Role of Muscle Pulleys in Producing Eye Position-Dependence in the Angular Vestibuloocular Reflex: A Model-Based Study

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INTRODUCTION

The angular vestibuloocular reflex (aVOR) has an important role in minimizing retinal image slip during angular head rotations. To achieve this minimization, the eye and head velocity axes must align, and the eye and head velocities must be opposite in direction but equal in magnitude. That is, the gain of the aVOR must be 1.0 when viewing a target at far distance (more than ~1.0 m) and when rotating about a head-centered axis. A number of studies have shown that, during yaw and pitch head rotations, the eye and head velocity axes do remain approximately aligned and the gain of the aVOR is approximately equal to 1.0, when the eye is positioned at or near the center of the ocular motor range at the start of the head rotation (Aw et al. 1996; Crawford and Vivil 1991). Interestingly, a number of recent studies have revealed that the eye and head velocity axes do not always align when there is a requirement to fixate a point away from the primary position. In fact, during low-frequency sinusoidal oscillations in yaw, pitch, and roll, the eye velocity axis has been observed to systematically tilt away from the head velocity axis in a manner that is dependent on eye-in-head position (Frens et al. 1996; Misslisch et al. 1994). For example, during yaw oscillations the eye velocity axis tilts back when gaze is directed up and forward when gaze is directed down. These eye velocity axis tilts result in mismatches between the roll eye and head velocities, and hence retinal image slip.

Recently, high acceleration passive (Aw et al. 1996; Halmagyi et al. 1990) and active (Foster et al. 1997) head-on-neck “impulses” have been utilized to study eye velocity axis tilts in human subjects fixating targets positioned away from primary position (Thurtell et al. 1999a). In response to the passive head impulses, no eye velocity axis tilt was observed for the first ~50 ms after the onset of the head rotation, for any eye position. Palla et al. (1999) have also observed close alignment of the head and eye velocity axes in the early part of the response to high velocity passive head impulses. Thurtell et al. (1999a) found, however, that the axis tilts did become apparent after the initial 50 ms of the response, and were observed to occur in the same direction as seen in previous studies. The eye velocity axis tilts were also observed in the responses to active...
The mechanisms responsible for producing the axis tilts are unclear. If the eye movements obeyed Listing’s law, a constraint on ocular kinematics (von Helmholtz 1866), the angle of eye velocity axis tilt would be half that of eye deviation away from primary position (Tweed and Vilis 1990). However, the angle of tilt of the velocity axis is less than this (Frens et al. 1996; Misslisch et al. 1994; Solomon et al. 1997). Misslisch et al. (1994) concluded that the tilts arose due to a compromise between no axis tilt (perfect image stabilization) and the constraints imposed by Listing’s law. The mechanism for achieving the compromise was thought to be neural in origin. Hence, in response to identical head rotation stimuli, the signal driving the eye muscles would alter depending on eye position. Misslisch et al. (1994) also posited that the goal of the compromise was to minimize retinal image slip on the fovea, while allowing retinal image slip to occur on the periphery of the retina.

Recently, it has been shown that the paths of the rectus extraocular muscle bellies are constrained by orbital tissue, the fibromuscular pulleys (Clark et al. 1998, 1999; Demer et al. 1995, 1997; Miller et al. 1993). If it is assumed that the pulleys implement a kinematic rotation of the torque axis that is approximately half the angle of eye deviation away from primary position, then Listing’s law is obeyed during saccades when the central drive is confined to the two-dimensional pitch-yaw plane (Raphan 1997, 1998). If the pulleys produce such a rotation of the torque axes, the torque generated by the muscles becomes eye position-dependent. As a result, the eye velocity axis will tilt as a function of eye position. Therefore it is no longer clear that eye position-dependence in the aVOR is neural in origin; it could well arise as a consequence of the eye plant properties.

The purpose of this study was to investigate the mechanisms by which the eye position dependence of the aVOR could be generated during active and passive head rotations, using a model-based approach. Specifically, we have investigated whether the eye position-dependence of the aVOR can be predicted by a model that incorporates a semicircular canal system (Yakushin et al. 1998), a commutative velocity-position integrator in the CNS (Schnabolk and Raphan 1994) and a pulley system in the plant (Raphan 1998). To evaluate the accuracy of the predictions, we have compared high-resolution data collected from normal human subjects (Thurtell et al. 1999a) with the predictions of the model. To maximize the validity of the model predictions, head velocity and initial eye orientation data were used as input for the model. We have also sought to determine whether and to what extent additional “neural processing” is required to predict the patterns observed in the data. The findings presented in this paper have previously been presented in abstract form (see Thurtell et al. 1999b).

METHODS

Conventions

The head and eye velocities from the data and model simulations were expressed relative to a right-handed head-fixed coordinate system. Positive yaw is a leftward rotation, positive pitch is a downward rotation, and positive roll is a clockwise rotation.

Data collection and analysis

The model simulations presented in this paper were compared directly with data obtained from a previous study (Thurtell et al. 1999a). The experimental procedures are briefly summarized here. See Thurtell et al. (1999a) for a complete and detailed description of the experimental setup and protocols.

Two experiments were conducted: one using high-velocity passive (manually generated) yaw head rotations, and the other using high-velocity active (self-generated) yaw head rotations. Eight normal human subjects were tested in each experiment. The head rotation stimuli typically had an amplitude of 15–25° (with peak velocity about 250°/s). The velocity vectors corresponding to the head rotation were approximately aligned with the z-axis of the head-fixed coordinate system (making the rotation predominantly yaw), although the rotations inevitably had pitch and roll components due to the mechanics of the neck joints and soft tissues. During these experiments, responses were recorded using the magnetic search coil technique (Collewijn et al. 1985; Robinson 1963) with subjects maintaining fixation on different targets (20° up, 0° and 20° down) located on a tangent screen 94 cm from the front of the cornea. The search coil signals were digitized at 1 kHz with a 16-bit analog-digital converter. Rotation vectors corresponding to eye-in-head and head-in-space position, and velocity vectors corresponding to eye-in-head and head-in-head angular velocity, were calculated from the search coil data (Haslwanter 1995; Haustein 1989; Hepp 1990; Tweed et al. 1990). Analysis was restricted to a 100-ms period, beginning 20 ms before the onset of head rotation, to exclude the effects of non-VOR systems such as the cervicoocular reflex and smooth pursuit (Bronstein and Hood 1986; Carl and Gellman 1987; Tychsen and Lisberger 1986).

In this study, the data and corresponding model predictions will be presented as time series, and then compared by projecting the predicted eye velocities onto the pitch (xz) and roll (yz) planes. The model predictions from the 100-ms period will be presented, as for data from Thurtell et al. (1999a). The predictions for the entire response will be presented in some cases.

Modeling

The model was implemented using the Microsoft Visual C/C++ programming environment. Integration processes in the model were performed using a regular trapezoidal rule algorithm, with temporal update every 0.001 s. Because the dominant time constant of the system is orders of magnitude larger than this value, the integration technique worked well (Raphan 1998; Yakushin et al. 1998).

Since the model assumed that the reference eye position corresponds with the primary position, we determined primary position from subjects’ Listing’s plane data and recomputed the rotation vectors and velocity vectors relative to primary position. That is, the data were rotated so that each subject’s Listing’s plane aligned with the roll plane of the head-fixed coordinate frame. These computations were conducted using the methods of Tweed et al. (1990). The new coordinate frame, which is close to the stereotaxic coordinate frame, is what we will refer to as being the head-fixed coordinate frame.

The analysis of the model predictions was conducted using MAT-LAB 5.2 running on an IBM-compatible PC under Windows NT. The figures presented in this paper were generated using Splus running on a DECstation 5000/240 under Ultrix, and Canvas (Version 6.0) running on an IBM-compatible PC under Windows NT.

Model organization and conceptual basis for study

OVERVIEW OF THE aVOR MODEL. The model of the aVOR is comprised of a number of major components that, in concert with one another, produce an eye rotation response to a head rotation stimulus (Fig. 1). While detailed descriptions are given elsewhere (Raphan...
axes (roll, pitch, and yaw). The components of the gain matrix (G) describing the canal dynamics, the transformation of the head velocity to aVOR with gain approximately 1.0. The gain matrix was represented as a commutative vector integrator, characterized by gain matrices (G<sub>p</sub> and C<sub>p</sub>) that determines the integrator’s dynamics (see APPENDIX B for further details). The parameters of the velocity-position integrator were set as in Raphan (1998). The magnitudes of rotation of the torque (δ) and the eye (Φ) axes are related by a pulley coefficient, k<sub>Φ</sub> (Fig. 2), such that

\[ \delta = k_\Phi \Phi \]  

The semicircular canal model was based on the canal model presented in Yakushin et al. (1998), a brief description of each of the model components is included below and in APPENDICES A and B.

MODEL OF SEMICIRCULAR CANALS AND VESTIBULAR AFFERENTS. The semicircular canal model was based on the canal model presented in Yakushin et al. (1998). Since each semicircular canal responds to angular acceleration about an axis normal to the canal plane, the canal model must incorporate a kinematic transformation of the head velocity from head-fixed coordinates into canal coordinates. Thus the head velocity is projected onto each of the canal plane normals, which form a nonorthogonal basis in humans. In the model, the orientations of the canals were adjusted to agree with those reported for humans (Blanks et al. 1975).

The canal model also incorporates a first-order dynamical system, to produce vestibular afferent firing that is temporally related to the input angular head acceleration (Yakushin et al. 1998). The dominant time constant for each canal was set to 4 s (Fernández and Goldberg 1971), as there is now evidence that this may be the time constant in humans as well as in monkeys (Dai et al. 1999). The equations describing the canal dynamics, the transformation of the head velocity signal into canal coordinates, and the transformation of the vestibular afferent signal back into head-fixed coordinates are given in APPENDIX A.

The vestibular afferent signals activate second-order neurons in the vestibular nuclei (Waespe and Henn 1977, 1978) (Fig. 1). The sensitivities of the second-order neurons were determined by a gain matrix (G) relating eye rotation to head rotation along each of the coordinate axes (roll, pitch, and yaw). The components of the gain matrix (G<sub>11</sub>, G<sub>22</sub>, and G<sub>33</sub>) were initially adjusted to give gains consistent with those observed during passive roll, pitch, and yaw head impulses (Aw et al. 1996; Thurtell et al. 1999a). Roll rotations produced an aVOR with gain approximately 0.7, while yaw and pitch rotations produced an aVOR with gain approximately 1.0. The gain matrix was represented with respect to head-fixed coordinates. The effects of velocity storage were neglected in the model, since the head rotations being considered in this paper were of short duration (<250 ms).

MODEL OF THE OCULAR MOTOR PLANT. Torque (m) is generated by the extraocular muscles as a result of activity in the motoneurons (m<sub>n</sub>). Due to the effects of the fibromuscular pulleys, the torque axis is rotated in a manner depending on eye position (Fig. 2). For example, when the eye looks up by an angle Φ, the pulley changes the pulling direction of the muscle, thereby rotating the torque axis by an angle δ. In the model, a muscle matrix M implements the transformation from motoneuron firing to torque. M is a rotation matrix that incorporates the actions of the pulleys in three dimensions. The transformation is given by

\[ m = Mm_n \]  

The rotation of the torque axis is about the eye orientation axis, and the angle of rotation is a fraction of the eye rotation angle. The angle of torque axis rotation is determined by a pulley coefficient, k<sub>Φ</sub> (Fig. 2), such that

\[ \delta = k_\Phi \Phi \]  

FIG. 1. Schematic diagram of the 3-dimensional (3-D) model of the vestibuloocular reflex, with saccadic pulse generator. The matrix M, which transforms motoneuron firing into torque, incorporates the pulley effect by bringing about an eye position-dependent rotation of the torque axis. See text for a description of the model and explanations for the symbols.

FIG. 2. The fibromuscular pulleys keep the rectus muscle bellies fixed in the orbit, regardless of the orientation of the eye. However, the pulling directions of the extraocular muscles, and hence the torque axis, are altered in a manner depending on eye position. In the model, the magnitudes of rotation of the torque (δ) and the eye (Φ) axes are related by a pulley coefficient, k<sub>Φ</sub> (figure adapted from Quaia and Optican 1998).
A pulley coefficient of 0.5 constrains the trajectory of a saccadic eye movement driven by a pitch-yaw command, so that it perfectly obeys Listing’s law. A pulley coefficient of 0.0, on the other hand, will result in a large torsional transient and hence a violation of Listing’s law, since there is no tilt of the torque axis during the saccade (Raphan 1998).

The plant itself was modeled as a second-order dynamical system governed by the inertia of the eyeball, viscous damping by the fluid and tissue surrounding the eye, and the elasticity of surrounding membranes. See Appendix B and Raphan (1998) for further details.

Optimal Model Parameters. To determine the optimal pulley coefficient to fit the data in this study, we calculated the pulley coefficient at which the mean square error ($E^2$) between roll eye velocities for data [$\omega_{r,\text{data}}$] and model prediction [$\omega_{r,\text{pred}}$] was a minimum. The pulley coefficient was varied from 0 to 1, in 0.01 increments. The mean square error was computed for each pulley coefficient value as

$$E^2 = \frac{1}{N} \sum_{i=1}^{N} (\omega_{r,\text{data}}[i] - \omega_{r,\text{pred}}[i])^2$$  

where $N$ is the number of samples in the temporal sequence of corresponding model and data sets. Since the data were sampled at 1 kHz and the length of the analysis period was 100 ms, $N$ was equal to 100 in this study. The optimal pulley coefficient, which gave the minimum mean square error, was determined for each subject and eye velocity trajectory, and over a wide range of roll aVOR gains.

It should be noted that the value of the optimal pulley coefficient reflects the pulley configuration only for a given roll gain. If the signal activating the extraocular muscles is a pure pitch-yaw signal, then any tilting of eye velocity axis in the pitch plane occurs due to the pulley effect. If there is a roll component to the signal, as during vestibular slow phases, eye position—dependent tilting of the eye velocity axis in the pitch plane may occur due to the pulley effect and/or due to an eye position—dependent alteration in the roll signal activating the muscles.

**RESULTS**

Data-model comparison for active head impulses

Subject 0031m executed active yaw head impulses that had a large yaw component, and minimal pitch and roll components throughout the head movement (Fig. 3A). The initial fixation point of the subject did not affect the starting head position or the head trajectory (Thurtell et al. 1999a). When the subject was looking 20° up, the yaw and pitch eye velocities approximately compensated for the yaw and pitch head velocities, respectively (Fig. 3A, heavy and dashed shaded lines). However, the roll eye velocity was inappropriately clockwise, as there was little roll head velocity. When the subject was fixating a central target, all components of eye velocity were approximately compensatory for the head velocity stimulus. When the subject was looking 20° down, the yaw and pitch eye velocities compensated for the yaw and pitch head velocities, but the roll component was again inappropriate (as in the 20°

![Active Head Impulses (subject 0031m)](image-url)
up condition), on this occasion being counterclockwise. These patterns are consistent with those observed in data collected from human subjects during low-frequency yaw oscillations (Misslisch et al. 1994). A complete description and analysis of the data for a range of subjects can be found in Thurtell et al. (1999a).

The head velocity trajectories from the data were used as input for the model, as were the initial eye position data. The curve representing mean square error between data and model torsional eye velocities, as a function of pulley coefficient, was approximately parabolic for both upward (Fig. 4, – – –) and downward (Fig. 4, · · · ·) gaze. For the 0° initial fixation position, the mean square error was not of great magnitude and varied little over the range of pulley coefficients (Fig. 4, · · ·). The curve representing the mean square error for the average of all gaze positions had a minimum corresponding to a pulley coefficient of 0.53 (Fig. 4, 2).

Consistent with the finding that a pulley coefficient of 0.53 closely predicted the time course of the torsional component of eye velocity (Fig. 5A, middle), the axis tilt was also predicted at every instant of time during the response (Fig. 5B, middle). When the pulley coefficient was reduced to 0.00, thereby removing the effect of the pulleys, the torsional eye velocity mirrored torsional head velocity (Fig. 5A, bottom), resulting in approximate head and eye velocity axis alignment independent of eye position (Fig. 5B, bottom).

**FIG. 4.** Averaged mean square error (between data and predicted torsional eye velocities) plotted as a function of pulley coefficient ($k_F$), for subject 0031m executing active head impulses. The curves are approximately parabolic for fixation 20° up and 20° down. The curve for fixation at 0° is flat, indicating that the pulleys do not alter the roll eye velocity when fixation is near the primary position. The mean curve is parabolic; the minimum occurs when the pulley coefficient is 0.53.

**FIG. 5.** A: time series of torsional head and eye velocity data (top) from subject 0031m executing active head impulses, averaged from 20 ms before to 80 ms after head impulse onset. The small arrow indicates the time of head impulse onset. The model predicts the magnitude and direction of the torsional eye velocity when the pulley coefficient ($k_F$) is optimal (0.53) (middle). However, when the pulley coefficient is equal to 0, the model predicts loss of eye position-dependence; torsional eye velocity becomes compensatory for torsional head velocity (bottom). B: the averaged velocity vectors are plotted in the pitch plane for eye velocity data (top) and eye velocity modeled with pulley coefficients of 0.53 (middle) and 0 (bottom). Note that the roll eye velocity and, hence, velocity axis alignment is little affected by the change to the pulley coefficient when the fixation position is near the primary position (near 0° in this subject).
Active Head Impulses (all subjects)

A Mean Velocity Data (n=8)

B Mean Model Prediction (k_F = 0.5) (n=8)

Fig. 6. A: mean head and eye velocity data from active head impulses, averaged across 8 subjects, are plotted in the pitch (top) and roll (bottom) planes. B: for the optimal pulley coefficient (k_F), 0.5, the model predicts the direction and magnitude of the eye position–dependent axis tilts.

We also compared the averaged data from eight subjects (Fig. 6A), with model predictions (Fig. 6B). The optimal pulley coefficient value for each subject is given in Table 1. Seven of the subjects had optimal pulley coefficients ranging from 0.27 to 0.58, with only one of the eight subjects having an optimal pulley coefficient <0.25. While the mean square error curves from the subjects demonstrate a single minimum, the gradient of the curve for most subjects was small over a broad range of values close to the optimal pulley coefficient, representing a relative insensitivity in using this method for determining optimal model parameters. However, introducing weights to different parameters would bias our results and would not increase confidence in our findings.

The optimal pulley coefficient across all subjects occurred when the median of the mean square error over all trials and subjects was minimal; it was found to be 0.5 (Fig. 7A; Table 1).

Data-model comparison for passive head impulses

As previously shown (Thurtell et al. 1999a), there are eye position–dependent velocity axis tilts during passive head impulses as during active head impulses. The optimal pulley coefficient for passive head impulses was computed in all subjects using a gain matrix equal to that used for active head impulses; the values of these pulley coefficients are given in Table 1. Subjects’ optimal pulley coefficients ranged from 0.03 to 0.31. The optimal pulley coefficient was calculated across all subjects, as for the active head impulses; it was found to be 0.21 (see Fig. 7B; Table 1).

For subject 0036m, the optimal pulley coefficient was found to be 0.19 for a roll gain of 0.7. Using this value of pulley coefficient, the model predicted the fundamental features of the axis tilts (Fig. 8). However, the dynamics of the axis tilts

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Median optimal k_F 0.5 Median optimal k_F 0.21
Mechanisms for VOR eye position-dependence

When Misslisch et al. (1994) studied eye position–dependent eye velocity axis tilts in humans using 0.3-Hz sinusoidal whole-body rotations, they noted that the tilts were consistent with a compromise between Listing’s law and perfect compensation for head rotation. After studying the predictions of the SQUINT model of extraocular muscle geometry (Miller and Robinson 1984), they concluded that the central signals driving the extraocular muscles must already encode the appropriate eye velocity axes, and that orbital mechanics contribute very little to the production of the tilts. They had not, however, considered the effects of the rectus fibromuscular pulleys (Clark et al. 1998, 1999; Demer et al. 1995, 1997; Miller et al. 1993) in their study. Preliminary work by Raphan (1997) indicated that the pulleys might have an important role in bringing about the tilts. More recently, however, it has been suggested that even with an ocular motor plant that incorporates pulleys, no integrator model can predict the eye position dependence of the aVOR, and consequently a neural integrator that is quaternion-based and noncommutative is required (Smith and Crawford 1998; Tweed 1997). However, our model, which incorporates a commutative vector velocity-position integrator, muscle pulleys, and a three-dimensional semicircular canal system, predicts the axis tilts.

The role of the pulley system was first considered in studies concerned with modeling eye movement trajectories during saccades. In those studies, it was shown that if the pulleys are correctly positioned and the command signal is confined to the pitch-yaw plane, kinematically accurate saccades can be produced by models that incorporate a commutative vector velocity-position integrator (Quaia and Optican 1998; Raphan 1997, 1998). The value of the pulley coefficient is critical in the saccadic model, because it determines the magnitude of the eye velocity axis tilt when the driving signal is in the pitch-yaw plane. It is therefore possible that a combination of dynamic pulley coefficient and roll gain modification is responsible for producing the initial axis alignment for each subject.
FIG. 8. Head and eye velocity data from subject 0036m during passive head impulses is plotted in the pitch plane (top). While the model predicts the general features of the eye position–dependent axis tilts (bottom), when the pulley coefficient \( k_F \) is optimal for that subject’s data (0.19), it does not predict the initial alignment of the eye and head velocity axes (for example, at the arrows).

FIG. 9. Head and eye velocity data from subject 0030m during passive head impulses is plotted in the pitch plane (top). Only the velocity data \( \leq 100^\circ/s \) have been plotted. For this range, there is almost perfect eye and head velocity axis alignment for each fixation position. The model was unable to predict perfect axis alignment when the pulley effect was eliminated \( (k_F = 0) \), although there was no eye position dependence (middle). However, when the pulley coefficient was maintained at 0.5, axis alignment could be achieved by modification of the angular vestibuloocular reflex (aVOR) roll gain (bottom). The roll gains required to bring about axis alignment are indicated.
impulses, the model accurately predicted, on average, the variance in eye velocity axis tilt as a function of eye position and head velocity. Thus the model predicts that the axis tilt patterns may essentially arise as a result of two factors: the pulley effect and the less-than-unity roll gain. As we have shown, a pulley coefficient of 0.0 gives approximate eye and head velocity axis alignment and no eye position dependence (Fig. 5B, bottom), whereas a pulley coefficient of 0.5 would tilt the eye velocity axis by half the angle of gaze deviation from primary position. A pulley coefficient <0.5 gives an eye velocity axis tilt that is less than half the angle of gaze eccentricity. The less-than-optimal roll gain of the aVOR (which is ~0.7 during passive head impulses) would further diminish the relative tilt of the eye velocity axis if there is a roll component to the head movement. Variations in the pulley configuration and roll gain between individuals, in addition to different stimulus and species characteristics, could account for the variations in the amount of tilt from subject-to-subject and for the differing results reported in different studies. Thus for active head impulses, there is no need to postulate an axis tilting mechanism in the central vestibular structures (Müller and Tordai 2000). We found that removing the effect of the orbital layers of the rectus muscles (Raphan 1998) to bring about this simple result.

**Passive-active differences**

While the tilt of the eye velocity vector as a function of eye position was a prominent aspect of the response to active head impulses, there were striking differences when active and passive head impulses were compared (Thurtell et al. 1999a). For active head impulses, the tilts became apparent within the first 5 ms of the response and were maintained throughout the trajectory, as predicted by the model. For passive head impulses, there was little tilt of the eye velocity axis during the first 50 ms (Thurtell et al. 1999a). These findings are consistent with data showing negligible axis tilt in the averaged eye velocity vectors during the first 10° of head movement during passive head impulses (Palla et al. 1999). The axis of eye velocity was noted to tilt gradually after the initial 50 ms period (Thurtell et al. 1999a). Thus passive head impulse axis tilts are not uniform over time but evolve over the duration of the head trajectory. We found that the initial alignment of the eye and head velocity axes was inconsistent with model predictions for a fixed pulley coefficient of 0.5 and a fixed aVOR roll gain of 0.7.

We considered a number of mechanisms that might be responsible for the temporal evolution of eye velocity axis tilt. Dynamic changes in pulley effect may arise as a result of the insertion of the orbital layers of the rectus muscles into the connective tissue of the pulley structures (Demer et al. 2000). We found that removing the effect of the pulleys, by adjusting the pulley coefficient to 0.0 and maintaining the roll gain of the aVOR at 0.7, resulted in closer initial axis alignment and loss of eye position-dependence. The model still did not, however, predict the degree of alignment observed in the data. Thus a dynamic modification in pulley coefficient could not completely account for the initial axis alignment during passive head impulses. In addition, such a peripheral mechanism would have to be specific to the passive aVOR because these dynamic changes in eye velocity axis tilt were not observed during
active head rotations and have not been observed during the execution of saccades.

We considered whether the axis tilts were due to a neural-based preprogrammed mechanism, which was delayed and therefore responsible for the initial axis alignment. Eye velocity tilting is functionally appropriate for eye positioning mechanisms, such as the saccadic system, which attempt to reduce torsional transients and maintain the eye orientation axis within Listing’s plane. Relative tilting of the eye and head velocity axes is functionally counter to the goal of the aVOR, which is to compensate for head velocity both in magnitude and direction, thereby bringing about retinal image stabilization. Thus a preprogrammed mechanism to misalign the eye and head velocity axes would be functionally inappropriate for the aVOR and unlikely to be responsible for generating the axis tilts.

In contrast to preprogrammed axis tilts, we found that the axis alignment could be predicted well by modifying the roll gain of the aVOR during the initial 50-ms period while maintaining the pulley coefficient at a constant value of 0.5. It is important to note that an almost perfect match to the data could be produced using a number of combinations of pulley coefficient and aVOR roll gain (Fig. 10). Therefore either a dynamic roll gain modification or dynamic change in pulley effect, or a combination of both, could be responsible for producing the initial axis alignment during passive head rotations. The roll gain modification would constitute a form of eye position–dependent processing in central vestibular structures, which would help counteract the tilting of the eye velocity axis produced by the pulleys, to bring the eye and head velocity axes into better alignment. A roll gain modification may be required in the aVOR and not during saccades because of their essentially different functional roles. The saccadic system functions to move the eyes from one fixation point to another. It is, therefore of benefit if the velocity axis tilts to minimize positional roll transients (Raphan 1998). The aVOR, on the other hand, functions to minimize retinal slip. It is, therefore inappropriate for the eye velocity axis to tilt. The roll gain modification that we are proposing is entirely different from other proposed mechanisms, such as the saccadic system, which attempt to reduce torsional transients because of their essentially different functional roles. The saccadic system functions to move the eyes from one fixation point to another. It is, therefore of benefit if the velocity axis tilts to minimize positional roll transients (Raphan 1998). The aVOR, on the other hand, functions to minimize retinal slip. It is, therefore inappropriate for the eye velocity axis to tilt. The roll gain modification that we are proposing is entirely different from other proposed forms of eye position–dependent central processing, because it brings about eye and head velocity axis alignment and increased retinal image stability, rather than the axis tilt and decreased retinal image stability that would result from the other mechanisms (Misslisch et al. 1994).

While it is probable that the pulleys are responsible for producing the observed axis tilts, as they have been anatomically demonstrated, the site of the proposed roll gain change is not clear. One possibility is that the otoliths are involved in the gain modification. During these yaw head rotations, there would be centripetal acceleration generated at each macula due to their eccentricity relative to the rotation axis of the head. During head-on-neck yaw rotations, the head rotates about the atlantooccipital joint. The distance from this rotation axis to the maculae is <5 cm (Curthoys et al. 1977). As the velocity during the initial 50 ms of rotation is <200°/s, the centripetal acceleration at each macula would be very small (<0.05 g). In addition, the centripetal accelerations at each macula would be toward the rotation axis. The effect would be similar to accelerating forward and would not be expected to generate strong compensatory roll eye velocity. Indeed, there has been no report of compensatory roll eye velocity during fore-aft acceleration in squirrel monkeys (Paige and Tomko 1991). Furthermore, the latency of compensatory linear vestibuloocular reflex responses are in the order of 25 ms (Bronstein and Gresty 1988), so the effects we are examining would almost be over by that time. Therefore it is unlikely that the otoliths significantly contribute to the responses of either active or passive head impulses in normal human subjects.

The alterations in roll gain may be, in part, related to rapid feedback from the roll state of the velocity-position integrator to the secondary vestibular neurons. Such a mechanism would affect the dynamics of vestibular-evoked eye movements, although its effect on saccades is probably negligible, since the roll state of the velocity-position integrator is inactive during saccades in our model (see Raphan 1998). More fundamental physiological studies are required to determine where such a roll gain change might occur in the central vestibular structures.

Recent evidence has been presented that neuron responses in the vestibular nucleus may be attenuated during active head movements (Cullen and Roy 1999; McCrea et al. 1999) and may be related to the mechanism that disables a roll gain modification during active head movements. Cullen and Roy (1999) found that some, but not all, neuron responses were attenuated during the gaze stabilization period of an active head movement. McCrea et al. (1999) suggested that reafferent neck proprioceptive and efference copy signals could be responsible for the attenuation.

The underlying functional reason for the different dynamic characteristics of the axis tilts in passive and active head impulses may result from the different goals of the system during these types of movements. Roll gain modification may not occur during active head impulses because the goal of the system during normal eye-head refixations is to shift gaze from one target to another, rather than maintain fixation on a fixed target. For these refixations, there is considerable preprogramming but no effort to stabilize the retinal image initially. Hence there is no reason for the roll gain of the aVOR to be modified in the initial phase of the response to active head rotations. In fact, normal aVOR function is probably suppressed during the initial period of active eye-head refixations (Laurutis and Robinson 1986), supporting the idea that the proposed modification of the initial roll gain of the aVOR during passive head impulses might be suppressed during active head impulses. Passive head movements may therefore be unmasking an important underlying functional component of the pure aVOR.

**Optimal pulley coefficient calculations**

The optimal pulley coefficient varied considerably between subjects during the active head impulses, ranging from 0.15 to 0.58. Five of the eight subjects had optimal pulley coefficients between 0.39 and 0.6, a range that can be used to predict normal saccadic torsional transients (Raphan 1998). Our data on the range of pulley coefficients are therefore consistent with the finding that there are large and reproducible inter-individual differences in both the magnitude and direction of torsional transients in normal subjects (Fig. 4d in Straumann et al. 1995). Our findings on the range of optimal pulley coefficients are also consistent with the corresponding range of eye velocity tilt.
angles that have been reported when making saccades from secondary to tertiary positions (Table 1 in Palla et al. 1999).

The optimal pulley coefficients calculated for the passive head impulse stimulus also varied considerably between subjects and were, on average, smaller in magnitude in comparison with the values obtained for active head impulses. However, as discussed above (see Model organization and conceptual basis for study), the values of the optimal pulley coefficient that we have reported do not necessarily reflect the actual configuration of the pulleys in the plant. Hence we are unable to determine the actual pulley configuration in subjects’ orbits from the calculated optimal pulley coefficient value. The trajectories of saccadic eye movements would be more useful for determining actual pulley configuration, as any eye velocity axis tilt that occurs during these eye movements presumably arises due to the effect of the pulleys alone (Raphan 1998). We have shown, however, that in response to passive head impulses the same eye velocity data can be closely predicted with a number of different combinations of pulley coefficient and roll aVOR gain. Indeed, the pulley coefficient need not be changed from 0.5 to achieve the desired effect; the data can be predicted just by changing roll aVOR gain. Therefore it is possible to have a fixed pulley configuration in the orbit that would not require radical readjustment to execute different types of eye movements.

In summary, we have presented a model of the aVOR that incorporates the kinematics and dynamics of the semicircular canals, central processing through a modifiable gain matrix, a vector velocity-position integrator, and an ocular motor plant that includes muscle pulleys. With muscle pulleys present, the model predicted the eye position–dependent axis tilts that occur during both active and passive head impulses. Removal of the pulley effect resulted in loss of aVOR eye position–dependence and approximate eye and head velocity axis alignment. It was possible to predict the initial alignment of the eye and head velocity axes, seen in response to passive head impulses, by introducing an eye position–dependent modification in the roll gain of the aVOR. A change in pulley effect alone was insufficient to bring about perfect eye and head velocity axis alignment for those data, but a combination of changing pulley effect and roll gain change was found to be as effective as a roll gain change alone. So, the presence of pulleys takes away the need for the axis tilts to be centrally programmed, and the roll gain modification serves as a means of counteracting the pulley effect, to produce good axis alignment and retinal image stabilization during high acceleration impulsive head rotations.

**APPENDIX A**

The model of the three-dimensional semicircular canals (Fig. 1) was simplified from vector Eqs. 9–18 given in Yakushin et al. (1998)

\[
\frac{dx_{\text{cup}}}{dt} = T^{-1}_{\text{can}}(T_{\text{can}}\omega_h - x_{\text{cup}})
\]

\[\omega_h = T^{-1}_{\text{can}}x_{\text{cup}} - \omega_h\]  

(A1)

where \(x_{\text{cup}}\) is the cupula state, \(\omega_h\) is the angular head velocity, and \(\omega_h\) is the vestibular afferent signal, referenced to the head-fixed coordinate frame. The matrix \(T_{\text{can}}^{-1}\) which transforms head velocity from head-fixed to canal coordinates, is given by

\[
T_{\text{can}} = \begin{bmatrix}
\cos \theta_5 \cos \phi_5 & \sin \phi_5 & -\sin \theta_5 \cos \phi_5 \\
-\cos \theta_5 \cos \phi_5 & \cos \phi_5 & \sin \theta_5 \sin \phi_5 \\
\sin \phi_5 & \sin \phi_5 & \cos \theta_5 \\
\end{bmatrix}
\]

(A2)

where \(\theta_5 = \theta_i = -40^\circ, \phi_5 = \phi_i = 135^\circ, \phi_5 = 0^\circ, \) and \(\theta_i = -30^\circ\) (Yakushin et al. 1998). \(T_{\text{can}}^{-1}\) transforms the vestibular afferent signal from canal coordinates back into head-fixed coordinates. The diagonal matrix \(T_c\) is given by

\[
T_c = \begin{bmatrix}
4 & 0 & 0 \\
0 & 4 & 0 \\
0 & 0 & 4 \\
\end{bmatrix}
\]

(A3)

\(T_c\) represents the cupula time constant of all canals in the head-fixed coordinate frame. Since we studied the responses of normal subjects, we assumed that the time constants for all canals were identical. When the time constants are altered for specific canals, such as when plugged, more general equations must be utilized (see Yakushin et al. 1998).

**APPENDIX B**

The velocity-position integrator (Fig. 1) was implemented in the model as in Raphan (1998)

\[
\frac{d}{dt} x_p = H_p x_p + G_p w
\]

\[m_p = C_p x_p + D_p w\]  

(B1)

where \(x_p\) is the integrator state, \(w\) drives the integrator, and \(m_p\) is the motoneuron activity. The matrices were chosen as

\[
H_p = -0.03333/s \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}
\]

\[G_p = 0.03333/s \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}\]

\[
C_p = 59.0 \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}
\]

\[D_p = 0.278 \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}\]

(B2)

The plant was approximated by a second-order system, given by

\[
\frac{d}{dt} \omega = -\Omega_h \omega - \frac{d}{dt} \omega_h - J^{-1}(B \omega + K \Phi \hat{n}) + J^{-1}m
\]

(B3)

where \(\omega\) is the eye velocity relative to the head, \(\omega_h\) is the head velocity relative to space, and \(\Phi \hat{n}\) is the orientation of the eye relative to the head. \(\Omega_h\) is given by

\[
\Omega_h = \begin{bmatrix} 0 & -\omega_{hx} & -\omega_{hy} \\ \omega_{hx} & 0 & -\omega_{hz} \\ -\omega_{hy} & \omega_{hz} & 0 \end{bmatrix}
\]

(B4)

where \(\omega_{hx}, \omega_{hy},\) and \(\omega_{hz}\) are the components of head velocity relative to space.

The matrices in the equations were chosen as

\[
J = 5 \times 10^{-7} \text{ kg} \cdot \text{m}^2 \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}
\]

\[
K = 4.762 \times 10^{-4} \text{ kg} \cdot \text{m}^2/\text{s}^2/\text{rad} \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}
\]

(B5)

\[
B = 7.47 \times 10^{-7} \text{ kg} \cdot \text{m}^2/\text{s}^2/\text{rad} \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}
\]
A complete derivation of these equations and a description of how eye orientation is updated based on the Euler-Rodriguez equations can be found in Raphan (1998).

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