

Modeling Control of Eye Orientation in Three Dimensions. I. Role of Muscle Pulleys in Determining Saccadic Trajectory

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Raphan, Theodore. Modeling control of eye orientation in three dimensions. I. Role of muscle pulleys in determining saccadic trajectory. *J. Neurophysiol.* 79: 2653–2667, 1998. This study evaluates the effects of muscle axis shifts on the performance of a vector velocity-position integrator in the CNS. Earlier models of the oculomotor plant assumed that the muscle axes remained fixed relative to the head as the eye rotated into secondary and tertiary eye positions. Under this assumption, the vector integrator model generates torsional transients as the eye moves from secondary to tertiary positions of fixation. The torsional transient represents an eye movement response to a spatial mismatch between the torque axes that remain fixed in the head and the displacement plane that changes by half the angle of the change in eye orientation. When muscle axis shifts were incorporated into the model, the torque axes were closer to the displacement plane at each eye orientation throughout the trajectory, and torsional transients were reduced dramatically. Their size and dynamics were close to reported data. It was also shown that when the muscle torque axes were rotated by 50% of the eye rotation, there was no torsional transient and Listing's law was perfectly obeyed. When muscle torque axes rotated >50%, torsional transients reversed direction compared with what occurred for muscle axis shifts of <50%. The model indicates that Listing's law is implemented by the oculomotor plant subject to a two-dimensional command signal that is confined to the pitch-yaw plane, having zero torsion. Saccades that bring the eye to orientations outside Listing's plane could easily be corrected by a roll pulse that resets the roll state of the velocity-position integrator to zero. This would be a simple implementation of the corrective controller suggested by Van Opstal and colleagues. The model further indicates that muscle axis shifts together with the torque orientation relationship for tissue surrounding the eye and Newton's laws of motion form a sufficient plant model to explain saccadic trajectories and periods of fixation when driven by a vector command confined to the pitch-yaw plane. This implies that the velocity-position integrator is probably realized as a subtractive feedback vector integrator and not as a quaternion-based integrator that implements kinematic transformations to orient the eye.

INTRODUCTION

Studies of eye rotation about a yaw axis have led to a model that posits a neural velocity-position integrator that transforms central velocity command signals into position-related signals that drive the oculomotor plant (Robinson 1971, 1973, 1975; Skavenski and Robinson 1973). When modeling eye movements in three dimensions, a natural extension of the velocity-position integrator to three dimensions would be a vector feedback integrator whose output corresponds to the roll, pitch, and yaw axis of the head. Tweed and Vilis (1987) have argued that such

an extension would not give appropriate eye positions, because of the noncommutativity of eye rotations. Rather, they proposed a quaternion-based "multiplicative" three-dimensional neural velocity-position "integrator" that codes the three-dimensional kinematics of eye rotation from the primary position relative to the head (Tweed and Vilis 1987, 1988, 1990). This will be referred to as the "quaternion model." Key assumptions of the model are as follows. 1) The axes corresponding to the pulling direction of the eye muscles remain fixed relative to the head. 2) The parameters of the "quaternion integrator" are precisely matched to those of the plant so that the output of the quaternion integrator is equal to the orientation of the eye. 3) Eye velocity is equal to the neural signal driving the quaternion integrator (Tweed and Vilis 1987). Because of the construct of the quaternion-based model, all saccades have fixed axes of rotation (Tweed and Vilis 1987). If these axes were confined to a single plane, Listing's law (Helmholz, 1867) would be obeyed not only for each eye position, but during the saccadic trajectory as well (Tweed and Vilis 1987). This model has led to the postulate that there is a "Listing's law operator" governing saccades in the CNS (Crawford and Vilis 1991; Hepp 1994; Hepp et al. 1992; Tweed and Vilis 1990; Crawford 1997), although at present there is no evidence for such a specialized operator.

A basic difficulty associated with the quaternion model is that it is conceptually based on rejecting the subtractive integrator model (Tweed and Vilis 1987) without a full exploration of its performance capabilities. Tweed and Vilis (1987) concluded that "subtractive feedback models must continuously adjust the axis of rotation throughout a saccade, and they generate meandering, dysmetric gaze saccades." This conclusion, however, was based on examining the integrator's output and not on the eye orientation, and there is no a priori reason for these variables to be identical. If the output of the velocity-position integrator is to drive the motoneurons, which in turn drive the eye muscles, the velocity-position integrator output should be more closely related to torque than to eye orientation. Because torque is a vector quantity (Halliday and Resnick 1978), it has commutative properties. Eye rotations are not vectors and do not obey commutative relationships. Therefore, to appropriately evaluate the subtractive feedback vector integrator model of velocity-position, the properties of the plant that relate these two disparate mathematical objects need to be investigated.

Schnabolk and Raphan (1994) devised a model for relating torque to orientation based on the idea that there is passive elastic restoring torque developed by the orbital tissue (Collins 1971; Collins et al. 1969; Levin and Wyman 1927; Robinson 1964; Robinson et al. 1969), which would restore the eye to primary position as it rotates. The crucial relationship between torque that has commutative properties and eye orientation that has noncommutative properties was represented by $T(R) = K\Phi\hat{n}$ (Schnabolk and Raphan 1994). The function $T(R)$ is the restoring torque, $\Phi\hat{n}$ is the axis-angle representation of eye rotation from primary position, and K is the elasticity of the surrounding tissue. This simple relationship expresses the idea that the elastic restoring torque is always along an axis that would optimize the rotation back to the primary position and is proportional to the angle of eye rotation (Schnabolk and Raphan 1994). In the steady state, the restoring torque is equal to the applied muscle torque, and equilibrium is reached. When the orbital tissue torque-orientation equation is incorporated into Newton's equation of motion governing the rotation of the eye, it forms a three-dimensional dynamic model of the oculomotor plant. Using this plant model, Schnabolk and Raphan (1994) proposed a "vector integrator model" of the velocity-position integrator that drives the motoneurons that innervate the muscles, which in turn generate the torque to position the eye. During eye movements, the velocity-position integrator combines with the direct pathway to determine the saccadic trajectory in the presence of counter-torque due to viscous damping and elasticity.

The vector and quaternion integrator models were compared, assuming that the muscle axes remained fixed in the head during eye rotations. The vector integrator model predicted saccadic trajectories accurately for eye movements smaller than $\sim 15^\circ$ (Schnabolk and Raphan 1994). None of the nonphysiological type of eye movements, such as dysmmetric or meandering saccades, attributed to the vector integrator model (Tweed and Vilis 1987), actually occurred (Schnabolk and Raphan 1994). The models were also compared regarding their prediction of Listing's law. Operationally, the quaternion integrator lacks dynamic components and predicts that Listing's law is perfectly satisfied throughout the saccadic trajectory (Hepp et al. 1992; Tweed and Vilis 1987, 1990). In the vector-integrator model (Schnabolk and Raphan 1994), Listing's law is generated naturally if the pulses driving the velocity-position integrator have only pitch and yaw components and no roll components in head coordinates. Under the assumption of fixed muscle axes, however, the vector-integrator model predicts that Listing's law is only satisfied for steady-state eye orientations and during centripetal and centrifugal saccadic trajectories. This is because in the steady state the applied and restoring torques remain aligned. During saccadic trajectories from secondary to tertiary positions, when the torques are not aligned, Listing's law is only approximately satisfied. Under these circumstances small deviations from Listing's law were predicted. For saccadic eye movements of $< 15^\circ$, which constitute the majority of spontaneous eye movements, the predicted deviations from Listing's law are well within experimental variations in Listing's plane (Schnabolk and Raphan 1994).

A number of experiments have been performed to test the predictions of the vector-integrator model (Straumann et al. 1995; Tweed et al. 1994). The results indicate that contrary to the quaternion model predictions (Tweed and Vilis 1987), but as predicted by the vector-integrator model (Schnabolk and Raphan 1994), there are transient roll components, i.e., "roll blips," during saccadic trajectories from secondary to tertiary eye positions (Straumann et al. 1995; Tweed et al. 1994) that violate Listing's law. However, simulations of large saccades by the vector integrator model (Tweed et al. 1994) predicted considerable discrepancies between the predicted torsional transients and the experimental data.

Raphan (1997) had suggested that the reason for the discrepancies between the vector integrator model and data were that the data exceeded the bounds of definition of the model. It was assumed in the development of the vector integrator model that the muscle-torque axes were fixed in the head and did not vary as a function of eye orientation, a postulate in both the vector and quaternion models (Schnabolk and Raphan 1994; Tweed et al. 1994). This assumption was based on the idea that the muscle bellies were stable and the point of tangency of the muscle and globe remained fixed relative to the orbit (Miller and Robins 1987; Miller and Robinson 1984; Robinson 1975). As a consequence, the plane determined by point of tangency, muscle origin, and the center of rotation, whose normal is the torque axis, would remain approximately fixed in the head (Miller and Robins 1987). For small eye deviations ($< 15^\circ$) from primary position, this is a good approximation, and the muscle matrix could be chosen as a constant diagonal matrix. However, for large gaze shifts, this approximation may not be valid. Studies using magnetic resonance imaging (MRI) and surgical division of the membranes during transposition surgery showed that there is little or no affect on muscle paths even for large gaze shifts (Miller 1989; Miller et al. 1993). More detailed analysis of the muscle paths indicated that there are pulleys that would alter the torque axes and the resultant muscle matrix as the eye moves into different orientations (Demer and Miller 1995; Miller 1989).

The purpose of this study was to extend the vector integrator model to include the effects of muscle axis shifts due to eye muscle pulleys. Because the pulleys rotate the torque vector on the eyes, as the eye moves, it was of interest to study their effects on eye movement trajectories and the implementation of Listing's law during saccades as well periods of fixation. Aspects of this work have been presented in preliminary form (Raphan 1997).

METHODS

Model simulations were developed using the Microsoft Visual C/C++ programming environment. The output of the model was sent as a file to a MacIntosh computer where the output files were graphically represented using Canvas 3.1.

Coordinate conventions

To facilitate comparisons between the results presented in this study and those obtained by others (Straumann et al. 1995;

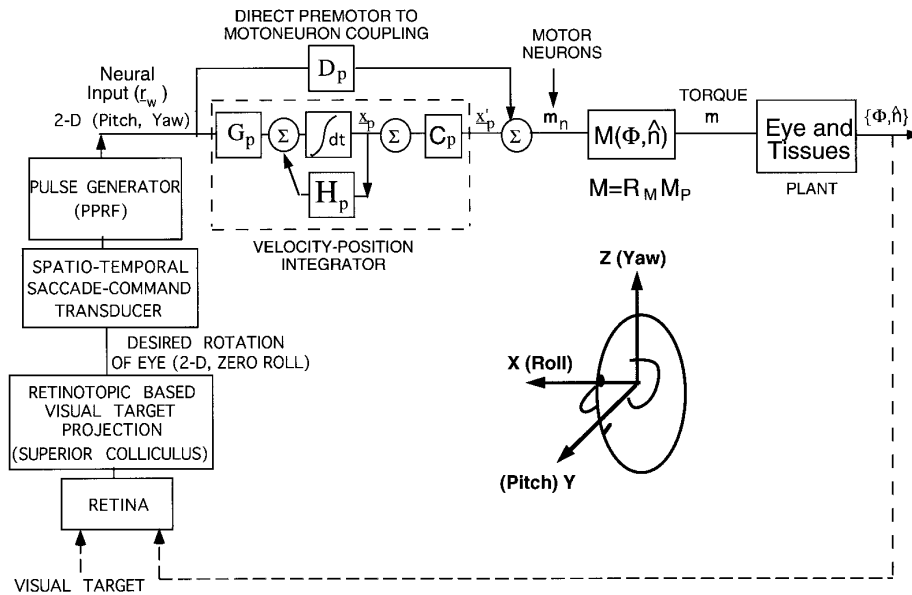


FIG. 1. Three-dimensional model of eye movement control mechanism for visually guided saccades. See text for details.

Tweed et al. 1994), the head-based coordinate convention was chosen in accord with the coordinate system utilized by Tweed et al. (1994). Positive roll is chosen along the naso-occipital axis emanating from the nose. The positive pitch axis comes out of the left ear, and the positive yaw axis out of the top of the head (see Fig. 1, *insert*). This convention, a modification of the coordinate frame utilized by Schnabolk and Raphan (1994) and Raphan (1997), changes the direction of the positive roll axis, using the sequence of vector components as (roll, pitch, yaw) rather than (pitch, roll, yaw).

RESULTS

Conceptual basis and model organization

The organizational model of the saccadic orienting mechanism in three dimensions is shown in Fig. 1. It is assumed that when the eye is in a given orientation, $\{\Phi, \hat{n}\}$, a visual target will project onto the retina at some position relative to the fovea. The displacement is coded in the retinotopic projection of the superior colliculus (Robinson 1972; Van Opstal et al. 1991), whose output generates a desired rotation of the eye, which will align the visual axis with the target axis relative to the head. The desired rotation of the eye that is spatially coded in the superior colliculus is processed by a spatiotemporal saccade-command transducer to drive the pulse-generating network in the paramedian pontine reticular formation (PPRF) (Cohen and Henn 1972a,b; Henn and Cohen 1976; Hepp et al. 1989; Keller 1974). The Neural Input (\mathbf{r}_w) in the model is the output of the pulse-generating network and drives the Velocity-Position Integrator as well as the Direct Premotor to Motoneuron Coupling. The sum of the output of the "velocity-position" integrator dynamical system (\mathbf{x}'_p) and the direct premotor to motoneuron coupling drives the motoneurons (\mathbf{m}_n). The motoneuron signal generates the muscle torque (\mathbf{m}) to orient the eye.

When the eye is fixed in a given orientation, equilibrium is reached between the restoring torque developed due to eye rotation from the primary position and the applied torque from the integrator signal. Thus the state

of the integrator is a "position" command that approximates the orientation of the eyes during periods of fixation or for input frequencies well below the reciprocal of the dominant time constant of the eye plant. An important aspect of the model is that all signals up to and including the torque are neural vector signals. The operators G_p , C_p , and H_p associated with the velocity-position integrator as well as D_p , associated with direct Premotor to Motoneuron Coupling, are vector transformations on the neural vector signals. The transformation M , transduces the neural vector signal to a torque vector generated by the eye muscles. Thus all signals obey rules of commutativity associated with vector addition. On the other hand, eye orientation does not obey the rules of commutativity and cannot be represented by a vector. Thus the eye plant dynamical system in three dimensions is an important dynamical transformation that must convert torque, that is a vector, to orientation, which is not a vector.

We will now show that by incorporating pulleys into the muscle transformation, a two-dimensional neural signal, confined to the pitch-yaw plane can explain the dominant features of saccadic trajectories as well as the steady-state behavior without the need for a quaternion integrator.

Modeling rotational kinematics of the eye

The rotational kinematics of the eye relative to the head can be described by a rotation matrix whose columns represent an orthonormal basis (Lang 1966) attached to the eye. The rotation matrix can be parameterized in a number of ways (Altmann 1986). In oculomotor studies, rotations of the eye have been parametrized using Euler angles (Collewyn et al. 1988; Fick 1854; Helmholtz 1867; Nakayama 1978) and variations of Euler-Rodriguez parameters such as quaternions (Altmann 1986; Tweed and Vilis 1987), rotation vectors (equivalent to the Euler Symmetric Parameters) (Haustein 1989; Klein 1884), and axis-angle representations (Altman 1986; Goldstein 1980; Schnabolk and Raphan

1994; Tweed et al. 1994). The dynamics of eye rotations can then be described as a dynamical system relating the rates of change of the parameters, such as axis-angle, in terms of their values at any given time (Schnabolk and Raphan 1994).

A conceptually simpler, but more sophisticated method for describing the dynamics of the rotation than is presented in Schnabolk and Raphan (1994), is to consider any eye orientation as comprised of a sequence of incremental rotations from the primary position to the final eye orientation. The trajectory of the eye is then governed by eye velocity, which determines the incremental rotation at any intermediate eye orientation. This can be implemented as a matrix dynamical system that is more easily programmed to perform the simulations. Mathematically, this can be described as follows.

Let $R(t)$ be the rotation matrix associated with the eye position in the head at any given time, t . Further, let $R(t + \Delta t)$ be the rotation matrix at time, $t + \Delta t$, and $R_{\text{inc}}(t)$ be the incremental rotation at time, t , due to an eye velocity, ω , which will take the eye from orientation, $R(t)$ to $R(t + dt)$. Let $\hat{n}(t)$ be a unit vector along the axis that describes the rotation at time, t , and $\Phi(t)$ the angle of rotation about that axis. Let \hat{n}_{inc} and Φ_{inc} be the axis and angle describing the infinitesimal rotation, R_{inc} . For incremental rotations, the axis is along ω and the incremental change in Φ , Φ_{inc} , is equal to the magnitude of ω , $\|\omega\|$, multiplied by Δt (Goldstein 1980). Therefore the following relationships are obtained:

$$\begin{aligned}\hat{n}_{\text{inc}} &= \frac{\omega}{\|\omega\|} \\ \Phi_{\text{inc}} &= \|\omega\| \Delta t\end{aligned}\quad (1)$$

With the use of Eq. 1, and the finite rotation formula (Goldstein 1980; Rodrigues 1840), the incremental rotation matrix can be given as

$$R_{\text{inc}} = \begin{bmatrix} \cos \Phi_{\text{inc}} + n_{1\text{inc}}^2(1 - \cos \Phi_{\text{inc}}) & n_{1\text{inc}}n_{2\text{inc}}(1 - \cos \Phi_{\text{inc}}) - n_{3\text{inc}} \sin \Phi_{\text{inc}} & n_{1\text{inc}}n_{3\text{inc}}(1 - \cos \Phi_{\text{inc}}) + n_{2\text{inc}} \sin \Phi_{\text{inc}} \\ n_{2\text{inc}}n_{1\text{inc}}(1 - \cos \Phi_{\text{inc}}) + n_{3\text{inc}} \sin \Phi_{\text{inc}} & \cos \Phi_{\text{inc}} + n_{2\text{inc}}^2(1 - \cos \Phi_{\text{inc}}) & n_{2\text{inc}}n_{3\text{inc}}(1 - \cos \Phi_{\text{inc}}) - n_{1\text{inc}} \sin \Phi_{\text{inc}} \\ n_{3\text{inc}}n_{1\text{inc}}(1 - \cos \Phi_{\text{inc}}) - n_{2\text{inc}} \sin \Phi_{\text{inc}} & n_{3\text{inc}}n_{2\text{inc}}(1 - \cos \Phi_{\text{inc}}) + n_{1\text{inc}} \sin \Phi_{\text{inc}} & \cos \Phi_{\text{inc}} + n_{3\text{inc}}^2(1 - \cos \Phi_{\text{inc}}) \end{bmatrix} \quad (2)$$

Using the matrix of Eq. 2, the rotation matrix at time $t + \Delta t$, $R(t + \Delta t)$, can be found from the rotation matrix at time t , $R(t)$, by the following matrix multiplication

$$R(t + \Delta t) = R_{\text{inc}}R(t) \quad (3)$$

The axis-angle for each eye rotation can be determined from the rotation matrix by using an equation similar to Eq. 2, which specifies the rotation matrix in terms of the axis-angle

$$R = \begin{bmatrix} \cos \Phi + n_1^2(1 - \cos \Phi) & n_1n_2(1 - \cos \Phi) - n_3 \sin \Phi & n_1n_3(1 - \cos \Phi) + n_2 \sin \Phi \\ n_2n_1(1 - \cos \Phi) + n_3 \sin \Phi & \cos \Phi + n_2^2(1 - \cos \Phi) & n_2n_3(1 - \cos \Phi) - n_1 \sin \Phi \\ n_3n_1(1 - \cos \Phi) - n_2 \sin \Phi & n_3n_2(1 - \cos \Phi) + n_1 \sin \Phi & \cos \Phi + n_3^2(1 - \cos \Phi) \end{bmatrix} \quad (4)$$

The axis and angle can be extracted from the rotation matrix R at each time from the Euler-Rodriguez relationships as follows

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix} = \begin{bmatrix} \frac{r_{32} - r_{23}}{2 \sin \Phi} \\ \frac{r_{13} - r_{31}}{2 \sin \Phi} \\ \frac{r_{21} - r_{12}}{2 \sin \Phi} \end{bmatrix} \quad (5)$$

$$\Phi = \cos^{-1} \frac{\text{Tr}R - 1}{2} \quad (6)$$

Thus, by multiplying the previous rotation matrix at any time t , by R_{inc} , the updated rotation matrix can be found. Because R_{inc} is completely specified by the angular velocity, ω , the rotation of the eye in the head can be determined from knowledge of the angular velocity. We now consider how the eye velocity is generated from the torque generated in the eye muscles.

Modeling the dynamic torque-orientation relationship of the eye

The dynamical system representing changes in eye velocity and orientation can be given by Newton's equation of motion in the inertial space fixed frame

$$J \frac{d(\omega + \omega_h)}{dt} = \sum_i T_i \quad (7)$$

Equation 7 states that the sum of the torques, $\sum T_i$, acting on the eye is equal to the moment of inertia, J , multiplied by the angular acceleration of the eye in an inertial space fixed frame of reference, i.e., derivative of angular eye velocity, $\omega + \omega_h$, relative to space and given in the space-fixed coordinate frame. The angular eye velocity, ω , is relative to the head, and ω_h is the angular velocity of the head relative to space. The vectors

can be referenced to the head-fixed frame by using the following transformation (Goldstein 1980)

$$\left[\frac{d(\omega + \omega_h)}{dt} \right]_{\text{space}} = \left[\frac{d(\omega + \omega_h)}{dt} \right]_{\text{head}} + \Omega_h(\omega + \omega_h) \quad (8)$$

where

$$\Omega_h = \begin{bmatrix} 0 & -\omega_{hz} & \omega_{hy} \\ \omega_{hz} & 0 & -\omega_{hx} \\ -\omega_{hy} & \omega_{hx} & 0 \end{bmatrix} \quad (9)$$

Thus Eq. 7 can be simplified as follows

$$\frac{d\omega}{dt} = -\Omega_h\omega - \frac{d\omega_h}{dt} + J^{-1} \sum T_i \quad (10)$$

The sum of the torques, $\sum T_i$, includes the applied muscle torque, viscous counter-torque and elastic counter-torque due to the surrounding tissue and higher order terms. This is given by

$$\sum T_i = \mathbf{m} - B\omega - K\Phi\hat{n} - \sum B_i \frac{d^i\omega}{dt^i} \quad (11)$$

The vector \mathbf{m} is the applied torque generated by the muscles to rotate the eye. The matrices B and K represent the viscosity and elasticity respectively. The B_i matrices are related to higher order plant dynamics (Robinson 1964) and could be considered as a refinement of the present model at some future time. Substituting Eq. 11 into Eq. 10 and ignoring the higher order terms, the dynamic system governing the plant is given by

$$\frac{d\omega}{dt} = -\Omega_h\omega - \frac{d\omega_h}{dt} - J^{-1}(B\omega + K\Phi\hat{n}) + J^{-1}\mathbf{m} \quad (12)$$

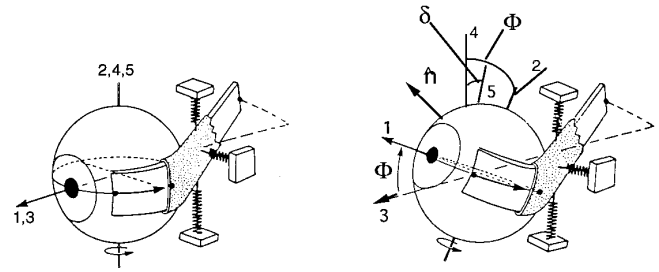
This equation is a superset of that presented in Schnabolk and Raphan (1994). Eye velocity is referenced to a head frame, which could possibly move. When the head is stationary, ω_h is zero and the equations are identical to that of Schnabolk and Raphan (1994).

Effects of muscle pulleys on saccades

The torque in the muscles, \mathbf{m} , is generated from activity in motoneurons, \mathbf{m}_n . This transformation is represented by matrix M , where

$$\mathbf{m} = M\mathbf{m}_n \quad (13)$$

On the basis of effects of transposition surgery and computerized tomography, it has been shown that the paths of the muscle bellies are considerably constrained by orbital connective tissue (Miller 1989; Miller et al. 1993; Simonsz 1990; Simonsz et al. 1986, 1988; Simonsz and van Dijk 1988). The biomechanical model of the globe has therefore been modified so that the tendons of the rectus muscle slide through fascial pulleys (Miller 1989). MRI imaging has shown that the paths of the rectus extraocular muscle bellies remain fixed in the orbit during large eye rotations and across large surgical transpositions of their insertions (Demer et al. 1996). The pulleys are comprised of collagen and elastin sleeves and are supported by connective tissue containing smooth muscle (Demer et al. 1997). The smooth muscle suspensions receive innervation involving multiple transmitters (Demer et al. 1997). As a consequence of the soft pulley action, the muscle axes could change approximately



Φ = ANGLE OF EYE ROTATION
 \hat{n} = AXIS OF EYE ROTATION FROM
 PRIMARY ORIENTATION
 δ = ANGLE OF MUSCLE AXES ROTATION

1. VISUAL AXIS
2. EYE YAW AXIS
3. HEAD ROLL AXIS
4. HEAD YAW AXIS
5. MUSCLE TORQUE YAW AXIS

FIG. 2. Demonstration of the Pulley Effect due to the lateral rectus eye muscle. In primary position (*left cartoon*) the torque axes are aligned with the head axes. When the eye rotates about an axis n (*right cartoon*), through an angle Φ , from primary position, the eye yaw axis (2) rotates by an angle Φ relative to the head yaw axis (4). The visual axis (1) is orthogonal to the eye yaw axis and therefore rotates by the angle Φ relative to the head roll axis (3). Because of the pulley (Springs and hashed sheath), the muscle torque yaw axis (5) rotates by an angle δ relative to the head yaw axis (4). Adapted from Miller et al. (1993).

symmetrically when the eye rotates (Fig. 2). A reasonable approximation for describing the property of muscle axes rotation is as follows: for an eye orientation that is described by a rotation angle Φ , about an axis, \hat{n} , the muscle-axes rotate about the eye rotation axis, \hat{n} (Fig. 2). The angle of the muscle-axis rotation, δ , is taken as some fraction of the angle of eye rotation, Φ , which is defined as the pulley coefficient k_Φ . This is an important refinement of the original model (Schnabolk and Raphan 1994) in that the torque axes that rotate the eye become dependent on the orientation of the eye. For small angles of eye deviation from primary position ($<15^\circ$), the model is virtually unaltered from that presented by Schnabolk and Raphan (1994). However, for larger angles of rotation from secondary to tertiary positions, these axis shifts modify the direction of torque and in turn modify the ensuing eye rotation.

The concept of muscle axes rotation as a function of eye orientation can be incorporated into the model by considering the muscle matrix, M , as a product of a rotation matrix, R_M , with the matrix in the primary position, M_P , and is given by

$$M = R_M M_P \quad (14)$$

The muscle matrix, M_P , represents the tension dependence on innervation when the eye is in the primary position and is a diagonal matrix (Schnabolk and Raphan 1994). The rotation matrix, R_M , represents the action of the pulley in redirecting the tension generated in each muscle pair as the eye moves into different orientations within the orbit and can be given by a rotation matrix

$$R_M = \begin{bmatrix} \cos \delta + n_1^2(1 - \cos \delta) & n_1 n_2(1 - \cos \delta) - n_3 \sin \delta & n_1 n_3(1 - \cos \delta) + n_2 \sin \delta \\ n_2 n_1(1 - \cos \delta) + n_3 \sin \delta & \cos \delta + n_2^2(1 - \cos \delta) & n_2 n_3(1 - \cos \delta) - n_1 \sin \delta \\ n_3 n_1(1 - \cos \delta) - n_2 \sin \delta & n_3 n_2(1 - \cos \delta) + n_1 \sin \delta & \cos \delta + n_3^2(1 - \cos \delta) \end{bmatrix} \quad (15)$$

The pulley effect can be described mathematically by the following key relationship between the angle of the axis rotation and the angle of eye rotation

$$\delta = k_\Phi \Phi \quad (16)$$

where Φ and δ are the angles of rotation of the eye and muscle torque axes, respectively, and are assumed to be related by the pulley coefficient, k_Φ . The axis, \hat{n} , is assumed to be a common axis of both eye rotation and the muscle torque axis rotation, and M represents a composite transformation of muscle innervation to muscle torque. It is assumed that the magnitude of the torque generated by each muscle pair is not changed by the pulley effect. For small deviations of the eye, R_M is approximately the identity matrix and M reduces to M_p , a constant matrix (Schnabolk and Raphan 1994). More detailed effects of eye orientation on the muscle torque could be handled by incorporating the length-tension characteristics of the muscle, but is beyond the scope of this presentation.

We now consider how the motoneuron activity, \mathbf{m}_n , is generated by the velocity-position integrator and a direct pathway around it.

Velocity-position transformation

The velocity-position integrator is a dynamical system that transforms neural signals related to an angular velocity command to a state that is related to torque. Thus the integrator is given by (Schnabolk and Raphan 1994)

$$\begin{aligned} \frac{d\mathbf{x}_p}{dt} &= H_p \mathbf{x}_p + G_p \mathbf{r}_w \\ \mathbf{m}_n &= C_p \mathbf{x}_p + D_p \mathbf{r}_w \end{aligned} \quad (17)$$

where H_p is the system matrix for the “velocity-position” integrator, G_p is the coupling to the integrator from a neural signal coding the “eye velocity” command, \mathbf{r}_w . The matrices C_p and D_p transform the state of the integrator and command velocity to the motoneuron signal, \mathbf{m}_n . The dynamical system given by Eq. 20 can encompass both position and slide component associated with saccades (Goldstein 1983; Goldstein and Reinecke 1993) by choosing \mathbf{x}_p , H_p , G_p , and C_p as follows

$$\begin{aligned} \mathbf{x}_p &= \begin{bmatrix} \mathbf{x}_{pi} \\ \mathbf{x}_{ps} \end{bmatrix} \quad H_p = \begin{bmatrix} H_{pi} & 0 \\ 0 & H_{ps} \end{bmatrix} \\ G_p &= \begin{bmatrix} G_{pi} \\ G_{ps} \end{bmatrix} \quad C_p = \begin{bmatrix} C_{pi} & C_{ps} \end{bmatrix} \end{aligned} \quad (18)$$

The state vectors \mathbf{x}_{pi} and \mathbf{x}_{ps} are the components of the state vector corresponding to “step” and “slide” compo-

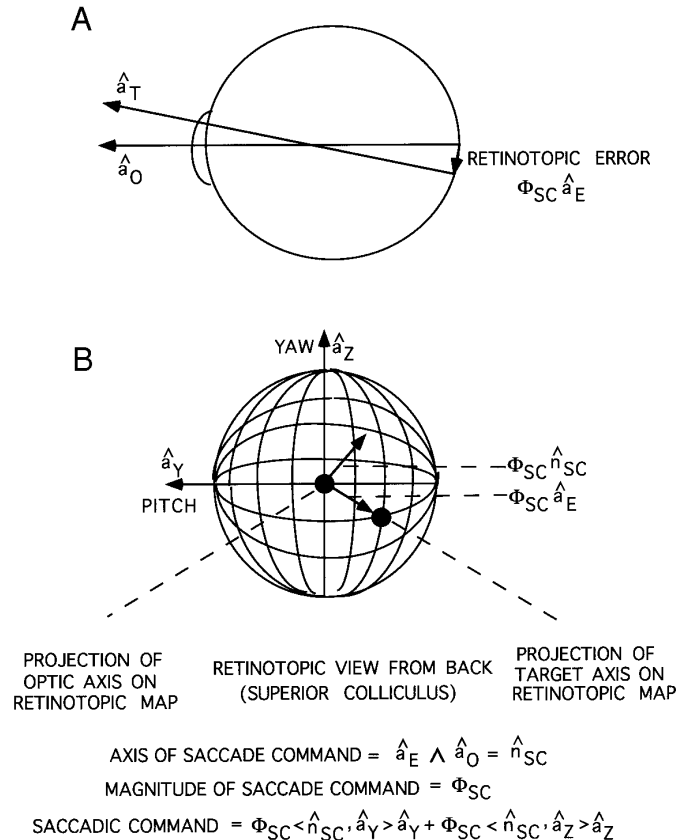


FIG. 3. Simple model of the 2-dimensional control signal for driving saccades. A: projection of a visual target along a unit vector \mathbf{a}_T on the retina relative to the projection of the visual axis along \mathbf{a}_O resulting in a retinotopic error, $\Phi_{SC} \mathbf{a}_E$. B: the retinotopic error is projected to the retinotopic map of the superior colliculus. The vector \mathbf{a}_O is represented as normal to the collicular plane, and the retinotopic error is projected into the 2-dimensional map of the superior colliculus. The cross-product is a vector along the axis of desired eye rotation (Axis of Saccade Command, \mathbf{n}_{SC}), and the magnitude of the retinotopic error is how much the eye must rotate (Magnitude of Saccade Command, Φ_{SC}). The saccade command is a 2-dimensional vector with pitch (Y) and yaw (Z) components representing the desired axis-angle of the eye rotation (Saccade Command).

nents. Similarly, H_{pi} , G_{pi} , and C_{pi} are the matrices that transform the “step” component during dynamic changes in state. The matrices H_{ps} , G_{ps} , and C_{ps} transform the slide state. It should be noted that in the state space formulation, the velocity-position integrator is a multidimensional integrator that encompasses both the three-dimensional space of eye rotations and the multidimensional dynamical system space. Thus higher order dynamics of the velocity-position integrator can be readily incorporated into this model.

Modeling the input to the velocity-position integrator during saccades

The vector integrator model suggests that a two-dimensional control signal drives the saccadic pulse generator. The plane of this neural command in head coordinates determines Listing's plane (Schnabolk and Raphan 1994) and is taken as the pitch-yaw ($Y-Z$) plane. This concept leads to a simple formulation of how visually guided saccades are generated based on the two-dimensional organization of superior colliculus neural activity (Hepp et al. 1993) (Fig. 3). To a first approximation, for a fixed eye position, any target along the visual axis projects to a point at the center of the retina (Fig. 3A). This in turn activates the center of the collicular map (Fig. 3B). Let us assume that the collicular representation of a unit vector along

this visual axis is given by \hat{a}_O . Because of the retinotopic organization of the superior colliculus (Robinson 1972), the vector \hat{a}_O is the same for all positions of fixation and is by definition normal to what we will refer to as the "collicular plane." A target of interest off the visual axis will project to a retinotopic point that can be described by a vector, $E_R = \Phi_{SC}\hat{a}_E$, from the center of the map and lies in the collicular plane (Fig. 3B). If a cross product is taken between E_R and \hat{a}_O , a vector that is in the collicular plane is obtained whose magnitude is Φ_{SC} and whose direction is along an axis about which the eye should rotate to acquire the new target. A unit vector along this axis is given by $\hat{a}_{SC} = \hat{a}_E \wedge \hat{a}_O$, where \wedge is the cross-product operator. If \hat{a}_O is taken to be \hat{a}_X , along the positive torsional axis, then the vector $\Phi_{SC}\hat{a}_{SC}$ is a saccadic command in the $y-z$ plane, with zero torsion, that will change

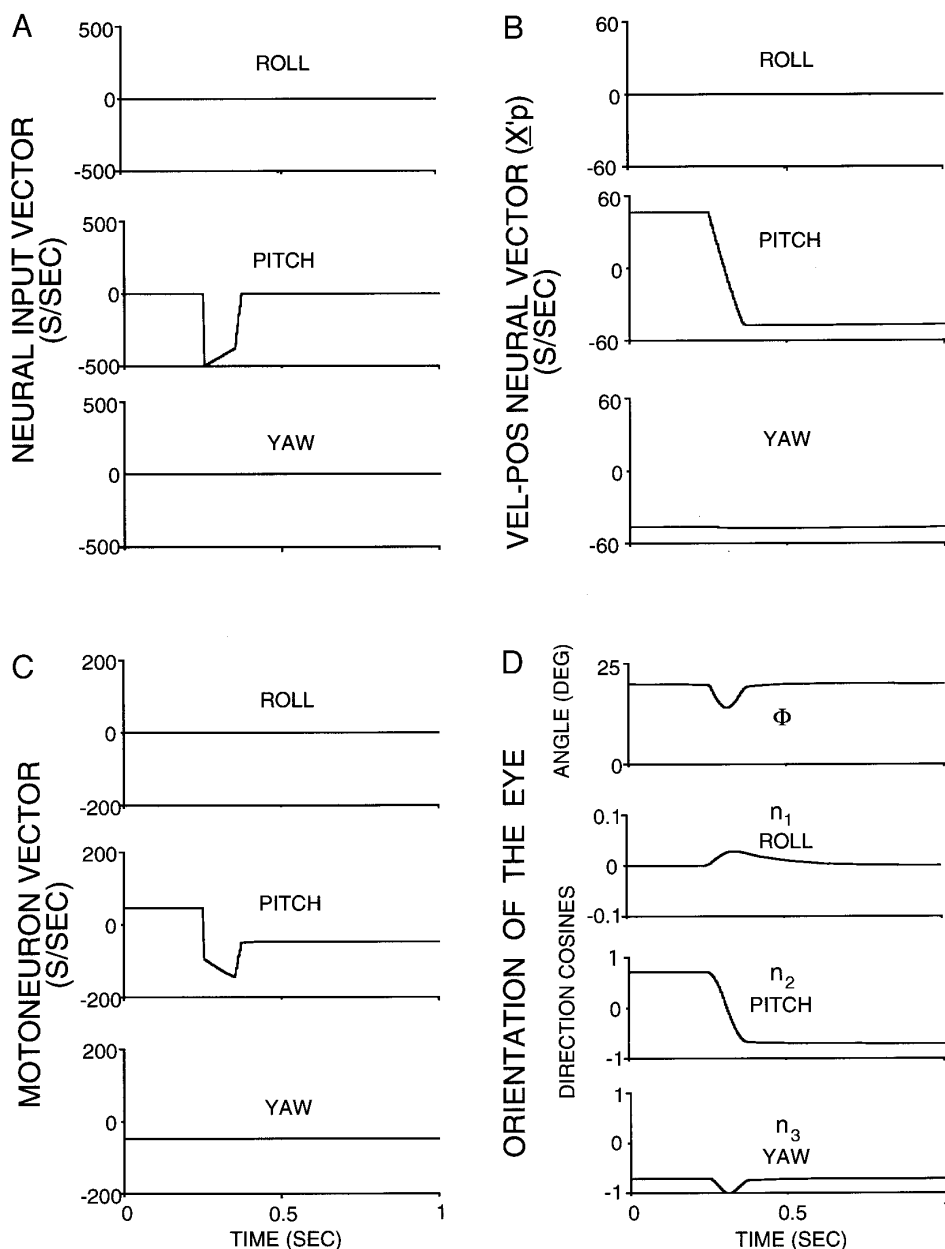


FIG. 4. Model simulation of the premotor and motor neural pulses as well as the eye orientation response for a movement from down right 20° to up right of 20° (28° movement). The Vel-Pos Neural Vector (B) was initialized by 2 simultaneous pulses (not shown) to give a positive pitch and negative yaw state. This initialized the eye to be oriented down and right with $n_2 = 0.707$ and $n_3 = -0.707$ (D) with an angle of 20°. When a negative pulse along the pitch axis was given (A), the velocity-position pitch state changed as did the pitch component of the motoneuron vector (C). There were transient changes in all parameters of eye orientation (D). In the steady state, the direction cosines and the angle corresponded to the Vel-Pos Neural Vector with only pitch yaw components.

the pitch and yaw states of the velocity-position integrator from any arbitrary state. This will maintain the steady-state torque such that Listing's law is obeyed. A similar cross product to represent the retinal error in three dimension provided by the components of the line of sight, when the target is to be foveated by a rotation from primary position, has been suggested by Hepp et al. (1993) (see DISCUSSION). We now show that by incorporating pulleys into the plant model, Listing's law can be obeyed during saccadic trajectories as well.

MODEL PERFORMANCE DURING SACCADIC SIMULATION. In the simulated experiments, the slide component of the velocity-position integrator and higher order terms of the plant dynamics were neglected. Subjects made saccades between five targets, in center position and at the corners of an upright square at eccentricity 20 or 40° in a lighted room (Tweed

et al. 1994). For these simulations, the parameters of the model were chosen in the following manner.

The matrix M_p was chosen as in Schnabolk and Raphan (1994), given as

$$M_p = 2.49 \times 10^{-6} \text{ (kg} \cdot \text{m}^2/\text{s}^2\text{)}/(\text{spikes/s}) \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \quad (19)$$

The matrices H_p and G_p , which represent the velocity-position system matrix and the input coupling to the integrator, were left unaltered (Schnabolk and Raphan 1994), although the output matrices, C_p and D_p were doubled compared with Schnabolk and Raphan (1994), so that the numbers could be more easily represented as unit firings. The pulse heights used in Schnabolk and Raphan

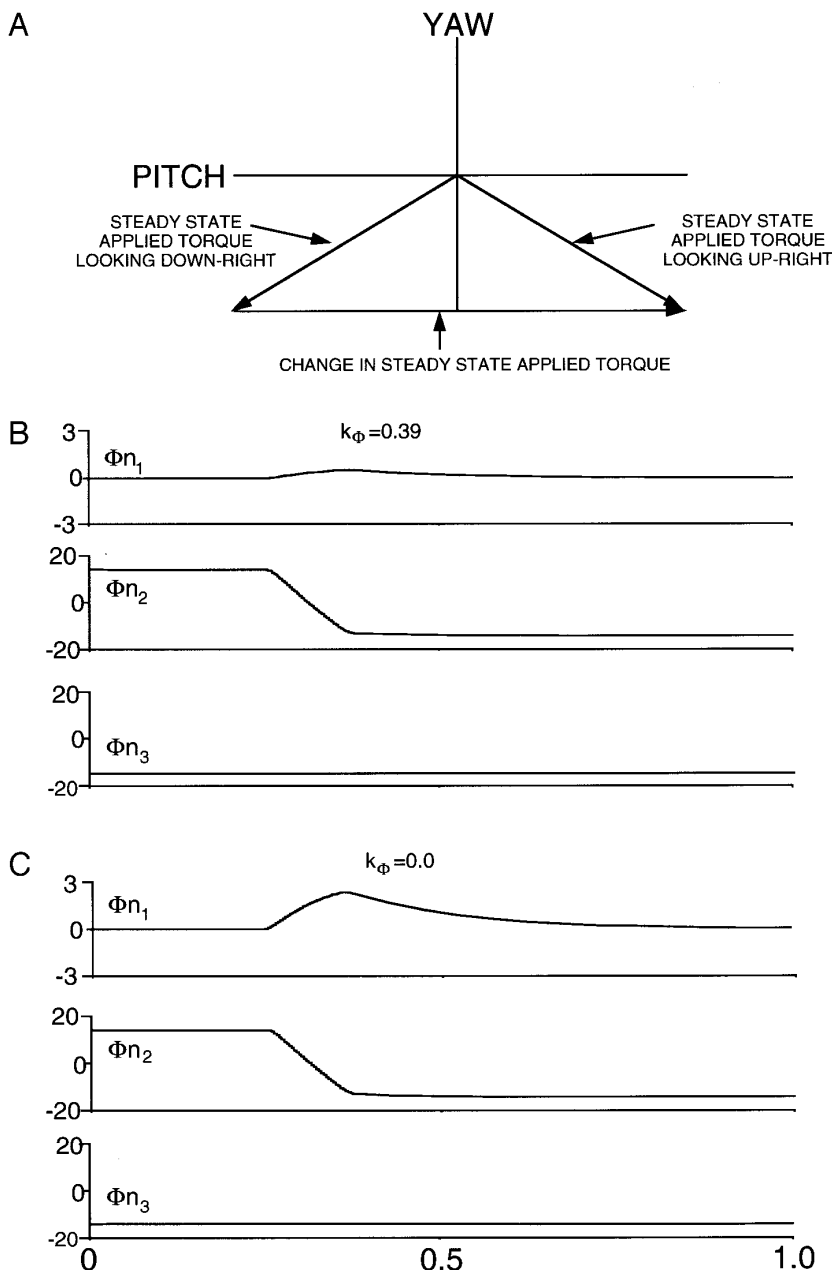


FIG. 5. Axis-angle product as a function of time during saccadic trajectory. A: vectors showing the steady-state applied torques and change in steady-state torque when marking a saccade. B and C: effects of pulley coefficient, k_ϕ , on the torsional transient. The peak value of the transient is significantly smaller for $k_\phi = 0.39$ (B) as compared with 0 (C; No Pulley).

(1994) were only approximately abstracted from single-unit activity in PPRF of monkeys (Henn and Cohen 1976; Hepp and Henn 1983; Keller 1974; Van Gisbergen et al. 1981). However, if we consider the large variation in unit activity and the abstraction from monkey to human data considered in this study, it seems more appropriate to increase the gain matrices and have a more reasonable range for the unit activity.

The matrices corresponding to the velocity-position integrator were therefore chosen as

$$\begin{aligned} H_p &= -0.03333/s \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} & G_p &= 0.03333/s \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \\ C_p &= 59.0 \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} & D_p &= 0.278 \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \end{aligned} \quad (20)$$

The parameters of the plant were chosen in accordance with known physiology as follows (Schnabolk and Raphan 1994)

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

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

$$B = 7.47 \times 10^{-5} \text{ kg} \cdot \text{m}^2 \cdot \text{s}^{-1} \cdot \text{rad}^{-1} \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \quad (21)$$

The simulation (Fig. 4) shows how the axis-angle of eye rotation changes when making a saccade from looking at the bottom right corner of the 20° eccentric square to its top right corner. The velocity-position-integrator state was initialized by applying equal pitch and yaw components to rotate the eye to look into the bottom right corner (Fig. 4B). When the eye reached steady state, the time, t , was set to zero. At time, $t = 0.25$ s, the neural input vector was changed by giving a negative pulse along the pitch axis to move the eyes to the up-right corner (Fig. 4A). In response to this pulse, the VEL-POS Neural Vector changed state along the pitch axis while the yaw and roll

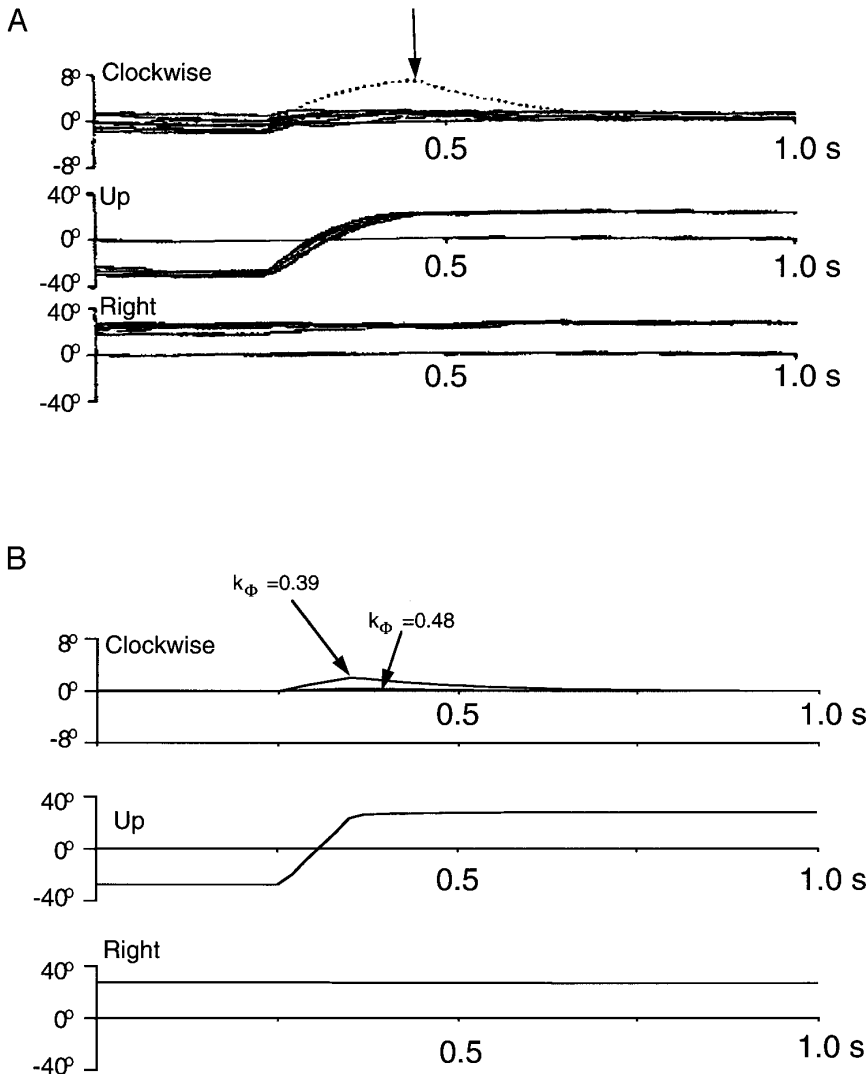


FIG. 6. Comparison of Tweed et al. (1994) simulation of Schnabolk and Raphan model (1994) overlaid on their data with simulations using pulley model. A: the data comprised saccades made from down-right 40° to up-right 40°. Without pulleys, simulation of the Schnabolk and Raphan model (1994) (···) reached peak torsional values higher than reached by data. B: when a pulley coefficient of 0.39 was used, the peak value and time course approximated the data. For a pulley coefficient of 0.48, there was virtually no torsional transient, and Listing's law was obeyed almost perfectly during the saccadic trajectory. In accordance with Tweed et al. (1994), clockwise, counterclockwise, up, and right are defined from the subject's viewpoint.

states remained invariant. The motoneuron vector (Fig. 4C) changed by a pulse-step along the pitch axis and generated the torque to change the orientation of the eye (Fig. 4D). There are transient changes in all direction cosines as well as a transient change in the angle of the movement. In the steady state, the angle of the eye orientation and the roll and yaw direction cosines are identical to that when the eye looks down-right. The pitch direction cosine changed from 0.707 to -0.707 (Fig. 4D). The corresponding steady-state torque vectors for the two eye orientations are shown in Fig. 5A. A torque-pulse along the pitch axis is necessary to execute this movement (Fig. 5A).

Tweed et al. (1994) represented orientation as components of the vector part of the quaternion along the roll, pitch, and yaw axes. To compare our model predictions with their data, we multiplied the eye orientation angle by the direction cosines and displayed the roll, pitch, and yaw components as a time series (Fig. 5B). The simulation clearly shows that for $k_\phi = 0.39$, the transient roll component (Tweed et al. 1994) was $<0.5^\circ$, well within any practical bounds defining Listing's law. We also tested the model

without any muscle axis change to show how small these effects really are. Figure 5C shows the saccadic trajectory without any shifts in muscle axes. The maximum torsional transient was $\sim 2.5^\circ$. This emphasizes the small effect that muscle axis change has on transient roll component even for saccades of 28° . It further indicates that muscle axes changes predominantly effect the system at much larger angles of eye deviation. It should be noted that the deviation of the axis of eye rotation from Listing's plane (Fig. 4D) appears larger than the torsional transient rotation (Fig. 5, B and C), because the latter is scaled by the size of the angle of rotation.

We also tested the model for saccades made from down-right to up-right using a 40° eccentric square. Again, the velocity-position integrator state was initialized to a vector that would generate a torque to keep the eyes in the down-right position as described above. A pulse was given along the pitch axis that resulted in a step change in the pitch component of the velocity-position integrator, a pulse-step change in the pitch component of the motoneuron vector, and a change in all direction cosines as a function of time

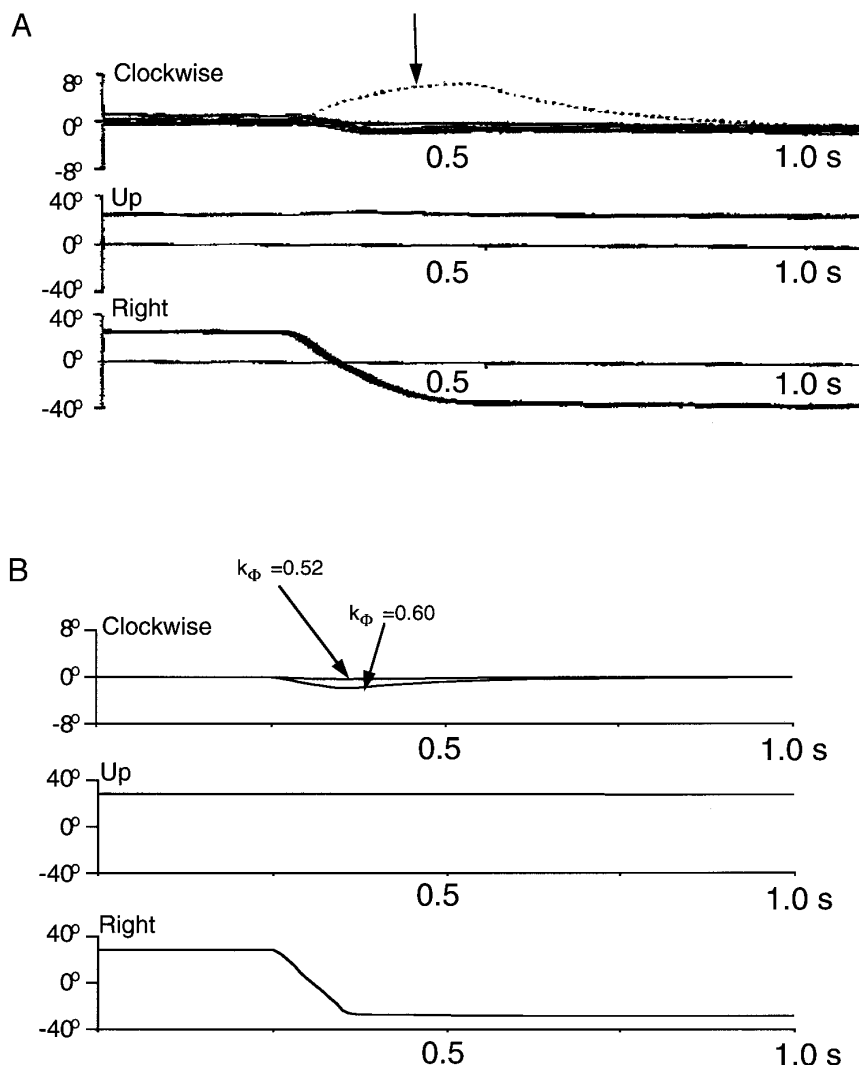


FIG. 7. Comparison of Tweed et al. (1994) simulation of Schnabolk and Raphan model (1994) overlaid on their data with simulations using pulley model. A: the data comprised saccades made from up-right 40° to up-left 20° . Without pulleys, simulation of the Schnabolk and Raphan model (1994) (\cdots) reached peak torsional values in the wrong direction relative to the data. B: when a pulley coefficient of 0.6 was used, the peak value and time course approximated the data. For a pulley coefficient of 0.52, there was virtually no torsional transient, and Listing's law was obeyed almost perfectly during the saccadic trajectory. In accordance with Tweed et al. (1994), clockwise, counterclockwise, up, and right are defined from the subject's viewpoint.

as the eye oriented to the up-right position. The steady-state orientation had a pitch direction cosine opposite to that when looking down-right. The results were a scaled version of that shown in Fig. 4. Each direction cosine was then multiplied by the rotation angle, and the time series of the rotation vector was compared with the data of Tweed et al. (1994) (Fig. 6). The data for a "typical subject" (*HM*) show that for a saccade from 40° down-right to 40° up-right, there is a torsional transient of $\sim 2^\circ$ (Fig. 6A). The simulation by Tweed et al. (1994) of the saccade trajectory using the three-dimensional vector integrator model (Schnabolk and Raphan 1994) shows a torsional transient reaching a maximum of 7° (Fig. 6A, \cdots). However, when changing muscle axes corresponding to $k = 0.39$ were considered, the torsional transient was maintained within 2° (Fig. 6B) and the vector integrator model closely approximated the data (Fig. 6B). Somewhat larger values of k , i.e., $k = 0.48$, maintained the torsional transient within 0.1° (Fig. 6B). This indicates that, depending on the movement of the axes for particular sub-

jects, there can be a wide range of torsional transients generated and accounts for the wide variability in the data (Tweed et al. 1994).

For saccades made from 40° up-right to 40° up-left, the typical subject (*HM*) had a torsional transient that went counterclockwise (Tweed et al. 1994) (Fig. 7A). The simulation done by Tweed et al. (1994) using the fixed-muscle axis integrator model predicted a 7° torsional transient in the wrong direction (Fig. 7A). When a muscle-axis change corresponding to $k = 0.52$ or $k = 0.60$ was implemented, it predicted the data both in magnitude and direction. The different values for k that predict the variations in data may be due to anisotropy in muscle axis shifts, or the center of mass of the eye may not be fixed in the head. A complete model-based study of these effects is beyond the scope of the analysis because there are no relevant data.

The simulations show that for $0 < k_\phi < 0.5$, the torsional transient is in one direction, whereas for $0.5 < k_\phi < 1.0$ it reverses direction for the given saccadic trajectories. The

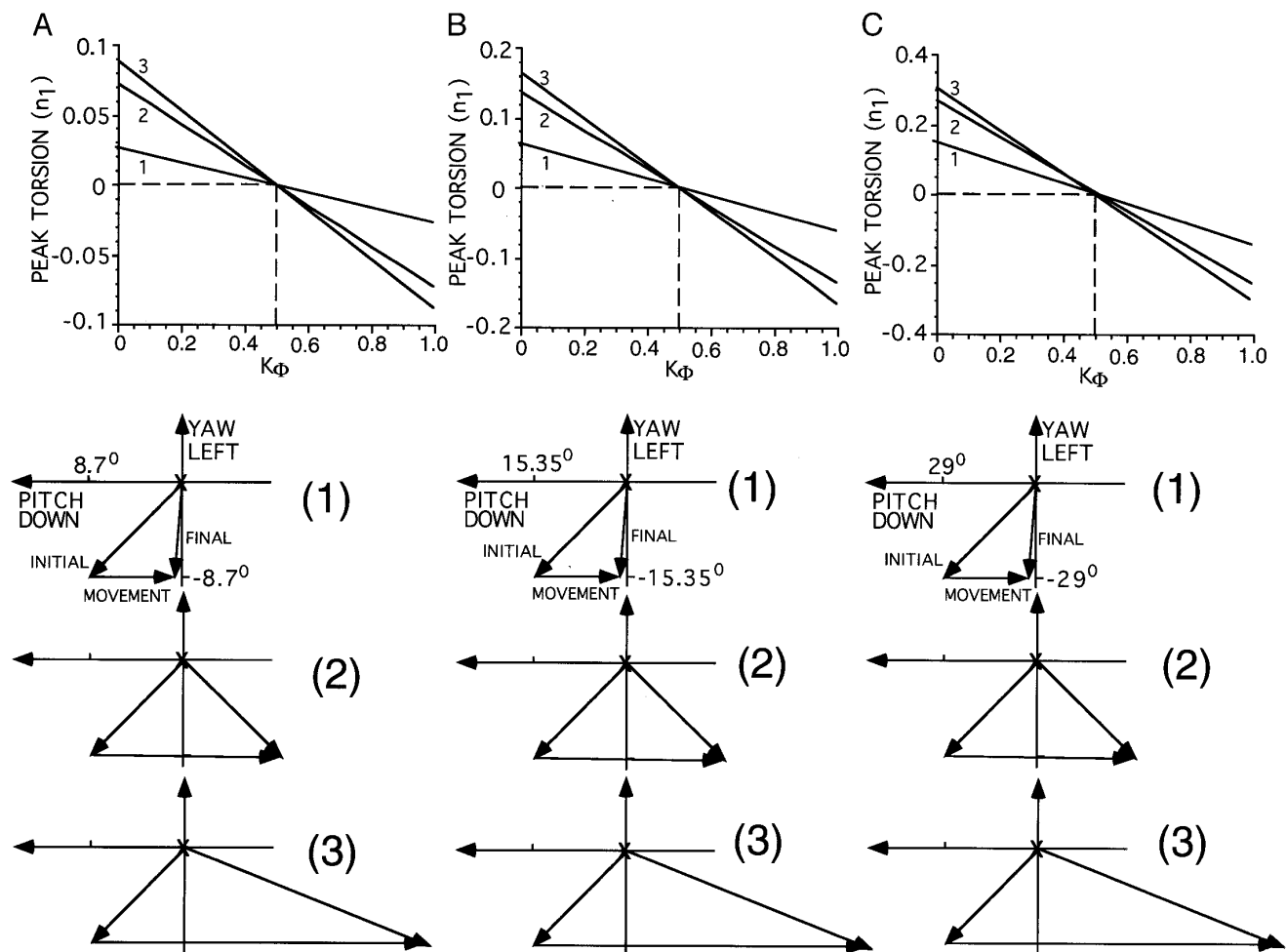


FIG. 8. Effects of the pulley coefficient, k_ϕ , on the peak value of the torsional transient for a wide range of saccadic movements and initial staring orientations. The peak torsional transient varies approximately linearly with pulley coefficient, k_ϕ when starting from right-down and making movements that bring the eyes looking approximately right (1), looking up-right in equal proportion (2), and looking up-right with a much greater up component (3). A: starting position of 10° down right. B: starting position of 20° down-right. C: starting position of 40° down-right. In all cases, the peak torsional transient was zero (0) for $k_\phi = 0.5$. There was also a reversal in sign of the transient torsional component when k_ϕ took on values on either side of 0.5 (see text for explanation).

following question arises: what is the underlying principle governing the size and magnitude of the torsional transient? To uncover this principle, we simulated saccades of varying amplitudes starting from a secondary position of $\sim 10^\circ$ down-right (Fig. 8A), 20° down-right (Fig. 8B) and 30° down-right (Fig. 8C). In each instance a saccade was made that brought the eye orientation to the right (Fig. 8, A, B, and C1), up-right approximately equal to the size of its initial orientation (Fig. 8, A, B, and C2) and up-right having a much larger angle (Fig. 8, A, B, and C3). Peak torsional transient was computed as a function of the pulley coefficient, k_Φ . In all cases, the peak torsional transient was approximately linearly related to k_Φ . The slope of the line increased with the size of saccade and initial eccentricity of eye orientation (Fig. 8). It was striking that for $k_\Phi = 0.5$, there was no torsional transient, regardless of the size of the saccade and eccentricity of the initial eye orientation. This comes about as a consequence of the half-angle rule relating the displacement plane associated with a particular eye orientation relative to primary position (Helmholz 1867; Tweed et al. 1990; Tweed and Vilis 1990). That is, when the visual axis rotates about an axis through some angle from primary position, the displacement plane for the new eye orientation has only rotated one-half the angle (Tweed et al. 1990; Tweed and Vilis 1990). By rotating the torque axis by one-half the angle of eye rotation and about the same axis as eye rotation ($k_\Phi = 0.5$), the torque is always maintained in the displacement plane at every eye orientation throughout the saccadic trajectory. Because the torque is responsible for changes in eye orientation, these changes will always obey Listing's law under this condition. Therefore torsion will always be zero for $k_\Phi = 0.5$ throughout the saccadic trajectory.

Tweed et al. (1994) evaluated the "goodness" of the vector integrator model by computing "blip area" of the torsional transient and comparing it with the quaternion model. Using the muscle axis rotations, this criteria is not meaningful, because any arbitrary blip area even zero can be achieved by the vector integrator model. In fact, any complex evaluative criterion of the model becomes moot, because Listing's law will be obeyed perfectly with a 50% pulley coefficient. The size of the torsional transient is the best indicator of the closeness of the eye trajectory to Listing's plane and how close the pulley coefficient is to 0.5. The direction of the transient indicates whether the pulley coefficient is greater or less than 0.5. The pulley coefficient could be found from data by computing the k_Φ that gives the best fit to the torsional transient. These results emphasize the point that the muscle pulleys have implemented an important rotation that maintains saccadic trajectories as well as eye orientations close to Listing's plane when activated by two-dimensional signals confined to the pitch-yaw plane.

DISCUSSION

This study indicates that the oculomotor plant performs important transformations that determine saccadic trajectories in three dimensions. One key transformation is the relationship between steady state eye rotation, Φ , and the

counter-torque generated by the tissue surrounding the eye. Schnabolk and Raphan (1994) had originally pointed out that the steady-state counter-torque-orientation relationship is important for implementing Listing's law. By assuming that the counter-torque relative to primary position is optimal, then it would be along the "Euler axis" defining the eye orientation (Goldstein 1980; Schnabolk and Raphan 1994). Therefore the axis associated with the eye orientation would be in the plane of the torque developed by the muscles when the eye was in equilibrium. If the muscle torque axis were in the pitch-yaw plane, i.e., Listing's plane, then Listing's law would be obeyed.

This simple idea has profound implications about the central control of saccades. It predicts that to hold positions of fixation in accordance with Listing's law, it is sufficient to have a vector velocity-position integrator with only its pitch and yaw states activated and its roll state equal to zero (Schnabolk and Raphan 1994). The model simulations contradict the idea that because eye rotations do not commute, there must be a noncommutative quaternion-based velocity-position integrator (Tweed and Vilis 1987). Because steady-state eye orientation is constrained by the torque-orientation relationship associated with surrounding tissue, there will always be a unique eye orientation for a given vector position command, and the noncommutativity of rotations is not a relevant issue. Any imprecise input that results in a nonzero roll state, and corresponding deviation from Listing's law, would necessarily have to be reset to return eye orientation to Listing's plane (Van Opstal et al. 1996). A conceptual mechanism to accomplish resetting proposes that torsional errors generated in a hypothesized Listing's box are processed via nucleus reticularis tegmenti pontis (NRTP) and are relayed to the burst generators (Van Opstal et al. 1996). In the model presented here, torsional eye orientation errors produced by noise would be reflected in a nonzero roll state. If the nonzero roll state is detected by NRTP, it need only send a roll pulse to clear this state when another saccade is made. This would automatically return eye orientation to Listing's plane, without the need to hypothesize a Listing's box.

Another key transformation that is implemented at the level of the plant is the rotation of the applied torque to the eyes due to the muscle pulleys (Miller 1989; Miller et al. 1993). Early work by Robinson (1975) had suggested that the muscle axes did not rotate with eye rotation, but remained fixed in the head. This led to differences in the implementation of Listing's law during saccades between the two models. For the quaternion model, the structural aspects of the plant were not relevant, because in this model the velocity-position integrator implemented the rotational kinematics (Hepp 1994; Tweed and Vilis 1987). The quaternion model predicted fixed axes saccadic trajectories with a Listing's law operator maintaining the axis of the eye movement confined to Listing's plane. With fixed muscle axes, the vector-based integrator model predicted that there would be small torsional transients during the saccadic trajectory when saccades are executed from secondary to tertiary positions (Schnabolk and Raphan 1994).

According to the vector integrator model, the reason for torsional transients during saccades is because of a mismatch

between the torque axes and the displacement plane associated with each eye orientation during the saccade. It should be noted that this mismatch is different from any pulse-step mismatch occurring due to the velocity-position integrator that causes glissadic eye movements during saccadic trajectories (Optican and Miles 1985; Optican and Robinson 1980; see Schnabolk and Raphan 1994, APPENDIX B for a time domain derivation of the pulse-step matching condition). Even matched pulse steps that induce accurate centrifugal saccades will produce torsional transients when the muscle axes are fixed relative to the head (Figs. 5). The muscle pulleys are important for reducing these torsional transients (Raphan 1997).

The prediction of the torsional transients by the vector integrator model (Schnabolk and Raphan 1994) was verified in studies of saccadic trajectories in humans (Straumann et al. 1995; Tweed et al. 1994). However, the fixed muscle axis vector integrator model predicted too large a value for the peak torsional transient when large saccades were executed. The obvious solution to this problem is to bring the muscle torque axis closer to the displacement plane during the saccadic trajectory; the closer it gets, the smaller will be the torsional transient. When the muscle torque axis is maintained within the displacement plane for each eye orientation during the saccadic trajectory, there should be no torsional transient throughout the saccadic trajectory. To a first approximation, this concept can be implemented by having the muscle pulleys implement a simple rotation of the torque axis by a fraction of the angle of eye rotation, but along the axis of eye rotation. With the use of this simple model, and the half-angle theorem (Tweed et al. 1990), a muscle axis rotation of 50% of the eye rotation would maintain the torque in the displacement plane for a saccadic command confined to the pitch-yaw plane, i.e., Listing's plane and is demonstrated by the simulations (Fig. 8). The pulleys are supported by smooth muscles that receive complex excitatory and inhibitory innervation (Demer et al. 1997). Therefore the neural and mechanical machinery exist to implement this rather precise rotation. The model simulations, however, suggest that these shifts are ~40% when making saccades from right-down to right-up. The data of Tweed et al. (1994) show that the muscle axes may rotate by as much as 60% when making saccades from up-right to up-left, inducing a torsional transient in a direction opposite to that expected if there were no muscle shifts. Thus the muscles appear to be situated so as to straddle Listing's plane during saccadic trajectories. Whether this is by design or a result of generating suboptimal performance is not clear. Nevertheless, saccadic trajectories from secondary to tertiary positions could be used as a base for mapping the full range of muscle axis shifts. If the peak torsional transient were normalized with regard to angle of rotation, this would be a measure of the peak torsional direction cosine. Because the sum of the squares of the direction cosines is equal to 1.0, the peak torsional directional cosine is a measure of the percentage of the rotation out of Listing's plane (Schnabolk and Raphan 1994). Therefore, if the peak torsional direction cosine could be related to what is now known about the structure of the pulleys, then the transient responses could be used as an effective parameter to assess the results of strabismus surgery

(Clark et al. 1997; Demer et al. 1995; Mehta and Demer 1994; Shin et al. 1996).

The vector model presented in this study also leads to a simple spatiotemporal interface between the superior colliculus and the brain stem pulse generators that drive the oculomotor system that is predicted by the quaternion model. Work done on stimulating the superior colliculus (Van Opstal et al. 1991) yielded saccadic trajectories that were in the pitch-yaw plane with a negligible torsional component. A "V" model was constructed that related the size of the saccade to the difference between rotation vectors that lie in Listing's plane. The conclusion from this study was that the superior colliculus motor map encodes the two-dimensional vector of target direction, but not the rotation axis of the eye and that Listing's law was implemented downstream of the superior colliculus. A later model (Hepp et al. 1993) implements a cross-product for retinal error in three dimensions by the components of the line of sight, when the target is to be foveated by a rotation from primary position, but still requires the implementation of a Listing's law box. In the model presented here, the superior colliculus encodes the axis-angle of eye rotation by implementing a cross-product of the retinotopic error vector with a vector normal to the collicular plane, the line of sight vector. The cross-product is a vector in the pitch-yaw plane of the head, which encodes the axis-angle neural command for properly rotating the eyes. Because the vector of pulses driving the velocity-position integrator have only pitch and yaw components and a zero roll component, Listing's law is generated naturally. Thus Listing's law is an emergent distributed property of the vector nature of signals in the CNS and how they activate the oculomotor plant. It is not linked to any specific site in the CNS, and no Listing's law box in the CNS need be postulated.

In summary, the pulley model for the eye muscles together with the torque orientation relation form a sufficient basis for support of the idea that Listing's law is due to the plant and a two-dimensional vector driving the system. Without the pulleys, Listing's law would hold only for steady-state eye orientations. The pulley system enables Listing's law to approximately hold during the saccade as well. A direct implication of this idea is that the velocity-position integrator is probably realized as a vector-based subtractive feedback dynamical system, simplifying the control of saccadic eye movements.

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