

Eye-position dependence of torsional velocity during interaural translation, horizontal pursuit, and yaw-axis rotation in humans [☆]

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Abstract

The translational vestibulo-ocular reflex (tVOR) stabilizes an image on the fovea during linear movements of the head. It has been suggested that the tVOR may share pathways with the pursuit system. We asked whether the tVOR and pursuit would be similar in their behavior relative to Listing's Law. We compared torsional eye velocity as a function of vertical orbital position during interaural translation, pursuit, and yaw-axis rotation. We found that the eye-position-dependence of torsion was similar during translation and pursuit, which differed from that during yaw-axis rotation. These findings further support a close relationship between the mechanisms that generate pursuit and the tVOR.

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1. Introduction

In the natural environment, visual and vestibular mechanisms work together to compensate for both head and object motion in order to maintain gaze stability. Head movements are compensated by the rotational (rVOR) and translational (tVOR) vestibulo-ocular reflexes. Whereas much of the neural circuitry underlying the rVOR has been described, less is known of the central pathways responsible for the tVOR. Due to similarities in their functions (stabilizing on the fovea of both eyes the images of an object of interest located at a

particular distance, while allowing background slip) and corresponding pursuit and tVOR deficits in patients with cerebellar disease (Baloh, Yue, & Demer, 1995; Wiest, Tian, Baloh, Crane, & Demer, 2001a, 2001b), one might hypothesize a relationship between the pathways of the pursuit system and the tVOR.

One distinguishing characteristic of different types of eye movements is their behavior with respect to Listing's Law (LL). For Listing's Law to hold during an eye movement, the axis (direction) of the angular velocity vector (the axis is calculated as the arctangent of the ratio of torsional to horizontal or vertical velocity) must vary by one-half the change in orbital position in the direction orthogonal to eye motion (Tweed & Vilis, 1990). This is known as the *half-angle rule* (see Fig. 2C and legend). For example, for horizontal eye movements, one can compare the angular velocity axis of the eye at different vertical positions in the orbit. The amount of ocular torsion approximates that predicted by Listing's Law during pursuit (Tweed, Fetter, Andreadaki, Koenig, & Dichgans, 1992) and saccades

[☆] For this paper, we use a head-fixed coordinate system. Thus, torsion refers to a rotation of the eye about an axis protruding forward from the head. Only when looking straight ahead does this correspond to a rotation about the line of sight.

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(Tweed & Vilis, 1990). During head rotation and optokinetic stimulation, when torsion would cause undesired retinal slip, there is less torsion, and LL is not obeyed (Fetter, Tweed, Misslisch, & Koenig, 1994; Misslisch & Hess, 2000; Misslisch, Tweed, Fetter, Sievering, & Koenig, 1994; Palla, Straumann, & Obzina, 1999; Thurtell, Black, Halmagyi, Curthoys, & Aw, 1999).

In the present study, we asked whether the relationship of torsional velocity to vertical orbital position during the tVOR more closely resembles that of pursuit or that of the rVOR. In other words, is the behavior of the tVOR with respect to Listing's Law more like that of pursuit or of the rVOR? If the tVOR and pursuit share brainstem neural circuitry, it is possible that they would have similar torsional behavior. Moreover, this question has additional importance, as torsional velocity during interaural translation has been used as a marker of the misinterpretation of interaural translation (for which the compensatory eye movement is horizontal) as compared to tilt relative to gravity (for which the compensatory eye movement is torsional) (Angelaki, Wei, & Merfeld, 2001; Merfeld & Zupan, 2002; Paige & Seidman, 1999). Preliminary results from these data were presented in abstract form (Walker, Zee, Shelhamer, Roberts, & Lasker, 2000).

2. Methods

Four normal subjects (two men and two women, ages 21–55) without neurologic or vestibular disease participated in this study. Before participating, all subjects gave written consent, under a protocol approved by the Johns Hopkins Medicine Institutional Review Boards, in accordance with the Declaration of Helsinki.

2.1. Experimental apparatus and recording techniques

For stimulation of translational responses, subjects were seated in a chair supported by air bearings, which was moved by a series of induction motors along a linear track. During motion, the head was held in position using a bite bar made of dental impression material and secured with padded blocks pressed tightly against both sides of the head. Pursuit was measured during the same experimental session as translation, with the subject stationary. The head was held in the same position for translation and for pursuit. The pursuit target was a red laser (subtending 0.2° at 100 cm distance), back-projected onto a tangent screen and moved horizontally and vertically by computer-controlled mirror galvanometers. In a separate session on a second day, subjects were rotated about the earth-vertical (yaw) axis with the head fixed in a rotary chair with a similar mirror-driven laser target.

Subjects in all experiments wore dual scleral search coils in both eyes (Skalar, Delft, the Netherlands). The subject was seated with the head upright and the nasal bridge centered within a cubic coil frame that generated three orthogonal magnetic fields of different frequencies. The signals from each coil were separated by frequency detectors, filtered (90 Hz Butterworth low-pass), digitized (500 Hz), and stored for later offline analysis.

2.2. Paradigms

Experimental paradigms consisted of sinusoidal interaural translations, yaw-axis rotations, and foveal pursuit. In all but one subject, responses to each stimulus were tested at three different frequencies: 0.2, 0.45, and 0.7 Hz. One subject could only be tested at 0.2 and 0.7 Hz. At 0.7 Hz only, tVOR and pursuit were tested at target distances of 43 and 100 cm in all subjects; all subjects but one were also tested at 200 cm. The peak linear acceleration during translation was approximately 0.06 g at 0.2 Hz, 0.33 g at 0.45 Hz, and 0.39 g at 0.7 Hz. The amplitudes of pursuit were chosen so that the eye trajectory would match that of the ideal response to the translational stimulus at the same frequency and target distance. The amplitude of rotation for rVOR stimulation was $\pm 10^\circ$.

To determine the effects of orbital position on the eye velocity axis, three vertical target positions (0° and $\pm 20^\circ$; 0° and $\pm 10^\circ$ for 0.7 Hz rVOR) were used. For translation, periods during which the target was always on were alternated with periods during which the target was flashing (20 ms duration every 1–10 s, depending on stimulus frequency, to provide a reference point for fixation without inducing retinal slip). Finally, at 0.7 Hz, subjects were also translated in darkness without the flashing target, to determine if the presence of the flashing target influenced the response. In three subjects, only an initial reference target was given each time the vertical position was changed. In the fourth subject, no target was present during the entire recording (verbal cues were given for vertical position).

2.3. Analysis

Data analysis was performed using MATLAB™ (The Mathworks, Natick, MA). First, raw coil signals were converted to rotation vectors (Straumann, Zee, Solomon, Lasker, & Roberts, 1995). An interactive program was used to select slow-phase segments for analysis, excluding quick phases, blinks, and other artifacts. After digital filtering (15 Hz) of the rotation vector data, angular velocity vectors in head-fixed coordinates, relative to the axes of the coil frame, were calculated with the following equation (Hepp, 1990):

$$\vec{\omega} = 2 \cdot \frac{\frac{d\vec{r}}{dt} + \vec{r} \times \frac{d\vec{r}}{dt}}{1 + |\vec{r}|^2} \quad (1)$$

where $\vec{\omega}$ is the angular velocity vector, \vec{r} is the rotation vector representing eye orientation, and $d\vec{r}/dt$ is the coordinate velocity vector (component-wise derivative of the rotation vector).

A cycle-by-cycle sinusoidal fitting method was performed, using data from selected slow-phase segments. Using a cross-correlation technique, these signals were multiplied by a reference sine and cosine at the known stimulus frequency (the frequency was not a parameter of the fits) to determine the amplitude and phase of each cycle, according to the following equations (Merfeld, Christie, & Young, 1994):

$$x = \int_0^T \sin(2\pi ft) \cdot \omega_x(t) dt \quad (2)$$

$$y = \int_0^T \cos(2\pi ft) \cdot \omega_x(t) dt \quad (3)$$

$$a = 2 \cdot \sqrt{x^2 + y^2} \quad (4)$$

$$\phi = \tan^{-1}(y/x) \quad (5)$$

where a is the amplitude and ϕ is the phase of the fitted sine, f is the stimulus frequency, T is the period ($1/f$), and ω_x is the horizontal component of angular eye velocity.

The gain was calculated as the ratio of the cycle-by-cycle horizontal eye velocity amplitudes to the chair (rVOR) or target (pursuit) velocity. For the tVOR, the “ideal” peak eye velocity for the given chair velocity and target distance was determined, and the gain was then calculated as the ratio of actual to ideal peak horizontal eye velocity. A limitation of this method is that some cycles have more data than others, based on what fraction of the cycle was excluded (for saccades, blinks, etc.). For the analysis, we used only cycles for which less than half of the data points were excluded. The average number of cycles used for analysis was 40 (range 18–76).

To determine the angular velocity axes, we calculated the ratio of torsional to horizontal eye velocity for each cycle, as determined by the same fitting technique, with the appropriate sign for the relative phase. The arctangent of this ratio is the *tilt angle*, the angle in the torsional–horizontal plane by which the eye velocity vector deviates, or tilts, from the purely horizontal axis of the stimulus. A linear regression of these tilt angles was performed with respect to the mean vertical eye position of each cycle to determine the *tilt angle slope* and the *tilt angle intercept*. Statistical comparisons of slopes and intercepts among the three groups (tVOR, rVOR, and pursuit) were performed using a one-way ANOVA, and the Bonferroni method was used to perform multiple comparisons of the groups ($\alpha = 0.05$).

All eye positions and velocities are given in head-fixed coordinates, according to the right-hand rule: positive velocities are leftward, downward, and clockwise, from the subject’s perspective. Thus, a positive tilt angle corresponds to a clockwise torsion during a leftward slow phase or a counterclockwise torsion during a rightward slow phase.

3. Results

The response gains for the tVOR, pursuit, and the rVOR are shown in Fig. 1, as a function of stimulus frequency. The tVOR gain was calculated as the ratio of the actual eye velocity amplitude to the ideal amplitude for the stimulus and target distance. Note the low tVOR gains.

3.1. Tilt angle slopes

Fig. 2 shows representative responses from one of our subjects. Fig. 2A illustrates the dependence of torsional eye velocity on vertical eye position during interaural translation. The torsional component of eye velocity is greatest when the subject is looking down, and there is a reversal of torsional phase between up and down positions. For the same subject, the eye velocity axis or *tilt angle* (in the torsional–horizontal plane) of the tVOR is plotted for each cycle as a function of vertical orbital position, along with a line representing the result of a least-squares linear regression (Fig. 2B). The slope of this line (0.61) is the *tilt angle slope*, a measure of the variation of the eye velocity axis as a function of vertical orbital position. For comparison, regression lines for pursuit and the rVOR are shown for the same subject.

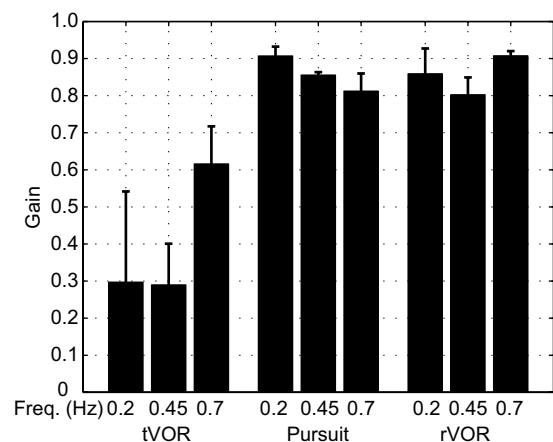


Fig. 1. Gains (horizontal eye velocity/stimulus velocity for pursuit and rVOR; horizontal eye velocity/ideal eye velocity for tVOR, see text) for each stimulus and frequency (all data shown as mean with 95% CI). tVOR and rVOR were measured when the subject was viewing a flashed target.

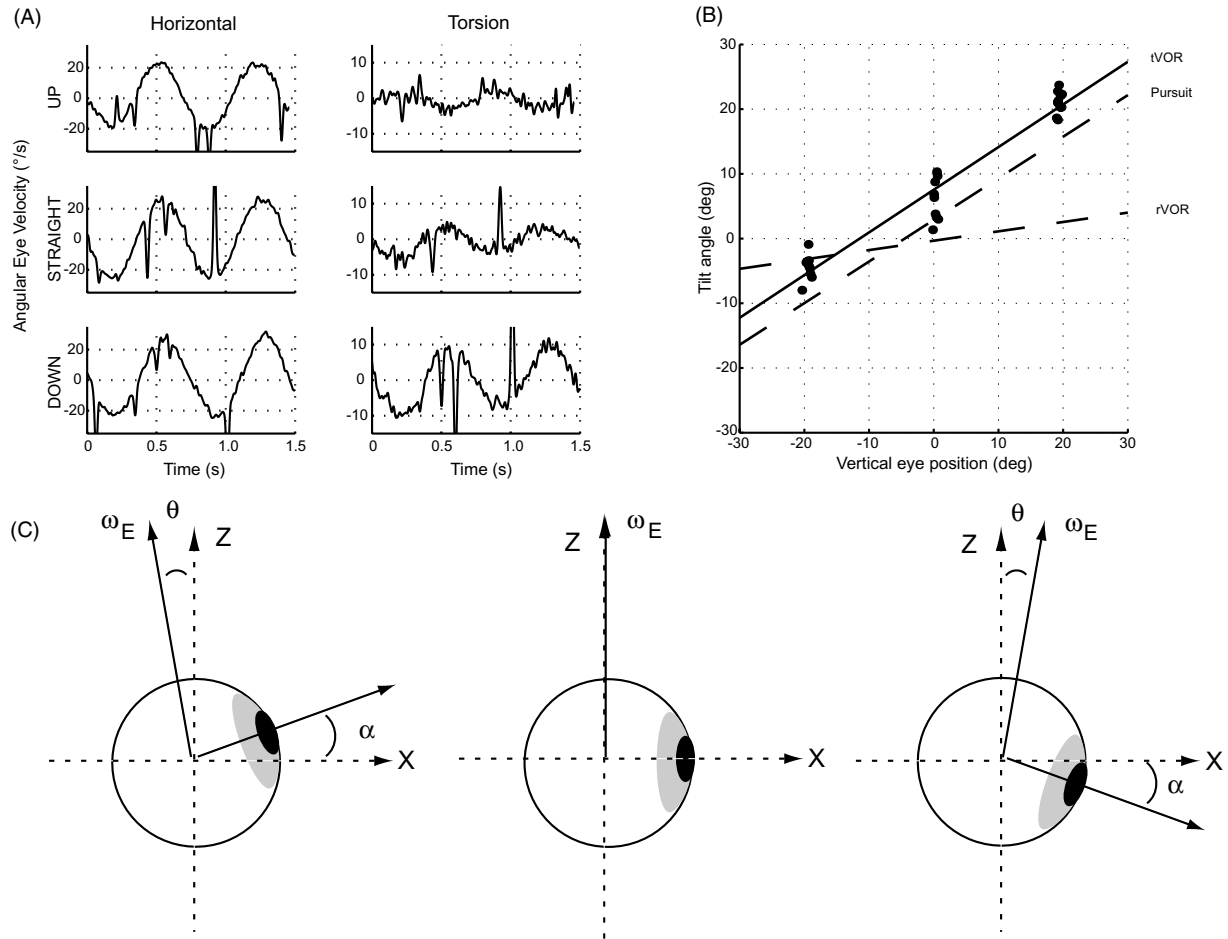


Fig. 2. Example of tVOR (0.7 Hz) in one subject. (A) Horizontal (left panels) and torsional (right panels) eye velocities at three vertical eye positions (straight ahead, up and down 20°). (B) Tilt angle for each cycle as a function of mean vertical eye position for that cycle. The solid line shows the result of a least-squares linear regression for these data. The slope is 0.66 (*tilt angle slope*) and the intercept is 7.6° (*tilt angle intercept*). For comparison, the regression lines for the same subject for both pursuit and the rVOR (also 0.7 Hz, 100 cm distance) are superimposed on the same plot (individual data points not shown). This illustrates that pursuit and the tVOR have similar slopes but different intercepts, whereas the slope for the rVOR is much lower. (C) Cartoon illustrating the variation of eye velocity axis with vertical orbital position. When the eye is looking straight ahead (center panel), the angular velocity of the eye is purely horizontal (according to the right-hand-rule, this would be a leftward velocity, since it is positive). When the eye looks down (left panel) by 20°, the eye velocity axis tilts forward by 10°, corresponding to a combination of leftward horizontal and clockwise (CW) torsional velocities. Similarly, when the eye looks up 20° (right panel), the eye velocity axis tilts backward by 10°, combining counterclockwise (CCW) torsion with leftward velocity. This is the same pattern as seen in (A), in which leftward eye velocity is associated with CCW torsion when the eye is looking up and CW torsion when the eye is looking down. In this example, the tilt angle slope would be 0.5 (20° difference in eye velocity axis/40° difference in vertical eye position). This corresponds to the *half-angle rule*, the prediction of Listing's Law. The tilt angle intercept is zero (torsional velocity is zero at zero vertical eye position).

The tilt angle slopes for all subjects and stimuli (translation, pursuit, rotation) are shown in Fig. 3. There was a highly significant difference among the means of the three stimulus conditions ($p < 10^{-9}$, one-way ANOVA combining data from all three frequencies). The means for tVOR and pursuit were each significantly different from that for the rVOR but not from each other (Bonferroni method of multiple comparisons). Tilt angle slopes for both translation (0.66 ± 0.05 , mean \pm 95% CI, $p < 0.001$, two-tailed t -test comparing mean to 0.5) and pursuit (0.65 ± 0.03 , $p < 0.00001$) were larger than 0.5, the value predicted by Listing's Law. For pursuit and translation, tilt angle

slopes were independent of frequency over the range tested. There was also no effect of viewing distance on slope over the range tested (0.7 Hz). For rotation, the tilt angle slope tended to decrease as frequency increased (Fig. 3), but this was not statistically significant, largely due to the presence of one outlier. In the other three subjects, however, there was a similar and large decrease in slope between 0.2 and 0.7 Hz.

The tilt angle slope during translation did not depend on the presence of the flashing target. The slope for data recorded during translation in darkness was 0.62 ± 0.09 . This was not different from slopes recorded with the flashing target ($p > 0.52$, two-tailed paired t -test). Even

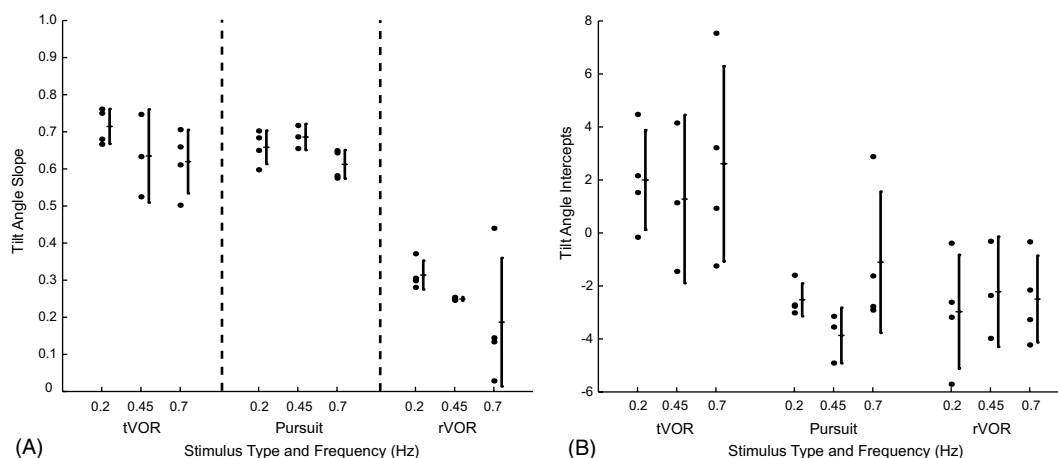


Fig. 3. (A) Tilt angle slopes for all subjects during tVOR, pursuit, and rVOR. Translation and rotation were done with flashing targets. In all cases, the target distance was 100 cm. Each point represents the value in a single subject. Next to each column of data points is depicted the mean and standard deviation of that group. (B) Tilt angle intercepts for all subjects during tVOR, pursuit, and rVOR (100 cm target distance, flashing targets for tVOR and rVOR).

in the subject who was translated in the dark with no target present during the entire recording, there was no difference in the slope (0.50 with the flashing target, 0.49 in the dark).

3.2. Tilt angle intercepts

The *tilt angle intercept* estimates the axis of eye velocity if the vertical position of the eye were on the horizontal meridian (Fig. 3B). Note that intercepts varied more widely than the slopes, although intercepts for pursuit and rotation were more negative than those for translation. This difference was highly significant (one-way ANOVA with Bonferroni method of multiple comparisons, $p < 0.0001$). One potential source of variability in these intercepts is differences in exact orientations of the orbits relative to the targets among subjects. However, this does not apply to a comparison of pursuit and the tVOR, since these were recorded in the same session (and therefore with the head in the same position). At all three frequencies, the intercept for translation was more positive ($4.4 \pm 1.7^\circ$, mean \pm s.d.). Under the right-hand rule, this corresponds to a relative excess of clockwise torsion for leftward slow phases (rightward translation) and counterclockwise torsion for rightward slow phases (leftward translation).

4. Discussion

The primary finding of this study is that torsional velocity during interaural translation in humans has a relationship to vertical eye position that is similar to that during pursuit and close to what is predicted by Listing's Law. However, at a given vertical eye position, there is a difference in the amount of torsion during pursuit and

the tVOR (different intercepts, which correspond to different torsional velocity offsets). Also, the relationship of torsion to vertical eye position is independent of frequency over the tested range (0.2–0.7 Hz) for both pursuit and the tVOR. For the rVOR, there was a trend toward decreasing tilt angle slope with increasing frequency that did not reach statistical significance. This trend is consistent with a prior study of Misslisch and Tweed (2001) and the finding of a small slope during impulsive (i.e., high frequency) head rotations (Palla et al., 1999).

This is the first study to investigate torsional eye velocity during translation as a function of vertical eye position in humans, although in a study of the tVOR in rhesus monkeys, the authors also found that torsion during the interaural tVOR depended on vertical eye position and that tilt angle slopes were greater than 0.5 (Angelaki, McHenry, & Hess, 2000). In a follow-up study, using a protocol similar to ours, Angelaki, Zhou, and Wei (2003) compared the tVOR, pursuit, and the rVOR. In general, their findings agreed with our initial data (Walker et al., 2000) and the full results presented here: tilt angle slopes for the tVOR were not statistically different from those for pursuit. They were able to extend that result to a higher frequency (4 Hz), although the amplitude was low (less than ± 5 mm).

4.1. Relationship between the tVOR and pursuit

Similar behavior relative to Listing's Law adds further support for a close relationship between pursuit and the tVOR. Such a relationship makes sense from a functional perspective. Whereas the rVOR ideally stabilizes the entire retinal image, for pursuit and the tVOR in general only the foveal image is important. Pursuit stabilizes a moving target on the fovea at the expense of

the stationary background. For the tVOR, the background is often at a different distance from the chosen target, again leading to motion of images on the peripheral retina (only images of objects at one distance can be stabilized).

For both pursuit and the tVOR, we found that tilt angle slopes were slightly higher than those predicted by Listing's Law. The reason is uncertain, although it does suggest that Listing's Law is not completely obeyed during pursuit or the tVOR. This is consistent with a prior study in which analysis of eye positions showed deviations from Listing's plane during pursuit (Straumann, Zee, Solomon, & Kramer, 1996). In monkeys (Angelaki et al., 2003), slopes were also greater than 0.5.

Although the tilt angle slopes were the same for the tVOR and pursuit, the intercepts were different. Specifically, the intercepts were more positive for the tVOR, meaning that there was more clockwise torsional velocity for an equivalent leftward horizontal eye velocity during translation than during pursuit. In monkeys, there was also a positive tilt angle when the animals were looking straight ahead (Angelaki et al., 2000). The reason for the difference between pursuit and the tVOR is not certain. It is true that the direction of this excess torsion is what one would expect if some of the translation were misinterpreted as tilt: linear acceleration to the right (leftward slow phases) is analogous to a left-ear-down tilt, which should elicit clockwise slow phases. However, such torsion was seen even at 0.7 Hz, a frequency thought too high to elicit this type of misinterpretation (Paige & Seidman, 1999; Wood, 2002). A difference in head orientation was not the cause of the difference in torsion, as these data were acquired in the same experimental session with the head in the same position. A difference in the vergence angle was not the cause because the vergence angle was nearly the same in the two conditions.

It has been suggested that the response to translation in this frequency range may involve extra-vestibular mechanisms, such as pursuit of an imagined target (Paige, Telford, Seidman, & Barnes, 1998). We agree that the similar kinematic behavior between the tVOR and pursuit may be due to shared pathways between the two reflexes, such that otolith input during translation may drive pursuit mechanisms. In fact, that was one hypothesis that motivated our study.

However, that pursuit pathways may be involved in the tVOR does not imply that the response is simply imagined pursuit and that otolith input is irrelevant. Whereas during such "pursuit" the task is to imagine a target moving in space, during translation the goal is to direct the eyes to a real or imagined point that is fixed in space, while the head is moving. This, in fact, is the purpose of the tVOR. Since the rVOR was measured under the same mental condition (stabilizing gaze on an imagined target location in space), one could argue that

imagined pursuit might be playing a role in this response as well. However, the kinematics during rotation are very different from those during pursuit and the tVOR and are more reflective of the role of the rVOR in stabilizing the entire retinal image. In addition, although in this study the responses to pursuit and the tVOR were similar, they were not identical. We found a difference in the torsional velocity bias, as measured by the tilt angle intercept, in the two conditions. Finally, Angelaki et al. (2000) showed that torsion strongly depended upon vertical position during translation up to 10 Hz. At these high frequencies, imagined pursuit is unlikely to be playing a major role. Thus, although the tVOR may be expressed via pursuit pathways, this does not mean that it is "simply" pursuit (Shelhamer, Peng, Ramat, & Patel, 2002).

4.2. Implications for the tilt-translation "ambiguity"

The acceleration due to gravitational force is a linear acceleration. Thus, there is no way to distinguish on a purely physical basis the acceleration due to interaural translation from that due to roll tilt. Nonetheless, under normal conditions, the brain can distinguish these two conditions, as reflected in the eye movement response. When the head is tilted, there is torsional ocular counterroll, and when the head is translated along the interaural axis, there is compensatory horizontal nystagmus.

The mechanism by which tilt and translation are resolved by the brain is still debated. One hypothesis is that the distinction is made based on stimulus frequency: very low frequencies imply tilt and elicit counterroll; higher frequencies imply translation and produce predominantly a horizontal nystagmus (Paige & Seidman, 1999). Additional evidence in support for this hypothesis is the misinterpretation of tilt when individuals are exposed to a prolonged constant linear acceleration, for example, during centrifugation (Merfeld, Zupan, & Gifford, 2001; Paige & Seidman, 1999).

Other data suggest that, at least at higher frequencies, canal and otolith information is combined in making the distinction between tilt and translation (Angelaki & Hess, 1996; Angelaki, McHenry, Dickman, Newlands, & Hess, 1999; Angelaki et al., 2001; Merfeld et al., 2001). Also of possible importance is the fact that tilt and interaural translation (with the head upright), although resulting in similar utricular stimuli, affect the sacculi differently (MacDougall, Curthoys, Betts, Burgess, & Halmagyi, 1999).

Our results, and similar data in monkeys (Angelaki et al., 2000, 2003), indicate an additional important factor determining the amount of torsion during interaural translation, namely that torsional velocity depends on vertical eye position. In fact, two different gaze positions may have torsional velocities that are opposite in

direction. This should be taken into account in any analysis that uses torsion as a measure of the response to real or perceived tilt. For example, responses at different frequencies could be compared with the eyes at the same vertical position or, as done here, measured at multiple vertical positions, comparing the intercepts across frequencies.

4.3. Functional consequence of torsional velocity

Finally, we consider the functional implications of the torsional eye velocity and its relationship to vertical eye position. Since the purpose of the VORs and pursuit is to stabilize gaze, a related question is what axis of eye velocity best stabilizes gaze in each case? This question encompasses two issues. First, what eye velocity axis is appropriate for the stability of foveal gaze? Second, what is the effect of torsional velocity on the peripheral retinal image? As described by Crawford (Crawford, Henriques, & Vilis, 2000) and discussed by Angelaki et al. (2003), the retinal projections of earth-horizontal lines curve vertically when the eye is in secondary vertical positions; the amount of curvature increases with increasing vertical displacement from the center position. Similarly, during pursuit of an earth-horizontal moving target, when the eye is looking up or down, a purely horizontal angular velocity would cause the fovea to move up or down relative to the target, as the eye moved more eccentrically into tertiary eye positions. This undesired vertical displacement of the fovea can be corrected by a torsional eye velocity (in head centered coordinates) that varies with vertical eye position according to the full-angle rule (tilt angle slope of 1) (Angelaki et al., 2003).

The kinematic requirements of the tVOR are analogous to those of pursuit. Even though the head is translating instead of the target, the relative motions of the eye and the target are the same during pursuit and the tVOR. For the rVOR, however, the relationship of the eye to the target is quite different. Because the head is rotating rather than translating (at a target distance of 100 cm, the effect of orbital translation is small), and the eye is simultaneously counterrotating in the head, the position of the eye (and thus the fovea) relative to the target should remain constant at a given vertical position. Thus, the kinematic considerations that require the full-angle rule for the tVOR and pursuit do not apply to the rVOR. Instead, foveal stability is optimal when the tilt angle slope is zero (zero-angle rule). Thus, the zero-angle rule is appropriate for image stability on both the fovea and the retinal periphery.

For none of these eye movements, however, do the optimal kinematics appear to be achieved. The tilt angle slope of the rVOR only approaches zero at the highest frequencies, and those of pursuit and the tVOR, al-

though greater than 0.5 (the value predicted by Listing's Law), are still much less than one. It has been suggested that the intermediate slope might be a compromise between keeping eye positions close to those during fixation and satisfying the requirements for gaze stability (Angelaki et al., 2003). However, this implicitly assumes that torsional velocity is the major factor determining gaze stability. In fact, particularly for the tVOR, this does not seem to be the case. The gain of the tVOR (relative to ideal eye velocity) is considerably less than unity, both for relatively low-frequency motion, as in this study, and for abrupt transient stimuli (e.g., Ramat & Zee, 2003). The reason why the gain should be so low is unclear, but it implies that there is substantial horizontal foveal slip during translation. Given this fact, torsional eye velocity would seem to have relatively little additional effect on vision during head translation.

4.4. Summary

In summary, this study demonstrates that the kinematics of the tVOR resemble those of horizontal pursuit more than those of the rVOR. In theory, this is more appropriate for foveal gaze stability, although due to the low tVOR gain, it is unlikely to have a substantial effect on vision. Whether this similarity of pursuit and tVOR indicates an overlap of their premotor pathways is uncertain; to address this question, specific electrophysiological studies will be required.

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References

- Angelaki, D. E., & Hess, B. J. (1996). Three-dimensional organization of otolith-ocular reflexes in rhesus monkeys. II. Inertial detection of angular velocity. *Journal of Neurophysiology*, *75*, 2425–2440.
- Angelaki, D. E., McHenry, M. Q., Dickman, J. D., Newlands, S. D., & Hess, B. J. (1999). Computation of inertial motion: Neural strategies to resolve ambiguous otolith information. *Journal of Neuroscience*, *19*, 316–327.
- Angelaki, D. E., McHenry, M. Q., & Hess, B. J. (2000). Primate translational vestibuloocular reflexes. I. High-frequency dynamics and three-dimensional properties during lateral motion. *Journal of Neurophysiology*, *83*, 1637–1647.
- Angelaki, D. E., Wei, M., & Merfeld, D. M. (2001). Vestibular discrimination of gravity and translational acceleration. *Annals of the New York Academy of Sciences*, *942*, 114–127.
- Angelaki, D. E., Zhou, H. H., & Wei, M. (2003). Foveal versus full-field visual stabilization strategies for translational and rotational head movements. *Journal of Neuroscience*, *23*, 1104–1108.

- Baloh, R. W., Yue, Q., & Demer, J. L. (1995). The linear vestibulo-ocular reflex in normal subjects and patients with vestibular and cerebellar lesions. *Journal of Vestibular Research*, 5, 349–361.
- Crawford, J. D., Henriques, D. Y., & Vilis, T. (2000). Curvature of visual space under vertical eye rotation: Implications for spatial vision and visuomotor control. *Journal of Neuroscience*, 20, 2360–2368.
- Fetter, M., Tweed, D., Misslisch, H., & Koenig, E. (1994). Three-dimensional human eye-movements are organized differently for the different oculomotor subsystems. *Neuro-Ophthalmology*, 14, 147–152.
- Hepp, K. (1990). On Listing's Law. *Communications in Mathematical Physics*, 132, 285–292.
- MacDougall, H. G., Curthoys, I. S., Betts, G. A., Burgess, A. M., & Halmagyi, G. M. (1999). Human ocular counterrolling during roll-tilt and centrifugation. *Annals of the New York Academy of Sciences*, 871, 173–180.
- Merfeld, D. M., Christie, J. R., & Young, L. R. (1994). Perceptual and eye movement responses elicited by linear acceleration following spaceflight. *Aviation Space and Environmental Medicine*, 65, 1015–1024.
- Merfeld, D. M., & Zupan, L. H. (2002). Neural processing of gravito-inertial cues in humans. III. Modeling tilt and translation responses. *Journal of Neurophysiology*, 87, 819–833.
- Merfeld, D. M., Zupan, L. H., & Gifford, C. A. (2001). Neural processing of gravito-inertial cues in humans. II. Influence of the semicircular canals during eccentric rotation. *Journal of Neurophysiology*, 85, 1648–1660.
- Misslisch, H., & Hess, B. J. (2000). Three-dimensional vestibuloocular reflex of the monkey: Optimal retinal image stabilization versus Listing's Law. *Journal of Neurophysiology*, 83, 3264–3276.
- Misslisch, H., & Tweed, D. (2001). Neural and mechanical factors in eye control. *Journal of Neurophysiology*, 86, 1877–1883.
- Misslisch, H., Tweed, D., Fetter, M., Sievering, D., & Koenig, E. (1994). Rotational kinematics of the human vestibuloocular reflex. III. Listing's Law 0. *Journal of Neurophysiology*, 72, 2490–2502.
- Paige, G. D., & Seidman, S. H. (1999). Characteristics of the VOR in response to linear acceleration. *Annals of the New York Academy of Sciences*, 871, 123–135.
- Paige, G. D., Telford, L., Seidman, S. H., & Barnes, G. R. (1998). Human vestibuloocular reflex and its interactions with vision and fixation distance during linear and angular head movement. *Journal of Neurophysiology*, 80, 2391–2404.
- Palla, A., Straumann, D., & Obzina, H. (1999). Eye-position dependence of three-dimensional ocular rotation-axis orientation during head impulses in humans. *Experimental Brain Research*, 129, 127–133.
- Ramat, S., & Zee, D. S. (2003). Ocular motor responses to abrupt interaural head translation in normal humans. *Journal of Neurophysiology*, 90, 887–902.
- Shelhamer, M., Peng, G. C., Ramat, S., & Patel, V. (2002). Context-specific adaptation of the gain of the oculomotor response to lateral translation using roll and pitch head tilts as contexts. *Experimental Brain Research*, 146, 388–393.
- Straumann, D., Zee, D. S., Solomon, D., & Kramer, P. D. (1996). Validity of Listing's law during fixations, saccades, smooth pursuit eye movements, and blinks. *Experimental Brain Research*, 112, 135–146.
- Straumann, D., Zee, D. S., Solomon, D., Lasker, A. G., & Roberts, D. C. (1995). Transient torsion during and after saccades. *Vision Research*, 35, 3321–3334.
- Thurtell, M. J., Black, R. A., Halmagyi, G. M., Curthoys, I. S., & Aw, S. T. (1999). Vertical eye position-dependence of the human vestibuloocular reflex during passive and active yaw head rotations. *Journal of Neurophysiology*, 81, 2415–2428.
- Tweed, D., Fetter, M., Andreadaki, S., Koenig, E., & Dichgans, J. (1992). Three-dimensional properties of human pursuit eye movements. *Vision Research*, 32, 1225–1238.
- Tweed, D., & Vilis, T. (1990). Geometric relations of eye position and velocity vectors during saccades. *Vision Research*, 30, 111–127.
- Walker, M. F., Zee, D. S., Shelhamer, M. J., Roberts, D. C., & Lasker, A. G. (2000). Variation of eye velocity axis with vertical eye position during horizontal pursuit, interaural translation, and yaw rotation in normal humans. *Society for Neuroscience Abstracts*, 26, 1718 (Abstract).
- Wiest, G., Tian, J. R., Baloh, R. W., Crane, B. T., & Demer, J. L. (2001a). Initiation of the linear vestibulo-ocular reflex in cerebellar dysfunction. *Annals of the New York Academy of Sciences*, 942, 505–507.
- Wiest, G., Tian, J. R., Baloh, R. W., Crane, B. T., & Demer, J. L. (2001b). Otolith function in cerebellar ataxia due to mutations in the calcium channel gene CACNA1A. *Brain*, 124, 2407–2416.
- Wood, S. J. (2002). Human otolith-ocular reflexes during off-vertical axis rotation: Effect of frequency on tilt-translation ambiguity and motion sickness. *Neuroscience Letters*, 323, 41–44.