponding values for the horizontal and vertical planes (Ferman, Collewijn & van den Berg, 1987a; Seidman & Leigh, 1989; Morrow & Sharpe, 1993). Furthermore, in humans, the torsional VOR lacks the "velocity storage" property that perseverates the horizontal VOR during sustained rotation (Seidman & Leigh, 1989; Cohen, Henn, Raphan & Dennet, 1981). To date, however, no study has attempted to determine the relative contributions of the vestibular organ, brain, and orbital tissues to the dynamic properties of the torsional VOR. Using a similar deductive approach to that applied to the horizontal VOR, we investigated the properties of the torsional VOR with two experiments. In the first experiment, we mechanically displaced the eye in the torsional plane and measured its return to resting position; this enabled us to quantify the dynamic properties of the ocular motor plant for intorsional and extorsional eye rotations. Using this information, and prior descriptions of the vestibular organ, we were able to conduct a second experiment that consisted of measuring the VOR response to position-step stimuli. This allowed us to determine the efficacy of neural integration of vestibular signals in the torsional plane.

To interpret our data, we made use of a mathematical model of the VOR that incorporated transfer functions for the semicircular canals, the central neural pathways, and the ocular motor plant (Fig. 1); this model was adapted from that presented by Robinson (1981), and modified slightly to better describe torsional eye movement. Because velocity storage is absent in the torsional plane (Seidman & Leigh, 1989), and the torsional optokinetic responses are very weak (Collewijn *et al.*, 1985; Morrow & Sharpe, 1993; Cheung & Howard, 1991), we were able to use a simplified description of the vestibular input and to assign published values to its parameters. The results of Expt 1 were used to determine the optimal values of the dominant time constant of the plant for inclusion in the model employed in Expt 2. To describe the brain's contribution to the torsional VOR in this model, we included two pathways: a direct pathway and a neural integrator (Robinson, 1981) (Fig. 1). The results of the position-step experiment were used to estimate the optimal values of parameters of the direct and integrated pathways, especially the parameter of primary interest, the time constant of the velocity-to-position neural integrator. Preliminary results of these experiments have been published as abstracts (Seidman, Tomsak, Grant & Leigh, 1991; Seidman, Leigh, Tomsak, Grant & Dell'Osso, 1994).

## METHODS

Three healthy men, aged 25, 30 and 45 yr served as subjects for both experiments. All three gave informed consent for the experimental procedures which were approved by our Institutional Review Board. Subject 1 was a myope who habitually wore spectacles (*od* − 3.00 D, *os* − 1.75 D), subject 2 was a myope who habitually wore contact lenses (*ou* − 5.00 D) and subject 3 was an emmetrope; no refractive corrections were worn during experiments. No subject was taking any medication.

Torsional, horizontal and vertical movements of each subject's non-dominant eye were recorded using a double-loop scleral search coil (Skalar, Delft, The Netherlands). The 6 ft, earth-fixed field coils (CNC Engineering, Seattle, Wash., U.S.A.) employed a phasic measurement system in the horizontal plane (Collewijn, 1977) and an amplitude system in the torsional and vertical planes (Robinson, 1963). Torsion is defined as absolute rotation about the line of sight, with a positive torsion indicating a clockwise rotation from the point of view of the subject. The search coil was pre-calibrated on

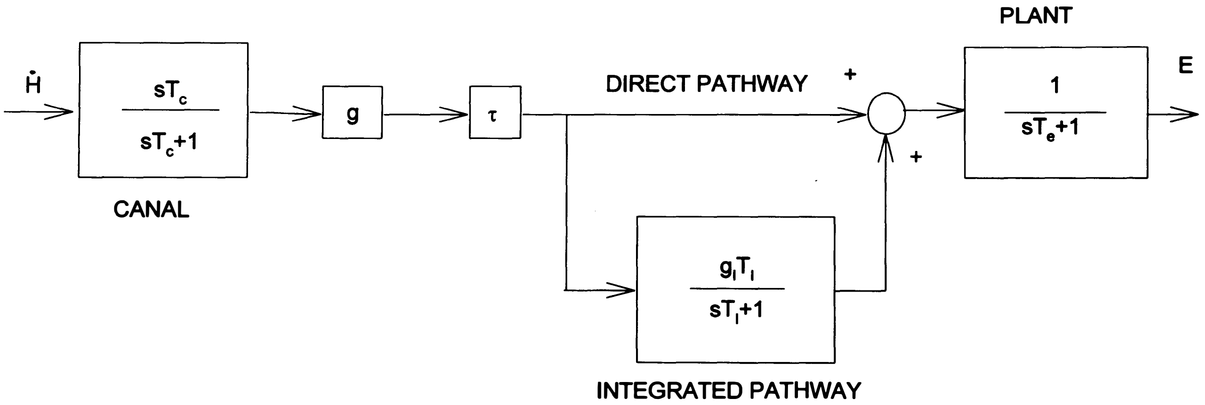

FIGURE 1. A model of the torsional vestibulo-ocular reflex. Model input is head velocity, $\dot{H}$; and output is eye position, E. Head velocity is transduced by the semicircular canals (described as a high-pass filter with time constant $T_c$). The latency of VOR is $\tau$, and its common gain is $g$. The vestibular signal projects to ocular motoneurons (OMN) through two separate pathways: a direct pathway, and an integrated pathway with gain $g_I$. The leaky integrator is approximated by a low-pass filter with time constant $T_I$. Note that as $T_I$ becomes large, the integrator becomes perfect. The signals of the two pathways are summed at OMN, and passed to a one-pole representation of the ocular motor plant. The Laplace operator is denoted by $s$.

protractors prior to placement on the subject's eye. The calibration of the coil system was $>98\%$ linear in all planes over an operating range of $\pm 20$ deg. Cross-talk on the torsional channel from horizontal movements was $<0.025$ degs torsion per deg of horizontal rotation. The eye was anesthetized with topical proparicaine prior to coil insertion. Subjects wore the coil for periods of time that were always less than 30 min.

### *Experiment 1*

The subject viewed a spot of light projected from a laser onto a tangent screen at a distance of approx. 1.3 m with his non-dominant eye. The other eye was occluded with a sheet of white, opaque paper at a distance of about 5 cm. The upper lid was gently retracted and a site on the temporal conjunctiva of the viewing eye was then anesthetized with topical lidocaine. Using ophthalmic forceps, the eye was gently grasped at the anesthetized site, and displaced in the torsional plane, either intorsionally or extorsionally, or abducted in the horizontal plane. The investigator performing these "forced ductions" verbally signaled a successful duction, and data collection began. The eye was then released, and its movement back to resting position was recorded. Periods of forced duction lasted only a few seconds for each trial. We chose this simple procedure because it was safe and comfortable and allowed us to estimate the dominant time constant of the plant sufficiently well for inclusion in the model of Expt 2; nevertheless, we restricted the number of trials during each of at least two sessions for each subject to no more than six, in order to avoid producing conjunctival hemorrhage or discomfort. Coil voltage signals were digitized at 1 kHz following analog filtering at 200 Hz to avoid aliasing. This procedure was conducted twice in each direction for subject 1, and three times in each direction for subjects 2 and 3. A total of six trials had to be discarded because of the presence of blinks or saccades early in the response, but at least two trials in each direction were used for estimation. No evidence of coil slippage on the eye was noted, as indicated by visual inspection and by *post hoc* confirmation of the constancy of resting position between trials.

Using non-linear parameter estimation techniques, data were fit to a one-pole (i.e. one time constant) model of the ocular-motor plant. Although a more complex model containing two time constants might more accurately describe the response, this simple model describes the plant sufficiently well to meet the goals of Expt 2 (see below).

For parameter estimation, we used a commercially available FORTRAN subroutine known as NL2SOL (Dennis, Gay & Welsch, 1981a, b; distributed by IMSL, Sugar Land, Tex.), that has been applied previously to models of the ocular motor system (Huebner, Saidel & Leigh, 1991). This routine is provided with a residual array (i.e. a point-by-point array which shows how the model's prediction differs from the actual data) and a Jacobian matrix (i.e. a matrix of sensitivities, showing how the prediction would change in response to a change in each parameter). It is the task of the estimation routine to minimize the sum-squared of the residual array. This quantity will be referred to as the error function. Using the information provided by the residual array and the Jacobian matrix, the routine modifies the parameter values iterively until they converge (i.e. a change in the parameter values ceases to significantly decrease the error function). In this first experiment, the estimation was simplified because the output variable and sensitivities could be expressed in closed form; thus the residuals and Jacobian matrix could be calculated directly.

Data were prepared for estimation using an interactive software package (ASYST Software Technologies, Rochester, N.Y.). The time of release of the eye from forced duction was determined. We defined resting position to be where the velocity of torsional eye movements first went to zero following the release from forced duction. After preparation in this manner, data were then stored in a file to be analyzed by NL2SOL, which provided estimations for $T_e$, the dominant time constant of the plant. Generally, the first 500 data points (i.e. the first 500 msec of data) were included in the estimation procedure. To help guarantee isotonic conditions, however, all data following blinks and saccades were discarded, and fewer points were used in these cases.

The algorithm usually converged to a final solution within 12 iterations. NL2SOL provides a variance/covariance matrix for each estimation, which is based on the Jacobian matrix. The diagonal elements of this matrix provide an indication of the precision of the estimate for each individual case (Huebner *et al.*, 1991). It should be noted that the precision of the estimation is calculated under the assumption that the model is correct (Meyers, 1990). Therefore, the precision of the estimation is not an indication of goodness of fit.

### *Experiment 2*

Coil linearity was the same as for Expt 1. Rotation of the vestibular chair within the earth-fixed magnetic field caused a minor artifact in the search coil signals, which is most likely due to the pickup of offset position signals as described by Kasper, Hess, and Dieringer (1987). To correct for this artifact, which was linear with chair position, the search coils were mounted on the chair and both were rotated in the magnetic field, referencing the coil signals to true angular chair position signaled by a 12-bit optical encoder mounted within the chair (BEI Motion Systems, Cincinnati, Ohio). By comparing coil output with the chair moving to our chair-fixed calibrations, the artifact was carefully measured prior to each experimental run, and was subsequently removed. Subjects wore the search coil on the same eye that was studied in Expt 1; the other eye was occluded with a patch. They also wore a search coil firmly attached to their foreheads to measure head position. Subjects sat in a vestibular chair with their faces oriented towards the ceiling, as previously described (Seidman & Leigh, 1989).

In this way we minimized otolithic contributions to the overall responses (Morrow & Sharpe, 1993; Seidman & Leigh, 1989). By the use of a plumb line, the eye of the subject containing the search coil was located as close as possible to the center of rotation of the chair. Foam pads were placed to one side of each subject's head to help in centering the eye, as well as behind the subject's back for comfort. The subject's head and body were then firmly fixed to the vestibular chair using restraints. Reid's line (Blanks, Curthoys & Markham, 1975) was always greater than 70 deg from earth horizontal. To minimize the effects of changing "false torsion" due to Listing's eye movements (Ferman, Collewijn, Jansen & van den Berg, 1987b), the tertiary gaze position of the subjects was held close to the axis of rotation of the chair by asking the subjects to view an earth-fixed light-emitting diode, 50 cm above their heads, which blinked with a duration of 2 msec at a frequency of about once per second, thereby minimizing retinal slip information. Prior to the beginning of each experimental run, the subject was slowly stepped to points within $\pm 30$ deg from starting position, and gaze was allowed to come to a final resting position. The eye always returned to a gaze position very near zero, showing that our methodology tended to minimize Listing's eye movements.

Position-step head rotations (range 5–30 deg) were then applied, moving the chair by hand (for safety reasons); stimuli were applied in a non-predictable manner. Position-step stimuli were selected since we were particularly interested in measuring gaze-holding at the end of the head rotation, i.e. maximizing sensitivity to the parameter of primary interest, and in minimizing the effects of saccades. More than 50 such position steps were applied during at least four sessions for each subject. Trials that included saccades were discarded, because saccades may influence neural integration characteristics (Sugie & Melvill Jones, 1971), and so contaminate the results. These discarded trials did not appear qualitatively different from the rest, but were simply not ideal for estimation purposes. For those trials not discarded, the median head perturbation in roll was 7.1 deg (range 4.1–11.1 deg) and median head speed was 24.6 deg/sec (range 17.0–37.5 deg/sec).

As control experiments, the ocular responses to self-generated horizontal (yaw) and torsional (roll) position-step stimuli were studied, as the subjects sat with their heads erect and imagined the location of a target 1.3 m in front of them in a dark room (i.e. no blinking LED). Median yaw rotation was 26.0 deg (range 14–43 deg) with median speed of 145 deg/sec (range 89–211 deg/sec). Motion profiles for self-generated roll were similar to the passive rolls described above. During these experiments with the head erect, subjects 1 and 2 wore scleral search coils on both eyes to measure the conjugacy of the eye movements. Coil voltage signals were sampled at either 1 kHz or 500 Hz, following analog filtering at 40 Hz.

After collection, the stored data were low-pass filtered at 40 Hz using a 99-point Hamming window technique, and then digitally differentiated with a two-point central difference algorithm. Parameter estimation techniques were then used to fit our data to the models shown in Fig. 1, which has six parameters:

| | |
|---|---|
| $g$ | common gain; |
| $\tau$ | VOR latency; |
| $T_c$ | canal constant; |
| $g_I$ | integrator gain; |
| $T_I$ | integrator time constant; |
| $T_e$ | plant time constant. |

Note that $g$ represents an internal gain common to both VOR pathways, and is not the overall gain of the VOR response; the VOR gain is dependent on all the model's parameters.

Certain simplifications were made to facilitate parameter estimation. The VOR latency, $\tau$, was fixed at 8 msec, a minimum value demonstrated for the horizontal VOR by Maas, Huebner, Seidman and Leigh (1989). The cupular time constant, $T_c$, was set at 7.0 sec, as estimated by Cohen *et al.* (1981). $T_e$ was fixed at the average values estimated for each subject during Expt 1. As will be demonstrated, it was necessary to use different values of $T_e$ for each direction of stimulation. For those trials in which head rotation drove the eye to a position of extorsion (intorsion), the time constant found for the return from a position of extorsion (intorsion) was used in the estimations, since this phase of eye movements dominated the response. Dynamic transitions between intorsion and extorsion were not included in this model; our goal was not to produce a model which would produce simulations of torsional eye movements in response to any stimulus, but to model the system sufficiently well to allow precise estimation of certain internal parameters given our particular stimuli. These simplifications leave us with a model in which three parameters ($T_I$, $g$, and $g_I$) are allowed to vary. The position-step stimuli were chosen to enhance sensitivity to $T_I$, since this was our primary interest.

Although the six-parameter model described above was chosen for these estimations, the choice of model did not greatly affect the estimate of $T_I$, the time constant of the neural integrator, despite possible increases or decreases in the error function. In preliminary analyses, we used a different and more complicated model, the pulse-slide-step model described by Robinson, Kapoula and Goldstein (1990); this did not change the estimate of $T_I$ by more than 1 sec, and so does not change our conclusions. Therefore, such an increase in model complexity is not justified, and the six-parameter model was used for all estimations.

For estimations of horizontal position-step data, because of the effects of velocity storage in the horizontal plane, the canal signal is perseverated (Cohen *et al.*, 1981). To account for this effect, the canal time-constant in our model was replaced with the time constant of the decaying eye velocity due to a 60 deg/sec velocity step in the dark. This value was measured to be 25 sec for subject 1, 14.5 sec for subject 2, and 13 sec for subject 3.

While the actual functioning of NL2SOL for Expt 2 did not differ from that during Expt 1, the implementation of the parameter estimation routine was different.

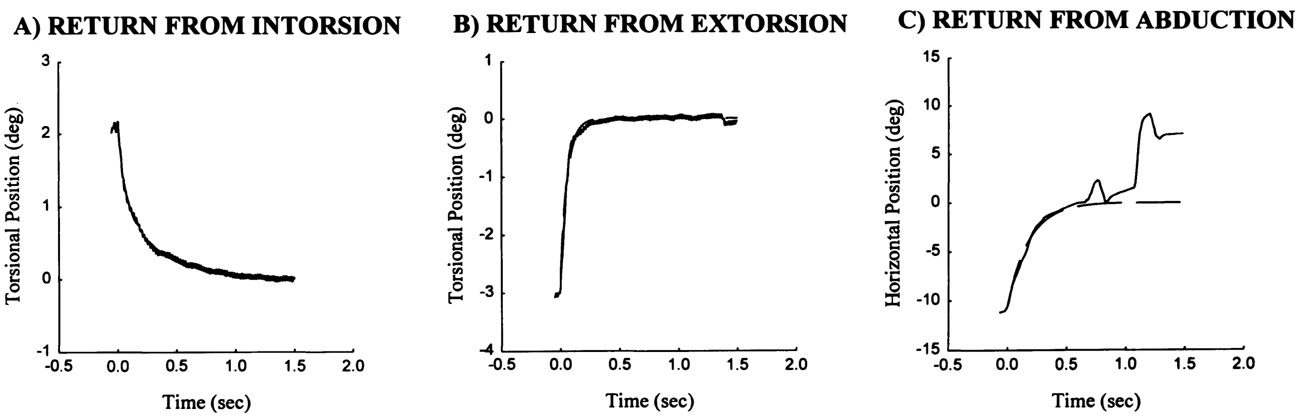

FIGURE 2. Time-course of the return to resting position after the eye was mechanically displaced and then released in subject 3. After the eye was released from intorsion (A) $T_e$ was 323 msec. Following return from extorsion (B), $T_e$ was 58 msec. Following abduction (C), $T_e$ was 183 msec. The solid lines show eye position, while the dashed lines show the fit to the model of Fig. 2. Note that in (A) and (B) the dashed line is almost totally superimposed on the data. The high-frequency sinusoidal oscillation present in the torsional data is noise, which did not influence the estimation process. Note also the two blinks and the saccade near the end of the horizontal record (C). Estimation, in this case, was performed on the data preceding the first blink.

Due to the varying nature of the input (each stimulus was unique) there is no closed-form solution to this model, and the predicted outputs must be calculated by numerically integrating the differential equations describing the system. NL2SOL was provided with an initial guess of parameter values. This guess was passed to ACSL (Mitchell & Gauthier Associates, Concord, Mass.), a numerical simulations package, which used parameter values to calculate eye position, as well as the three sensitivity functions. This information was passed to a file for use by NL2SOL, which used it to update the current parameter values. The process continued until convergence criteria were met.

The coefficient of variation (CV%) was used to assess precision of the estimations of parameter values (Huebner *et al.*, 1991). This is the ratio of the standard deviation of each estimated parameter (taken from the diagonal of the variance/covariance matrix of each estimation) to the estimated value of the parameter. The coefficient of determination, $R^2$, was used to assess goodness-of-fit of individual subject responses by the optimized model. This statistic represents the proportion of variation in the response data that is accounted for by the model (Meyers, 1990).

## RESULTS

### *Experiment 1*

Typical responses after the eye was released from intorsion, extorsion and abduction, from one subject are shown in Fig. 2. Intorsional ductions ranged between 2.4 and 6.4 deg. Extorsional ductions were between 2.8 and 9.2 deg. During intorsional ductions, the eye tended to move vertically upwards as well. These vertical movements ranged between 0.4 and 5.0 deg. Extorsional ductions were accompanied by upwards or downwards vertical movements, ranging between 5.3 deg down and 3.3 deg up. These vertical movements were uncorrelated with estimates of torsional time constants ($R^2 < 0.2$). Individual estimates of the dominant time constant, $T_e$, for the return from forced duction, for each subject, are shown in Table 1. The mean time constant for the return from extorsion was 83 msec, while the mean time constant for a return from intorsion was 210 msec. Although there was considerable variability of values from different trials, the time constants of return from intorsion or extorsion values were significantly different ($P < 0.02$, Wilcoxon rank sum test). The mean time constant from a return from abduction was 217 msec, similar to previous reports (Robinson, 1964). For each individual, the time constant for a return from extorsion was always shorter than the time constant for a return from intorsion. $R^2$ was $>0.99$ for 60% of our estimations, and was below 0.95 for only one estimation. CV% values are shown in Table 1 for each estimation. This value is usually below 3%, and exceeds 15% only once, showing good precision in our estimations.

TABLE 1. Dominant time constant ($T_e$, in sec) of return from forced duction

| Subject | Intorsion | Extorsion | Abduction |
|---|---|---|---|
| 1 | 0.126<br>CV% = 1.9 | 0.095<br>CV% = 2.3 | 0.345<br>CV% = 1.3 |
| | 0.186<br>CV% = 2.3 | 0.0705<br>CV% = 4.4 | |
| 2 | 0.155<br>CV% = 1.6 | 0.081<br>CV% = 12.0 | 0.204<br>CV% = 3.1 |
| | 0.134<br>CV% = 1.1 | 0.086<br>CV% = 43 | 0.180<br>CV% = 3.1 |
| 3 | 0.325<br>CV% = 3.1 | 0.146<br>CV% = 1.6 | 0.183<br>CV% = 1.7 |
| | 0.223<br>CV% = 2.0 | 0.058<br>CV% = 0.8 | |
| | 0.323<br>CV% = 1.9 | 0.041<br>CV% = 2.7 | |

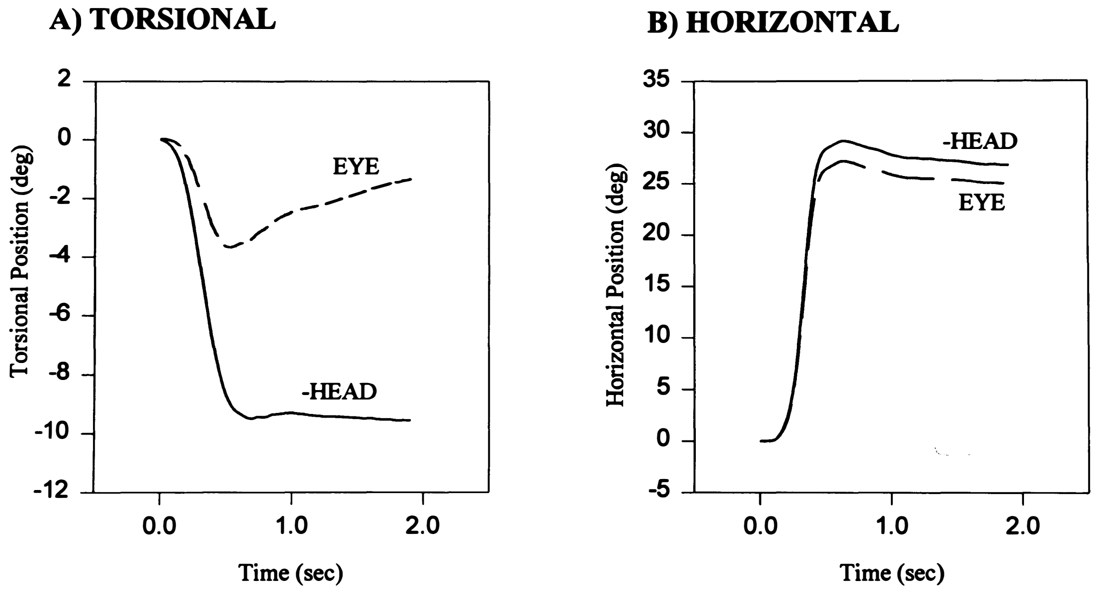

FIGURE 3. Typical responses to position-step stimuli in the torsional (A) and horizontal (B) planes from subject 1. The dashed lines show eye position, and the solid lines show head position, which has been inverted for clarity. Note that, following the horizontal stimulus (B), the eye retains its new eccentric position; in the torsional plane (A), however, the eye drifts rapidly back to its resting position. Note also that the gain of the torsional response is less than that of the horizontal. The positive direction indicates either rightward or clockwise movement from the subject's perspective, which for this particular subject is intorsion of the right eye.

*Experiment 2*

Typical responses to position-step stimuli in the torsional and horizontal planes are shown in Fig. 3; note that head position has been inverted in the figures for clarity of display. It is evident that, following the horizontal stimulus, the eye is held steady at its new eccentric position; in the torsional plane, however, the eye drifts rapidly back to its resting position. The drift of the eyes back to resting position following the roll head movement suggested a deficiency of velocity-to-position integration of vestibular signals. Note also that the overall gain of the torsional response is less than for the horizontal, which is closer to 1.0. These two characteristics—low gain and rapid drift back to the resting position were invariably present in over 150 torsional trials from our three subjects.

When we used those trials which were free of blinks and saccades to estimate the optimal values of the parameters of the model shown in Fig. 1, the time constant of neural integration, $T_I$ was always estimated to be $<5.2$ sec for subjects 1 and 3, and did not exceed 2.0 sec for subject 2 (see Table 2). The coefficient of determination, $R^2$, was always $>0.85$, and was $>0.98$ for more than 50% of all estimations, indicating that our model was well able to describe the data.

Median CV%, as well as the range of CV%s, are shown in Table 2 for each subject; medians and ranges are used because of the non-normal distributions. For subjects 1 and 2, CV% on the estimates of $T_I$, were always 2% or less, indicating precise estimations. For subject 3, CV%s of this parameter were $<10\%$ for extorsional trails. For the intorsional trial of subject three, $T_I$ was always estimated to be $<0.25$ sec. Because of these low values, these estimates are not as precise as in the other subjects, and CV% values were high. Note, however, that in subject 1, whose $T_I$ was estimated to be the greatest, CV%s of $g$ and $g_I$ were always under 2%.

The absence of drift of the eyes back to resting position after the horizontal head rotations suggested near-perfect integration of vestibular signals. When we estimated the optimal values of parameters for our model of the horizontal VOR (Table 2), $T_I$ was always estimated to be $>199$ sec, close to the maximum value allowed by our estimation. Note that because we used 1.5 sec epochs of eye movement data for parameter estimation purposes, a long $T_I$ (e.g. $>20$ sec) would appear infinite to our method of estimation; however, the estimated values of $T_I$ in the torsional and horizontal planes showed no overlap. For all parameters other than $T_I$ CV% were under 2% for all horizontal estimations. CV%s of $T_I$ were larger, reflecting low sensitivity at large values of this parameter.

Figure 4(A) shows a comparison of a typical response of the torsional VOR from subject 1 (same response as shown in Fig. 4) and the corresponding simulation of the response by the model (shown in Fig. 1), using optimal parameters for this subject. Head position is not shown for clarity of display. Figure 4(B) shows corresponding information for the horizontal VOR.

We also measured the torsional VOR with the head erect. The dynamic characteristics of these responses were similar to those with the head supine, consistent with reports from other laboratories (Fischer, Fetter, Tweed, Misslisch & Koenig, 1992; Morrow & Sharpe, 1993). One qualitative difference of these responses from those with the head supine, was the presence of a tonic ocular counter-roll component that had a gain typically of 0.25 or less (Collewijn *et al.*, 1985; Ott, 1992). Accordingly, we did not attempt to estimate the values of parameters using these data, since our model does not attempt to account for tonic counterrolling. We did, however, examine the responses of subjects 1 and 2, who wore scleral search coils on both eyes for these experiments, for conjugacy of eye movements in the torsional plane in response to roll movements with the head erect. We found a high degree of conjugacy of the torsional eye movements in both subjects; an example of conjugacy during ocular counterrolling (ear-to-shoulder head roll, beginning with head erect) is shown in Fig. 5.

## DISCUSSION

We have shown that the dynamic properties of the torsional VOR, tested using position-step head rotations, differ considerably from those of the horizontal VOR. We have attempted to determine how much of this difference is due to the influences of the ocular motor plant and how much can be attributed to the brain. Our first experiment was to compare the time–course of return of the eye to its resting position after it was mechanically displaced and then suddenly released from intorsion, extorsion or abduction. We found that return of the eye after it was released from extorsion was much shorter than after release from intorsion or abduction. Although this result was statistically significant, our results show considerable variability (Table 1); safety considerations limited the number of forced-duction trials that we could carry out. Since we made sure that the search coils were adherent to the conjunctiva our subjects' eyes, this variability might be due to movement of the conjunctiva (induced by the ophthalmic forceps) on the underlying sclera; note that the conjunctiva is tightly fixed to the sclera only at the limbus. Further human or animal studies that avoid such a possible source of error are needed to confirm our results.

If our finding of asymmetry of the time–course of return from forced intorsion and extorsion is correct, then what might be the explanation? One possible factor

TABLE 2. Torsional and horizontal VOR model parameters

| Subject | | | $g$ | $T_I$ (in sec) | $g_I$ | $T_e$ (in sec, fixed) |
|---|---|---|---|---|---|---|
| *Torsional VOR model parameters* | | | | | | |
| 1 | Extorsion | Mean | 0.041 | 3.66 | 11.39 | 0.083 |
| | ($n = 5$) | SD | 0.0049 | 1.10 | 1.20 | |
| | | CV% median | 0.54% | 0.77% | 0.65% | |
| | | CV% range | 0.31–0.62% | 0.47–1.49% | 0.37–0.78% | |
| | Intorsion | Mean | 0.076 | 2.12 | 5.56 | 0.156 |
| | ($n = 5$) | SD | 0.0062 | 0.59 | 0.66 | |
| | | CV% median | 0.68% | 1.5% | 1.1% | |
| | | CV% range | 0.45–0.97% | 1.06–1.65% | 0.70–1.48% | |
| 2 | Extorsion | Mean | 0.012 | 0.78 | 97.65 | 0.084 |
| | ($n = 8$) | SD | 0.0074 | 0.21 | 124.4 | |
| | | CV% median | 4.1% | 0.097% | 5.8% | |
| | | CV% range | 2.1–49% | 0.69–1.8% | 2.3–50.1% | |
| | Intorsion | Mean | 0.059 | 1.41 | 6.03 | 0.144 |
| | ($n = 5$) | SD | 0.022 | 0.65 | 3.96 | |
| | | CV% median | 0.81% | 1.7% | 1.4% | |
| | | CV% range | 0.61–2.6% | 1.4–7.7% | 1.2–4.1% | |
| 3 | Extorsion | Mean | 0.019 | 0.58 | 22.56 | 0.081 |
| | ($n = 5$) | SD | 0.012 | 0.37 | 33.76 | |
| | | CV% median | 4.1% | 6.7% | 8.8% | |
| | | CV% range | 1.7–23.4% | 1.7–8.5% | 5.1–24.1% | |
| | Intorsion | Mean | 0.073 | 0.11 | 1.14 | 0.290 |
| | ($n = 3$) | SD | 0.015 | 0.095 | 1.53 | |
| | | CV% median | 6.5% | >500% | >500% | |
| | | CV% range | 3.0–>500% | 6.2–>500% | 11.5–>500% | |
| *Horizontal VOR model parameters* | | | | | | |
| 1 | ($n = 8$) | Mean | 0.35 | 198.65 | 0.11 | 0.345 |
| | | SD | 0.055 | 3.01 | 0.11 | |
| | | CV% median | 0.32% | 69.1% | 0.43% | |
| | | CV% range | 0.19–0.77% | 52.4–>500% | 0.33–1.44% | |
| 2 | ($n = 10$) | Mean | 0.19 | 199.57 | 5.80 | 0.192 |
| | | SD | 0.0099 | 0.44 | 0.29 | |
| | | CV% median | 0.44% | 74.8% | 0.65% | |
| | | CV% range | 0.03–1.2% | 34.1–145% | 0.32–1.53% | |
| 3 | ($n = 4$) | Mean | 0.18 | 199.76 | 5.26 | 0.183 |
| | | SD | 0.0083 | 0.083 | 0.53 | |
| | | CV% median | 0.47% | 76.8% | 0.68% | |
| | | CV% range | 0.23–0.77% | 40.0–104% | 0.35–1.05% | |

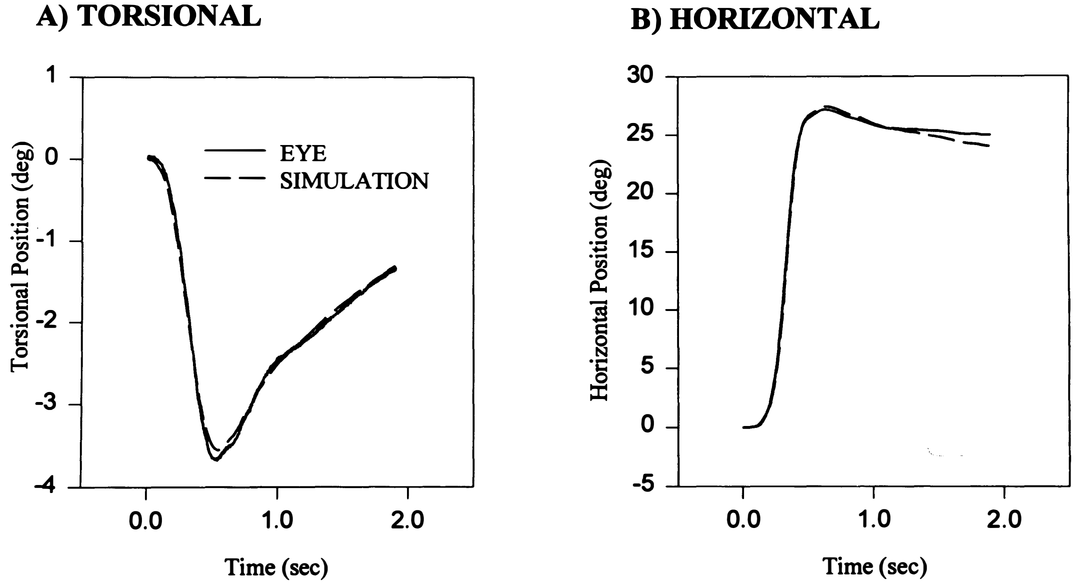

FIGURE 4. (A) Comparison of a typical response of the torsional VOR from subject 1 [same response as shown in Fig. 3(A)] and the corresponding simulation of the response by the model shown in Fig. 1, using optimal parameters for this subject. Head position is not shown for clarity of display. (B) Simulation for horizontal VOR in the same subject [same response as shown in Fig. 3(B)]. Solid lines show the actual response, and the dashed line shows the optimized model's simulated data.

concerns the unique course of the superior oblique tendon through the trochlea, resulting in stiffer properties than those of the inferior oblique or medial rectus muscles. Whatever the explanation, this finding raises the question of whether the brain compensates for any asymmetry of the torsional properties of the ocular motor plant during vestibular eye movements. When we examined the torsional eye movements of two of our subjects for conjugacy, the responses were indeed conjugate (Fig. 5). When we used the model of Fig. 1 to predict the response to head roll, holding values of brain parameters constant, we found that changing the value of the plant time constant $T_e$ from 82 to 210 msec, without re-optimizing the remaining parameter values of the model being used, substantially affected the conjugacy of the response (Fig. 6). Two explanations seem possible. Either the brain programmed vestibular eye movements differently for each eye, taking into account the asymmetrical properties of the orbit, or the movements of the eyes after the release from forced duction during Expt 1 did not provide an accurate description of the contribution of the ocular motor plant during active movements. Previous estimates of $T_e$ for horizontal movements from mechanical displacement experiments (Robinson, 1964) have correlated well with estimates based on electrophysiological studies (Fuchs, Scudder & Kaneko, 1988). However, as discussed above, we cannot exclude slippage of the conjuntiva (and search coil) on the sclera as a source of error. Nonetheless, our simulations show that the model was able to produce conjugate eye movements by assigning appropriate optimal values (i.e. re-optimizing the model) to the two neural pathways for each value of $T_e$ (see Fig. 6). Thus, conjugate torsional eye movements could be produced by this simple model, despite any asymmetry observed in the plant. This model behavior was reflected by the gain of the integration pathway, $g_I$, being estimated to be larger for extorsional trials than for corresponding intorsional trials in all three subjects, along with a corresponding change in $T_I$, perhaps indicating an attempt by the nervous system to yoke the eyes. If the measured

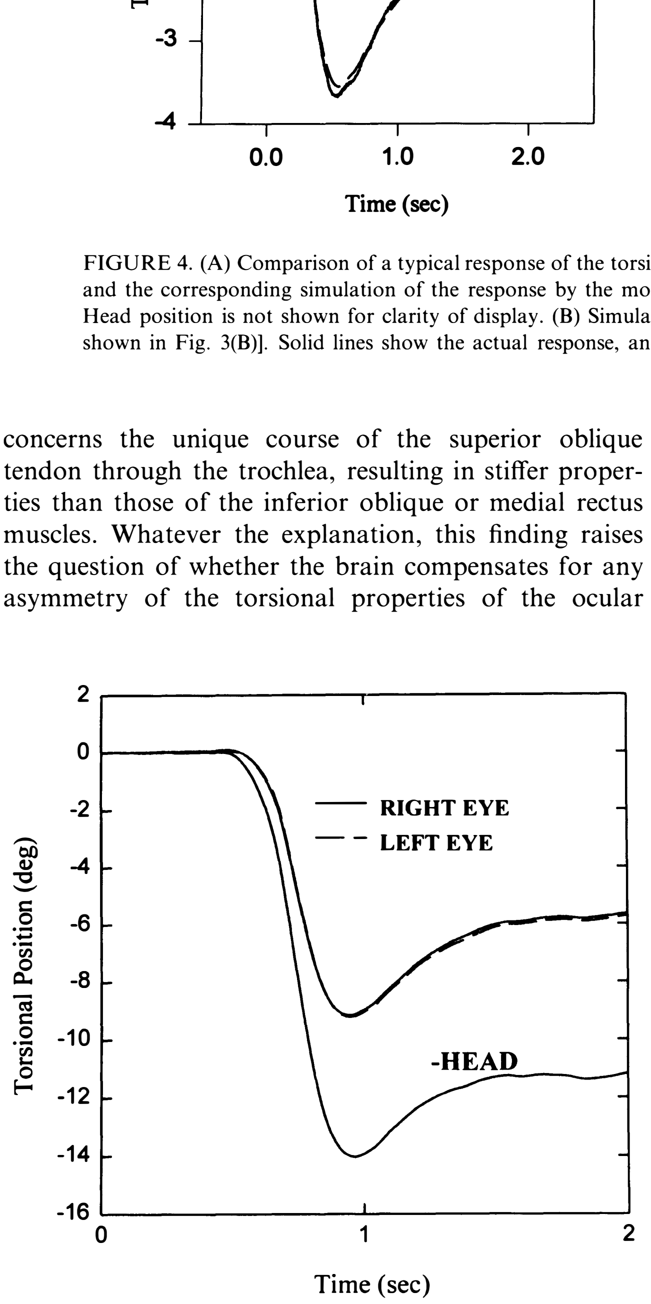

FIGURE 5. Demonstration of conjugacy of eye movements in the torsional plane. Torsional movements of both eyes and the head were recorded while the subject actively rolled his head in an ear-to-shoulder fashion, starting from the upright position. The response was conjugate. In addition, note that the data are similar to that occurring with the face supine [Fig. 4(A)], with the exception of a static ocular counterroll component present in this trial. Note that head position is inverted for clarity.

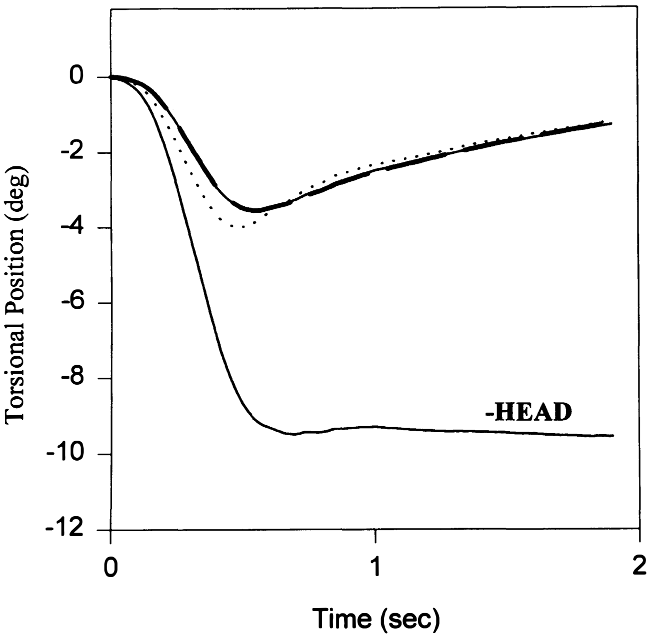

FIGURE 6. Simulated eye movements demonstrating the ability of our model to produce conjugate eye movements in the torsional plane despite asymmetries in the plant. Torsional head position (inverted for clarity) was recorded during an actual trial, and optimizations were performed to find parameters which would enable our model to reproduce the actual eye movements which were elicited. The solid line shows the simulated eye movements after the model had been optimized for $T_e = 156$ msec The dotted line shows the simulation after $T_e$ has been changed to 83 msec, with no re-optimization (i.e. other parameters remaining the same), resulting in a simulated movement that is disconjugate compared to the first simulation. The dashed line shows a third simulation following re-optimization of all parameters with $T_e = 83$ msec. This simulation produces eye movements which are conjugate to the first simulation, demonstrating how the model is capable of simulating conjugate eye movements even if plant asymmetries are large. $R^2$ was $>0.99$ for both optimizations, indicating a good fit of the model to the data.

plant asymmetries are, in fact, corrected by neural integration, this suggests independent integrator control for each extra-ocular muscle.

The finding of our second experiment was that the integration of the vestibular signal (head velocity) by the brain was much less complete for torsional than for horizontal eye movements. Specifically, the time constant of the torsional neural integrator was typically 2 sec, compared with a much larger time constant for the horizontal system. This finding holds true even if the asymmetry seen in plant behavior is an artifact of our methodology; a 100% change in the value assigned for the plant time constant causes a change of <2% in the time constant of integration. The reader can confirm this lack of gaze holding by observing in a mirror the torsional rotations that follow a position-step ear-to-shoulder roll of the head (most easily detected by observing the movement of a conjunctival vessel): initially the eye counterrolls, but then it promptly returns to its resting position. Note that this return of the eye occurs even during visual fixation. In contrast, a horizontal head rotation leads to a sustained deviation of the eye in the orbit; in this study, we show that this is the case even in darkness. Because we only measured gaze for 1.5 sec after the position step, we could not estimate $T_I$ in the horizontal plane with precision; thus all our estimates on horizontal position steps show time constants near 199.9 sec (the upper limit of the permitted range) for the integrator. Note that when $T_I$ becomes large, variation of this parameter affects the output progressively less (i.e. there is low sensitivity to this parameter). Therefore, our data are consistent with published values for neural integrator leak in the horizontal plane, which indicate a time constant of >20 sec (Becker & Klein, 1973; Robinson, Zee, Hain, Holmes & Rosenberg, 1984).

Recently, Crawford, Cadera and Vilis (1991) reported that stimulation of the interstitial nucleus of Cajal in rhesus monkeys causes vertical-torsional eye movements and that pharmacological inactivation of this nucleus apparently caused impairment of the torsional integrator. In this study, the investigators used saccades to tertiary orbital positions to generate tonic changes in ocular torsion. Thus, the deficiency in torsional gaze holding might have reflected the monkey's inability to hold a sustained tertiary eye position (due to centripetal drift of the eye in the vertical plane). Unfortunately, these investigators did not assess the neural integrator for torsional eye movements using vestibular stimuli. Preliminary data from another laboratory (D. Straumann & Quing Yue, personal communication, 1992) suggest incomplete integration of torsional eye velocity in rhesus monkeys, when evaluated with position-step stimuli. Caution is required, however, in comparing torsional eye movements of monkeys with humans. For example, the gain and velocity storage properties of the torsional optokinetic responses are well developed in rhesus monkeys (Schiff, Cohen & Raphan, 1986) but not in humans (Collewijn *et al.*, 1985; Morrow & Sharpe, 1993; Cheung & Howard, 1991).

Why should the brain's contribution to the torsional VOR differ so much from that in the horizontal plane? In order to account for the unique properties of the torsional VOR, it is pertinent to recall that the purpose of vestibular eye movements is to maintain clear and stable vision during head movements. In the horizontal and vertical planes, this is achieved by generating eye movements that largely compensate for head movements, thereby holding images of the surroundings fairly stable on the retina, and the image of an object of interest close to the fovea. However, in the torsional plane, the situation differs. It is not clear that perfect compensatory eye movements are necessary in this plane. Consider, for example, the consequences of absent torsional eye movements during head movements in roll. Torsional eye movements are not used to hold images steady on the fovea. This can best be conceptualized by the simple analogy of a point of light falling on the exact center of a large circle. Torsional movements of this circle will not displace the light from the center. Although retinal slip is induced by torsional eye movements while viewing non-point targets, the targets are still not displaced from the fovea. For this reason, smooth pursuit in the torsional plane is a meaningless concept (Robinson, 1982). Following the same reasoning, retinal slip caused by poor control of torsional eye movements is maximal in the periphery of the visual field (Enright, 1990), where photoreceptor density is low. Objects that fall in the periphery are not what our attention is directed to, suggesting that this type of retinal slip is well tolerated by perceptual mechanisms, and does not degrade vision during natural activity. Thus, from a visual standpoint, a modest VOR is probably all that is required to lessen image slip in the periphery and maintain visual acuity. Indeed, perceptual mechanisms involved in the processing of visual information appear to be better suited for handling torsional disturbances than corresponding horizontal and vertical mechanisms. For example, the stability of torsional gaze, though much less constant than horizontal or vertical gaze (Ferman *et al.*, 1987a; Ott, Seidman & Leigh, 1992) does not appear to impair visual acuity or perception. When these factors are taken into consideration, it seems unreasonable to expect that the properties of the torsional VOR would be the same as those of the horizontal VOR.

In the present study, we chose to use position-step stimuli in order to deduce the properties of the neural integrator. One reason for this choice was that we wanted to avoid quick-phases of nystagmus that have the effect of "resetting" a deficient neural integrator (Skavenski & Robinson, 1973; Sugie & Melvill Jones, 1971). To our knowledge, position-step stimuli have not been used before to test the torsional VOR, although Bello, Paige, and Highstein (1991) have studied the dynamic properties of the torsional VOR of the squirrel monkey using sinusoidal stimuli. They found smaller phase shifts at low frequencies than our data would predict; this discrepancy, however, may be due to the presence of many saccades during low-frequency stimulation, and the small range of torsional eye movements in this species.

In conclusion, the human VOR during roll head rotations shows different properties from horizontal systems that imply simpler neural processing of vestibular signals. One reason that the VOR has been so extensively studied is that it is a simple reflex capable of motor learning. The unique properties of the VOR is the torsional plane, and the special visual demands that they serve, may provide an opportunity for studying a special case of the same reflex with considerably different characteristics.

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