

Neural and Mechanical Factors in Eye Control

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Misslisch, H. and D. Tweed. Neural and mechanical factors in eye control. *J Neurophysiol* 86: 1877–1883, 2001. Soft tissue “pulleys” in the orbit alter the paths of the eye muscles in a way that may simplify the brain’s work in implementing Listing’s law, i.e., in holding ocular torsion at zero. But Listing’s law does not apply to some oculomotor systems, such as the vestibuloocular reflex (VOR), which shows a different kinematic pattern. To explain this different pattern, some authors have assumed that the pulleys must adopt a different configuration, retracting along their muscles when the eye switches from Listing’s law to VOR mode. The proposed retraction has not so far been observed, although the pulleys do move in other ways. We show that the hypothetical retraction of the pulleys would not in fact explain the full kinematic pattern seen in the VOR. But this pattern can be explained entirely on the basis of pulley positions and motions that have actually been observed. If one takes into account the neural processing within the VOR, specifically the fact that the reflex is weak in the torsional dimension, then a single mode of pulley action can serve both vestibuloocular kinematics and Listing’s law.

INTRODUCTION

There is evidence that our musculature is organized in a way that simplifies motor control. For instance, several studies (Demer et al. 2000; Miller 1989; Miller et al. 1993) report mobile, soft-tissue sheaths or “pulleys” in the orbit that influence the pulling directions of the extraocular muscles. These pulleys may simplify the brain’s work in implementing Listing’s law (Miller 1989; Quaia and Optican 1998; Raphan 1997; Tweed 1997; Tweed et al. 1994a), which says that during some types of ocular motion, the eye’s torsion (its rotation about a forward-backward axis) is zero (Helmholtz 1867). Might these same pulleys also play a role in other motor patterns besides Listing’s law?

A motor pattern distinct from Listing’s law is seen in the human vestibuloocular reflex (VOR), the reflex that holds the eyeball roughly steady in space during head motion. When the head turns, the VOR does not counterrotate the eye about exactly the same axis as the head, as one might expect. Rather, the eye’s axis swings away from the head’s depending on gaze direction. When your head yaws about a vertical axis, your eye’s rotation axis swings up when you look up and down when you look down, tilting a quarter to a third as far as the gaze line (Misslisch et al. 1994, 1996; Palla et al. 1999;

Solomon et al. 1997). Similarly, when your head pitches about an interaural axis, your eye’s rotation axis swings right when you look right and left when you look left (Fig. 1), again about a third as far as the gaze line (Misslisch et al. 1994, 1996). During roll head motion, about the forward-backward axis, the effect is larger and reversed (Fig. 1): your eye’s axis now swings almost as far as the gaze line but in the opposite direction (Misslisch et al. 1994, 1996).

As the VOR’s motor pattern breaks Listing’s law, it has been assumed that both patterns cannot be served by the same arrangement of pulleys. Some authors have therefore suggested that the pulleys might advance and retract along their muscle paths, adopting one arrangement for Listing’s law and the other for the VOR (Demer et al. 2000; Thurtell et al. 1999, 2000). But the proposed retraction is large (Fig. 2) and has not been observed; Clark et al. (1997) and Demer et al. (2000) found that the pulleys move as if dragged along with the turning eyeball (and therefore they move opposite the gaze line in some dimensions; see APPENDIX), but this motion resembled not at all the large backward shift that is proposed for switching from Listing’s law to the VOR. Further, we show here that the proposed retraction would not in fact explain the full pattern of eye axes seen in the VOR. We show that this pattern can be explained in full given only the observed actions of the pulleys, if one takes into account the known neural processing within the VOR, specifically the fact that the reflex is weak in the torsional dimension (Berthoz et al. 1981; Collewijn et al. 1985; Ferman et al. 1987; Misslisch and Tweed 2000; Robinson 1982; Seidman and Leigh 1989; Tweed et al. 1994b).

METHODS

Six normal human subjects rotated their heads sinusoidally through about $\pm 10^\circ$ in yaw, pitch, and roll in time to a computer metronome at three frequencies: 0.3, 0.6, and 1.2. As is usual in daily life, yaw was about an earth-vertical axis, pitch and roll about earth-horizontal axes. Subjects were trained, using a head-mounted laser, to make movements of the desired size and direction. Their head rotations varied somewhat and were usually larger at the lower frequencies, reaching $\pm 18^\circ$ in some subjects, but our function-fitting analysis described below removed the need for precisely controlled head motion. Before each trial, subjects fixated a laser spot 90 cm away. During the subsequent head motion, they tried to maintain this gaze

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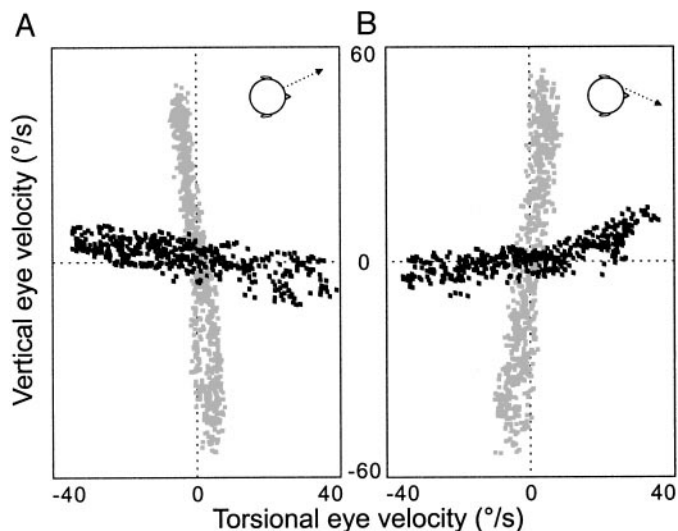


FIG. 1. The pattern of eye-velocity vectors in the vestibuloocular reflex (VOR). Each dot is the tip of an eye-velocity vector sampled during head oscillation in darkness. During head pitch at 0.6 Hz, eye velocities (gray dots) swing away from the interaural axis of head rotation (ordinates), moving left when gaze is 25° left (A), right when gaze is 25° right (B). During head roll at 0.3 Hz, eye velocities (black dots) swing away from the nasooccipital axis of head rotation (abscissas), opposite to gaze: right when gaze is 25° left (A) and left when gaze is 25° right (B). Subject DT.

direction. In *dark* trials, the laser was extinguished before the head movements began, and the trial ran in complete darkness except that the laser flashed for 5 ms once per second to keep the subjects' eyes

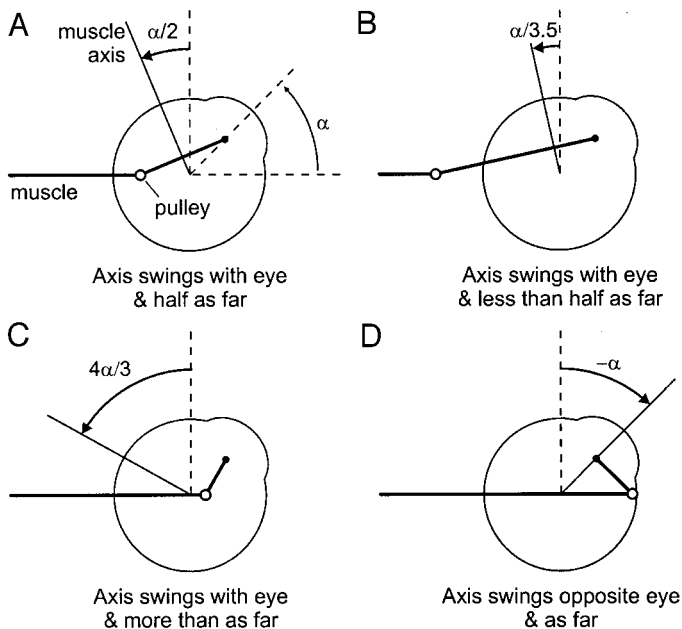


FIG. 2. Effects of pulley position on muscle action. A: if a pulley sits as far behind the eye's center of rotation as the muscle's insertion lies in front, then the axis of muscle action will swing with the eye when the eye moves, but only about half as far. This half-angle property may simplify the implementation of Listing's law (although exact half-angle behavior requires that the pulleys move slightly in the orbit when the eye moves). B: if the pulley is retracted, the muscle axis moves less when the eye moves. To achieve quarter- or third-angle behavior, the pulley would have to sit 2 or 3 times as far behind the ocular center as the insertion point is in front. C: if the pulley is pushed forward, the muscle axis moves more. D: advancing the pulley beyond its muscle's insertion makes the muscle axis swing opposite the eye's rotation.

from wandering. In *light* trials, the laser was constantly visible amid a field of larger white spots.

Rotations of the head and left eye were recorded at 100 Hz using search coils (Ferman et al. 1987; Robinson 1963; Tweed et al. 1994b). Eye and head-position quaternions and angular velocities were computed as described by Tweed et al. (1990). Angular velocities are expressed using the right-hand rule, i.e., if you point your right thumb in the direction of the vector, then your fingers curl round in the direction of spin; for instance a forward-pointing vector represents clockwise spin (from the subject's viewpoint). Quick phases and saccades were removed manually and by acceleration criteria chosen individually for each subject. To quantify the VOR we computed a best-fit quadratic equation expressing eye velocity as a function of head velocity and eye position; this form of function is very flexible and accurately approximates VOR behavior (Misslisch et al. 1994).

RESULTS

The motor pattern shown for one subject in Fig. 1 also held in general. Figure 3 plots the averaged behavior of our six subjects during head oscillations at 0.3 Hz in darkness. During head yaw and head pitch, the eye's rotation axis swung with the gaze line; during head roll, it swung opposite. This behavior was entirely consistent, with the complete pattern present in all six subjects, at all three frequencies, in both darkness and light. Quantitatively, the eye's axis swung 31% as far as the gaze line during head pitch; i.e., the angle between the responses for gaze 25° left and gaze 25° right averaged 15.5°, with angles for individual subjects ranging from 12.3 to 17.5°. During yaw, the eye's axis tilted 36% as far as the gaze line. During roll, the axis motion was more than twice as large, 81% as far as the gaze line for left or right gaze and 93% as far for up or down gaze.

Axis swing decreased at high frequencies of head rotation. Figure 4 plots the angle of swing for a 50° change in gaze direction, for the different frequencies of head rotation and the different visual conditions, averaged over the six subjects. Two

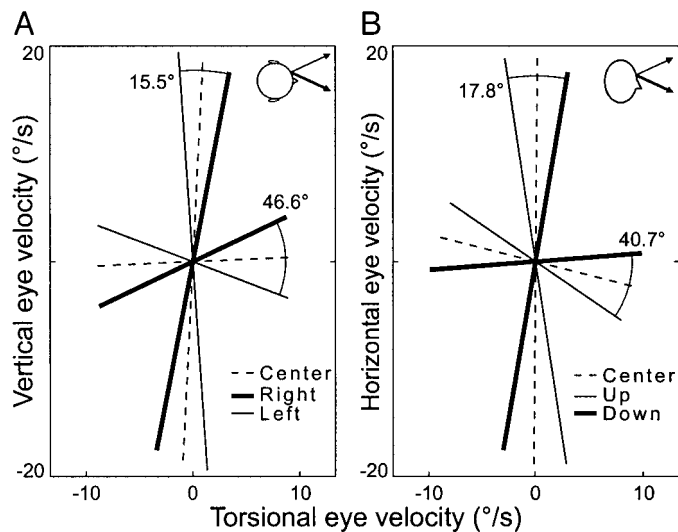


FIG. 3. VOR pattern for 0.3-Hz oscillation in darkness, averaged across subjects. Eye-velocity vectors are drawn as lines through the origin; in each panel, 3 line styles represent responses evoked with the eye in 3 positions: centered and 25° right and left (A), centered and 25° up and down (B). A: a 50° leftward change in gaze direction causes a 15.5° leftward swing of the eye-rotation axis during head pitch and a 46.6° rightward swing during roll. B: depressing gaze 50° makes the eye-rotation axis swing 17.8° downward during yaw and 40.7° upward during roll.

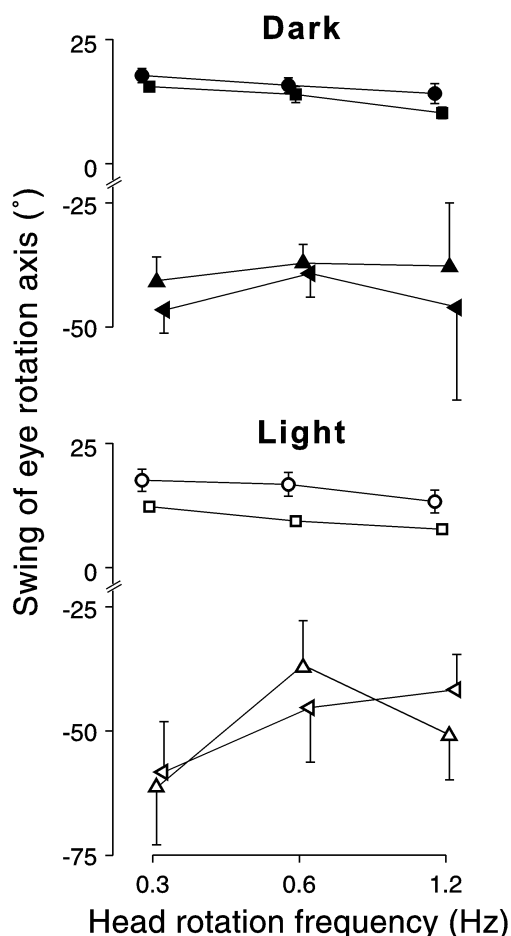


FIG. 4. Swing angles of eye-rotation axes for different frequencies of head rotation and different visual conditions, averaged across subjects. ●, ■, ▲, and ◄, dark trials (top); ○, □, △, and ◄, light trials (bottom). ● and ○, responses to head yaw; ■ and □, responses to pitch; ▲ and ◄, responses to roll with the gaze line 25° to the left and right; ▲ and △, responses to roll with gaze 25° up and down. The effect of eye position is much larger in roll than in yaw or pitch and decreases with increasing frequency. Bars show SE.

main results are revealed. First, the eye's rotation axis swung much farther during roll than during pitch and yaw, and in the opposite direction, at all frequencies. Second, swing tended to decrease with increasing frequency. Significant differences ($P < 0.05$) were found between the following conditions: pitch at 0.3 versus 1.2 Hz in darkness and light; pitch at 0.3 versus 0.6 Hz in light; yaw at 0.3 versus 1.2 Hz in light; roll gaze up/down at 0.3 versus 0.6 Hz in darkness and roll gaze right/left at 0.3 versus 0.6 Hz in light.

Our computer simulations (see DISCUSSION) showed that this pattern of axis motion is just what one would expect, given the known anatomy of the pulleys and the known neural processing within the VOR. Specifically, simulations showed that the axes swing because VOR responses are weaker in the torsional dimension than in the horizontal or vertical. This explanation implies a further, surprising prediction: if the axes swing because torsional gain is weak, then they should swing farther, the weaker the gain. This prediction is confirmed in Fig. 5, a plot of swing angles versus torsional gain. Regression analysis (Sokal and Rohlf 1998) of the eight data sets (yaw head motion, pitch head motion, roll while subjects looked up and down, roll while they looked right and left, all carried out in darkness and in light) showed, in all but

one condition (pitch in darkness), a significant ($P < 0.05$) inverse relation between swing angle and torsional gain: as torsional gain decreased, axis swing increased. Also as predicted (see DISCUSSION), the slope was steeper for head roll than for yaw or pitch. Other proposed explanations for axis swing do not predict this relation to torsional gain.

DISCUSSION

Some authors have assumed that pulleys can contribute to the motor pattern seen in the VOR only if they are strongly retracted along their muscle paths. But this retraction has not so far been observed and in any case would not, as we show below, explain in full the observed VOR responses. We show that VOR kinematics can be explained in full using only those pulleys properties that have actually been observed, if one takes into account the neural signals driving the reflex.

No one knows exactly how the pulleys affect muscle action, but the most popular idea is that they are arranged to implement the half-angle rule (Tweed et al. 1992) that is required for Listing's law. That is, they are placed so that the pulling direction of each muscle moves when the eye moves, turning in the same direction but only half as far (Fig. 2A) (Demer et al. 1995; Miller and Demer 1997; Raphan 1997; Smith and Crawford 1998; Thurtell et al. 2000; Tweed 1997). During the VOR, however, the half-angle rule fails: the eye's axis swing significantly less than half as far as the eye (during yaw and pitch)

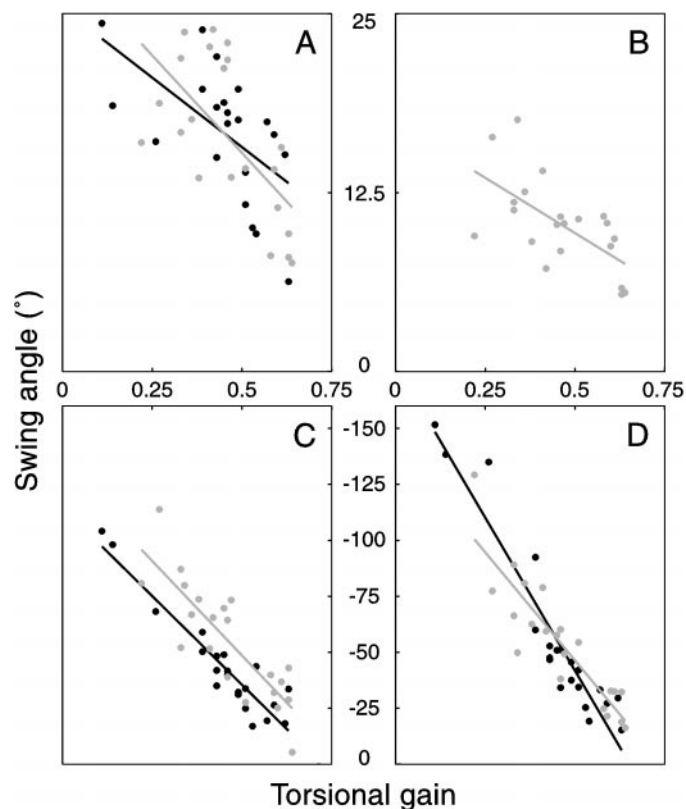


FIG. 5. Torsional VOR gain correlates with the eye-position dependence of the eye's rotation axis. The swing angle of the axis increases significantly with decreasing torsional gain in both light and darkness (gray and black symbols) during yaw (A), in light during pitch (B), and in both light and darkness during roll with gaze 25° up/down (C) and 25° left/right (D). Data are for all subjects, at all frequencies.

or significantly farther and in the opposite direction (during roll). To explain the reduced axis motion during yaw and pitch, Demer et al. (2000) and Thurtell et al. (2000) suggested that the pulleys might retract toward the muscle origins during the VOR (Fig. 2*B*; Thurtell et al. express this retraction as a change in their variable k_{ϕ}). But simulations using this retracted arrangement do not fit the data during roll: when the eye looks 25° right, for instance, the eye-rotation axes swing in the same direction as the eye (Fig. 6*B*), opposite the swing seen in the data (Fig. 6*A*). This *reversal error* is large: when the gaze line moves 25° right, the velocity vector, instead of turning about 25° left as in the data, turns about 8° right.

The reason is clear from Fig. 2. Retracting the pulleys would reduce the motion of the eye's axis (Fig. 2*B*) but would not make it swing opposite the eye, as seen in the roll VOR. The opposite adjustment, pushing the pulleys forward, would increase the axis motion (Fig. 2*C*), but would not reverse it unless the pulley advanced beyond its muscle's insertion (Fig. 2*D*). Figure 2 depicts just one muscle, but the principle is the same for the four muscles that roll and pitch the eye.

One might propose that pulley retraction explains the axis motion seen during yaw and pitch, whereas some other factor operates during roll. But as we show next, VOR behavior in all dimensions can be explained by a single, well-known mechanism—low torsional gain (Berthoz et al. 1981; Collewijn et al. 1985; Ferman et al. 1987; Misslisch and Tweed 2000; Robinson 1982; Seidman and Leigh 1989; Tweed et al. 1994b)—with no need for the hypothetical retraction of the pulleys. Of course ocular mechanics is complex and may have surprises in store, but at the moment there is no need to assume that the pulleys retract during the VOR. VOR kinematics are fully explained given the known properties of the pulleys and the neural drive.

VOR model

Figure 7 simulates a VOR with a weak torsional gain and pulleys that are set in a Listing configuration and move slightly

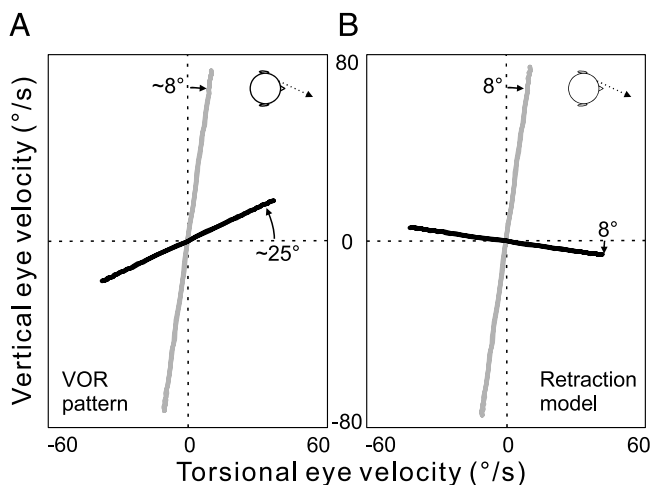


FIG. 6. Discrepancies between the pulley-retraction hypothesis and VOR behavior. Both panels plot the vertical vs. the torsional component of eye velocity during torsional and vertical head oscillations when the eye looks 25° right (same format as in Fig. 1*B*). *A*: typical behavior of the VOR. *B*: predictions of the retraction model. During head pitch the simulated responses match the data, but during roll the eye-velocity vectors swing the wrong way: when the gaze line shifts 25° right, the eye-velocity vector, instead of turning about 25° left as in the data, turns 8° right.

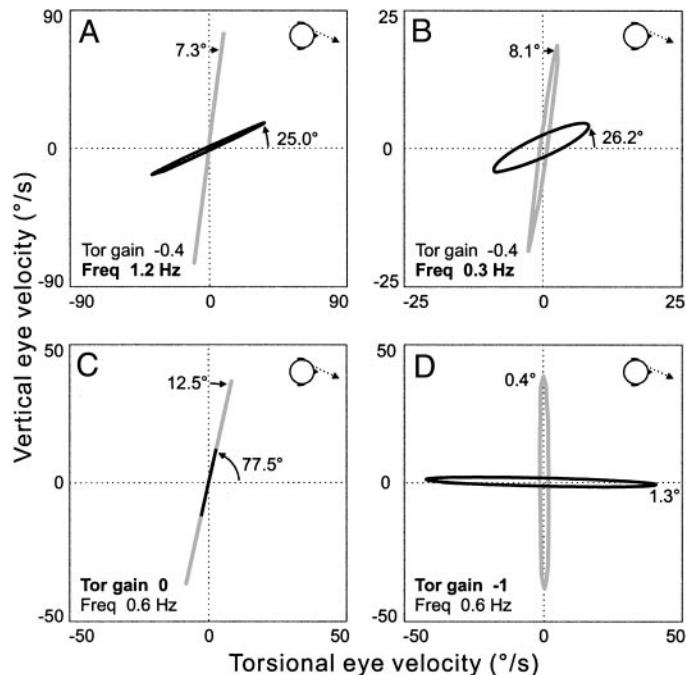


FIG. 7. VOR kinematics can be attributed to low torsional gain, without retracted pulleys. In these simulations the oculomotor integrator leaks torsionally with a time constant of 1 s. Plots show how the tip of the eye-velocity vector loops around as the head oscillates in pitch (gray lines) and roll (black lines) when the subject looks 25° right. *A*: the torsional gain of the VOR is set to -0.4 , and the head oscillates at 1.2 Hz. Vertical head oscillations evoke eye-velocity loops tilted 7.3° away from the ordinate; i.e., moving the eyes 25° right shifts the average axis of eye rotation 7.3°. The same change in eye position during torsional head oscillation shifts the eye's axis 25.0°. *B*: response of the same system to head oscillations of 0.3 Hz. Now the changes in eye position cause slightly larger shifts in the axis of eye rotation, because the leaky integrator magnifies the influence of eye position on the VOR at low frequencies of head motion. *C*: torsional gain is set to zero, flattening the eye-velocity loops and increasing the influence of eye-position dependence, so that a 25° change in eye position now causes a 12.5° shift in the response to head pitch, and a 77.5° shift in the response to head roll. *D*: torsional gain is set to 1.0, removing almost all eye-position dependence.

with the eye when it turns; the behavior seen by Clark et al. (1997) and Demer et al. (2000) (see APPENDIX for the model equations). Each panel of the figure shows how the tip of the eye-velocity vector looping around as the head oscillates. In Fig. 7, *A* and *B*, the torsional gain of the VOR is set to -0.4 . When the head oscillates vertically, at a high frequency of 1.2 Hz, the eye-velocity loops tilt away from the ordinate (Fig. 7*A*). That is, moving the eyes 50° left or right swings the average axis of eye rotation 14.6° in the same direction. When the head oscillates torsionally, the same change in eye position swings the eye's axis 50° in the opposite direction; i.e., this model, unlike the one in Fig. 6*B*, predicts the entire pattern of axis swing, including the reversal seen in the torsional cases. At a lower frequency of head oscillation, 0.3 Hz, the same change in eye position swings the axes of eye rotation farther: 16.2 and 52.4° (Fig. 7*B*). So the model may also explain the greater influence of eye position on the VOR at low frequencies of head motion, although the mechanism invoked here is not the only one possible (see below).

When torsional gain is reduced to zero in our model, axis swing is magnified (Fig. 7*C*); the eye-velocity loops flatten, and the responses to torsional and vertical head motion align. When torsional gain is strengthened to -1.0 , the

eye-velocity loops hardly swing at all (Fig. 7D). So in this model, swing depends on gain. The model therefore predicts the relations seen in Fig. 5 and also correctly predicts that monkeys, whose torsional gains are stronger than humans', should show less axis swing (Crawford and Vilis 1991; Misslisch and Hess 2000).

Why does low torsional gain reverse the axis tilt in the torsional case? Given that the pulleys are in their Listing configuration, any drop in torsional gain pushes the system closer to Listing's law. So what is the response to torsional head rotation of a VOR that follows Listing's law perfectly? If for instance the head is turning counterclockwise (thin gray arrow in Fig. 8) and the eye is looking 25° right, then what eye velocity, consistent with Listing's law, will best stabilize the retinal image? To calculate that optimal eye velocity, first multiply the head velocity by -1 to yield the eye-velocity vector (thin black arrow in Fig. 8) that would perfectly stabilize the retinal image (but would break Listing's law). Then project that vector orthogonally into the eye's velocity plane, which is tilted 12.5° right, in keeping with the half-angle rule. The dashed line in Fig. 8 depicts this projection and shows that the projected vector (thick black arrow) tilts leftward away from the vector of perfect stabilization. That is, the eye's rotation axis tilts opposite the gaze line (Misslisch et al. 1994).

The frequency effects in Fig. 7, *A* and *B* (smaller axis swings at higher frequencies of head motion) arise because the model incorporates a torsional leak in the oculomotor integrator (Seidman et al. 1995). When the head is stationary, the torsional eye-position command from the integrator does not hold steady but drains away to zero with a time constant that may be as low as 1 s. To emphasize the effect, we used this minimal value of 1 s in our simulations (Fig. 7), but if the true time constant is longer, one may need to invoke other mechanisms

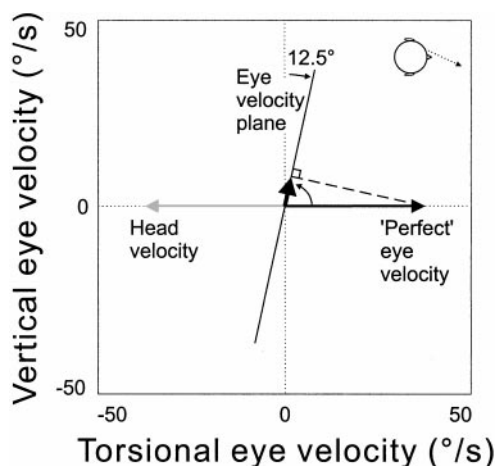


FIG. 8. Why a low torsional gain reverses the direction of eye rotation axis tilt in the roll VOR. In this example, the head rotates counterclockwise at 37.7°/s (gray arrow, peak velocity at 0.6 Hz), torsional gain is zero, and the eye is looking 25° right (cf. Fig. 7C). The eye velocity that is consistent with Listing's law and best stabilizes the retinal image must lie in the eye's velocity plane for that gaze direction, which is tilted 12.5° right. The eye velocity that stabilizes the entire retina (thin black arrow) is found by multiplying head velocity by -1 . Then the vector in the eye velocity plane (thick black arrow) is found by projecting the vector of perfect stabilization orthogonally (dashed line) into the eye velocity plane. Note that this roll VOR vector tilts leftward, away from the perfect image stabilization vector, and opposite the gaze line.

to explain the frequency effects. One possibility is miscalibration: it has been shown that if the brain's internal estimate of the plant's elasticity were low, that would explain the small torsional blips that accompany saccades (Tweed et al. 1994a); in the VOR, the same miscalibration would produce smaller axis swings at high frequencies (this can be simulated by setting $K_{11}^* < K_{11}$ in the equations in the APPENDIX). Another dynamic effect, the weakness or absence of axis swing during the initial response to an abrupt head jerk (Thurtell et al. 1999), may arise by the same mechanisms, simply because the head motion in this situation is very high frequency, or it may mean that the neural processes responsible for axis swing are slightly delayed.

Foveal VOR

Does the swinging-axis pattern serve any purpose? Misslisch et al. (1994) showed that it roughly halves the range of torsional eye positions generated by the VOR; i.e., it reduces deviations from Listing's law. And what is the advantage of better obeying Listing's law? Several suggestions have been made (e.g., Helmholtz 1867; Hepp 1990, 1995; Hering 1868; Tweed and Vilis 1990; Tweed et al. 1992). Perhaps the most important factor is that Listing's law keeps the eye near the center of its motor range, poised for a swift response in any direction.

Of course, when the eye's axis swings away from the head's, eye motion can no longer perfectly cancel head motion. The visual image is therefore imperfectly stabilized on the retina. This is an inevitable geometric consequence of staying close to Listing's law. But it is theoretically possible to approximate Listing's law while nevertheless preserving image stability over one small portion of the retina, the central high-acuity region called the fovea. Theoretically, the brain has a choice between two extreme strategies: it could eliminate optical flow entirely over the fovea, or it could minimize the average optical flow over the whole retina, with no special concern for the fovea. Or it could do something in between, keeping optical flow over the fovea somewhat smaller than the average flow elsewhere. All the strategies along this continuum are equally consistent with Listing's law; they can all be adjusted to yield any desired degree of adherence to the law, although it can be shown that the strategies that give special treatment to the fovea require higher eye velocities than the strategies that treat the whole retina more uniformly. Where does the actual VOR lie along this continuum? The best test is to measure how far the eye-velocity vector swings during head roll. If the brain is trying to eliminate optical flow over the fovea, the vector will swing 100% as far as the gaze line. If the VOR is treating the retina entirely uniformly, the vector will swing only 50% as far. Our data, showing ratios between 81 and 93%, support the foveal hypothesis. Misslisch et al. (1994) found ratios nearer 50%, perhaps because they used passive rather than active head motion, but more likely just because the swing angles vary a lot (Fig. 4). Presumably these angles need not be controlled with absolute precision. All that is required is a reasonable balance of several factors including energy output, ocular torsion, and image stability over various parts of the retina. In pursuit of this balance, the VOR

restricts its violations of Listing's law while partially preserving the stability of the foveal image.

APPENDIX

Model of the VOR

The rationale for this model is explained in Tweed (1997) and Tweed et al. (1999). The only differences between the 1999 version and the present one are the leaky integrator and the coefficients G and 1.5 in the matrix that multiplies canal outputs (see Eq. A1). G is torsional VOR gain, set to 1 in Tweed et al. (1999) and to various values in Fig. 7 here. The coefficients 1.5 yield the foveal-VOR behavior discussed earlier; when they are set to 1 as in Tweed et al. (1999), the VOR reduces global retinal slip with no special regard for the fovea.

At the sensory end of the model, the semicircular-canal activity vector c codes head velocity; c interacts with the brain's tonic, or eye-position, command T to yield an eye-velocity command E

$$E = \begin{pmatrix} -G & -GT_3 & GT_2 \\ 1.5T_3 & -1 & -T_1 \\ -1.5T_2 & T_1 & -1 \end{pmatrix} \times c/2 \quad (A1)$$

This interaction, or something closely equivalent, must exist in the VOR circuitry, because without it one cannot explain the noncommutativity of the reflex: the fact that the same head rotations applied in different orders yield different eye motions (Tweed et al. 1999). Of course the operation in the brain is unlikely to be represented in the matrix form of Eq. A1, with nine multiplier nodes; instead it presumably involves distributed processing in a network of nonlinear neurons. The network could be very small (Smith and Crawford 1998), or the operation expressed by Eq. A1 may be combined with other operations in a single larger network.

The phasic command E passes through the neural integrator to yield the tonic command T . Or rather, the vertical and horizontal components of E (E_2 and E_3) are integrated, while the torsional component E_1 is low-pass filtered with a time constant of τ s, to model the leak in the torsional signal: $dT_1/dt = E_1 - T_1/\tau$. (In Fig. 7, $\tau = 1$. In reality, many oculomotor signals in the brain are not divided into horizontal, vertical, and torsional components, and there are few purely tonic signals but rather mixed tonic-phasic, but neither of these complications fundamentally alters the model.) Motoneuron activity m is a weighted sum of tonic and phasic commands, T and E : $m = K^*T + R^*E$, where K^* and R^* are constants. Finally, the quaternion vector of eye position, q , is determined by the linear-plant equation

$$dq/dt = R^{-1}(m - Kq) \quad (A2)$$

In Fig. 7, $K^* = K = 6$ and $R^* = R = 1$, but if these variables are modeled as matrices rather than scalars, and if $K_{11}^* < K_{11}$, then various dynamic effects can be produced, including a stronger dependence of swing angles on the frequency of head oscillation.

It is Eq. A2 that implements the muscle pulleys (Tweed 1997 explains the connection between pulley action and this equation). First used in Tweed et al. (1994a), Eq. A2 is in all essential respects equivalent to the plant equations in other pulley models (Quaia and Optican 1998; Raphan 1997; Thurtell et al. 2000). Simulations show that Eq. A2, like any equation relating neural activity to eye motion, is consistent with a number of different muscle geometries, but perhaps the simplest is the one reported by Clark et al. (1997) and Demer et al. (2000): pulleys in a Listing configuration, moving with the eyeball or with their individual muscles when they stretch and contract. Clark et al. (1997) found that rectus pulleys, localized in the coronal plane, move a little in the direction opposite the gaze line; because the pulleys are behind the ocular equator, this means that the pulleys move with their local patch of eyeball; Demer et al. (2000)

found that rectus pulleys, visualized in a transverse plane, also move with the eyeball.

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