Commutative Saccadic Generator Is Sufficient to Control a 3-D Ocular Plant With Pulleys

CHRISTIAN QUAIA AND LANCE M. OPTICAN
Laboratory of Sensorimotor Research, National Eye Institute, Bethesda, Maryland 20892

Quaia, Christian and Lance M. Optican. Commutative saccadic concept of position must be replaced by the concept of orientation, which is less intuitive and more difficult to define mathematically. Second, the concept of velocity must be replaced by the concept of angular velocity. Third, and most important, it must be kept in mind that, for rotations around arbitrary axes, the derivative of orientation is not angular velocity (Goldstein 1980).

This last property, which applies to any rigid body rotating around a point fixed in space, is due to the noncommutativity of rotations, which can be described geometrically as follows: starting from the same initial orientation, a rotation of \( \alpha \) around an axis \( \hat{x} \) followed by a rotation of \( \beta \) around \( \hat{y} \) (with \( \alpha, \beta, \hat{x}, \) and \( \hat{y} \) arbitrary, as long as \( \hat{x} \) is not parallel to \( \hat{y} \)) does not produce the same final orientation obtained when the order of the rotations is reversed. For example, in the two panels of Fig. 1, a camera, starting from the same initial orientation (left column), is rotated around the same pair of axes (arrows in the figure) but in different order; clearly, the final orientations (right column) are different for the two sequences of rotations.

Because rotations around a single axis (i.e., when \( \hat{x} \) and \( \hat{y} \) are parallel) are commutative, in his model Robinson could use a simple integrator to transform eye velocity into eye position. However, because of the noncommutativity of arbitrary rotations, it is logical to conclude that a model that relies on the angular velocity being the derivative of orientation cannot be used to control a rotational plant in three dimensions. Consequently, to extend Robinson’s model from control of the eye around one axis to control around all three of its axes, Tweed and Vilis (1987) developed a model that uses noncommutative, rotational operators to generate the innervation signals. Subsequently, Schnabolk and Raphan (1994a,b) proposed that, in fact, a noncommutative neural system was not needed to control eye movements. Schnabolk and Raphan argued that the noncommutativity of rotations was not relevant because the innervation signals determine muscle torques (which are vectors, and thus commute), not eye orientation.

There is a fundamental difference in the behavior of the two models. The model developed by Tweed and Vilis (1987) is the correct extension to three dimensions of the model proposed by Robinson in one dimension (Robinson 1975), because eye orientation and angular velocity are neurally represented. Furthermore, this model assumes that the goal of the saccadic system is not only to move the eye from its current to a new orientation, but also to accomplish this as quickly as possible. In particular, any slow movement that follows a saccade and that is due to a mismatch between the tonic innervation signal present after the end of the sac-
And the orientation of the eye (Bahill et al. 1975), is avoided. These slow movements, which are called postsaccadic drifts (or glissades), can degrade visual perception (Westheimer and McKee 1975) and can be adaptively minimized by the brain (Optican and Miles 1985); by definition (Bahill et al. 1975), they encompass also the so-called torsional transients or blips.

Thus the Tweed-Vilis model (as well as the Robinson model) focused not only on the steady-state conditions (i.e., after stabilization of eye orientation) but also on the dynamics of the movement used to foveate the target. In contrast, Schnabolk and Raphan concentrated exclusively on the issue of eventually acquiring the target, without making any attempt to make a model that avoids (or minimizes) postsaccadic drifts. In fact, they explicitly stated: “there is of necessity a mismatch between the plant dynamics and the pulse-step driving it” (Schnabolk and Raphan 1994a, p. 634).

However, there is compelling physiological evidence that suggests that a model that does not account appropriately for the dynamics of the movement (i.e., that produces movements with large postsaccadic drift) is not a good approximation of the system implemented by the brain to control saccades. In fact, movements produced by normal subjects (either primates or humans) have very little postsaccadic drift (see Tweed et al. 1994a), and when the drift is induced artificially the innervation signals are adaptively modified to reduce the retinal slip (Optican and Miles 1985). Accordingly, the fact that a commutative controller is sufficient to guarantee a good steady-state behavior of the system does not imply that the brain can use such a strategy to drive the eye plant, as erroneously concluded by Schnabolk and Raphan.

Nevertheless, the need to account for the dynamics of the plant does not necessarily imply that the neural controller must be noncommutative. In fact, a noncommutative controller is necessary only if both orientation and angular velocity are encoded neurally, as was the case in the Tweed and Vilis (1987) and Robinson models. However, Tweed and colleagues (Tweed et al. 1994a; Tweed and Vilis 1990) pointed out that, if 1) eye orientation and 2) its derivative, but not angular velocity, were encoded neurally, the first signal could be computed by simply integrating the second. Under such an assumption, an essentially commutative saccadic generator could be used, and it would then be up to the plant to convert the innervation signal into the appropriate rotation of the eye; however, Tweed et al. (1994a) did not suggest any mechanism that would allow the plant to perform such conversion. Nonetheless, several recent studies have relied on the hypothesis that the derivative of eye orientation, as opposed to eye velocity, is neurally encoded (Crawford 1994, 1997; Crawford and Guitton 1997).

Recently, Raphan (1997) introduced a model of the ocular plant that incorporates the orbital pulleys discovered, and qualitatively modeled, by Miller and colleagues (Demer et al. 1995; Miller 1989; Miller et al. 1993; Miller and Robins 1987). As pointed out by Miller and colleagues (1993, 1997), the pulleys make the axes of action of the extraocular muscles depend on the orientation of the eye. Raphan proposed a simple mathematical approximation of the action of the pulleys. He used simulations to show that a saccade produced by a commutative controller driving a plant without pulleys had a large postsaccadic drift, whereas the same saccade made using a plant model with pulleys had a much smaller drift. However, no proof was offered that the improved dynamic behavior of the Raphan-Miller pulley model holds in general, i.e., for saccades different from those simulated. Furthermore, Crawford and Guitton (1997) pointed out that the pulleys have to react differently to phasic and tonic inputs, but neither they nor Raphan have offered a solution to this problem, which is critical for the pulley hypothesis.

The first goal of this paper is to verify that the Raphan-Miller pulley model always produces movements that have an accurate dynamic behavior. Using a novel quantification of the dynamic errors associated with the use of a commutative controller to drive a noncommutative plant, we compare, in a rigorous, mathematical way, the behavior of the Schnabolk-Raphan model with that of the Raphan-Miller pulley model. This is a departure from earlier approaches, when inferences drawn from the results of simulations of single movements (e.g., Schnabolk and Raphan 1994a; Straumann et al. 1995) were then proven incorrect by probing the behavior of the same models for other movements (Tweed 1997b; Tweed et al. 1994b). Using this quantitative approach, we demonstrate mathematically that the good dynamic behavior of the Raphan-Miller pulley model holds for all movements and that the saccadic generator (i.e., the network that converts the desired rotation of the eyes into the signals needed to produce that rotation) can be commutative.
The second goal of the paper is to explain, in an intuitive way, why this is possible and what the consequences of these results are for the neural signals that are generated by the oculomotor controller. The bottom line is that, if the pulleys are properly placed, the oculomotor plant (extraocular muscles, orbital pulleys, and eyeball) is seen by the saccadic controller as an essentially commutative system. We will elucidate the mechanisms underlying this surprising outcome, which gives new significance to the role of orbital pulleys; particular care will be given to explaining the effects of the pulleys on the different components (Pulse and Step) of the innervation signal.

Furthermore, we will discuss the consequences that the presence of the pulleys have for the overall organization of the saccadic system and for the neural implementation of Listing’s Law, which is simplified. We will also consider the import that these results have for strabismus, a disorder of ocular alignment, with regard to both its development and surgical treatment. Finally, we will propose several experimental paradigms that could be used to test the pulley hypothesis.

A brief description of these results appeared elsewhere (Quaia and Optican 1997a).

METHODS

Representation of orientation

The eyeball can be modeled as a sphere capable of rotating around any axis through its center, which is fixed in space. When an object can rotate around arbitrary axes, there are many different ways to define its orientation. For example, it is possible to describe the orientation by a sequence of three rotations around particular axes, as in the Fick and Helmholtz coordinate systems, with rotation matrices, or with quaternions (for review see Haslwanter 1995).

Of the many mathematically equivalent descriptions of rotations, we prefer the axis-angle form, which follows from Euler’s theorem. This theorem states that any orientation of a rigid body with one point fixed can be achieved, starting from a reference orientation, by a single rotation about an axis (through the fixed point) along a unit-length vector \( \mathbf{r} \) through a positive angle \( \Phi \) (Goldstein 1980). For example, in Fig. 2 we replot the left and right panels of Fig. 1; the vectors in the middle column are collinear with the Euler axes around which the cameras in the left column have to be rotated to assume the orientation represented in the right column through a rotation around a single axis. Thus the vectors in the middle column represent the Euler axes that describe the orientation of the cameras on the right; the top and the bottom vectors are different, as are the orientations of the rightmost cameras. The advantage of using this representation over others in studying the oculomotor system is that it represents the shortest path from the current orientation to the primary orientation (Nakayama and Balliet 1977; Schnabolk and Raphan 1994a). Consequently, we will use the Euler axis-angle form to represent orientation throughout the paper.

Simplifying assumptions and limitations

In this paper we treat each agonist-antagonist pair of muscles as a single ideal muscle, able to apply either a positive or a negative torque. With this simplification, which is, explicitly or implicitly, used also in the models developed by Tweed and Vilis and by Schnabolk and Raphan, the tension that the muscles develop is linearly proportional to their innervation (Haustein 1989), i.e., the tension-innervation ratio is constant. We introduce other simplifi-
Saccadic system in one dimension (rotations around a single axis)

In a first-order approximation, the oculomotor plant in one dimension (1 pair of muscles pulling around a single axis) can be described as a Voigt element (i.e., the parallel connection of a viscous element and an elastic element), which represents the passive characteristics of the plant, and a tension applied in parallel to it, which represents the action of the contractile elements (Robinson 1964). In theory, the inertia of the globe should also be taken into account, but its value is so small (Robinson 1964) that for our purposes it can safely be ignored (Tweed et al. 1994a).

Newton’s law states that the torque \( T(t) \) exerted by the muscles is the sum of the viscous and the elastic torque. If we indicate with \( \Phi(t) \) eye orientation at time \( t \) and with \( \omega(t) \) eye angular velocity at time \( t \)

\[
T(t) = B \cdot \omega(t) + K \cdot \Phi(t)
\]

where \( B \) is the viscosity and \( K \) the stiffness of the plant (muscles and orbital tissues).

In one dimension, rotations and translations are essentially equivalent, and angular velocity is the derivative of orientation. Thus the transfer function of the system in the Laplace domain is

\[
\Phi(s) = \frac{1}{K} - \frac{1}{sT_c + 1}
\]

The system has a single pole, and the step response of the system is an exponential with time constant \( T_c \), equal to the ratio of the viscosity to the stiffness. As shown by Robinson (1975), the value of this time constant in the monkey is \(~200\) ms.

The torque \( T(t) \) produced by the muscles is related to the innervation \( I(t) \) that the muscles receive from the motoneurons by the factor \( S \), called the tension-innervation ratio (see METHODS)

\[
T(t) = S \cdot I(t)
\]

Both Eqs. 1 and 3 define the same torque; consequently, at each instant of time

\[
I(t) = B_s \cdot \omega(t) + K_s \cdot \Phi(t)
\]

where \( B_s = B/S \) and \( K_s = K/S \).

To rotate the eye from its initial orientation \( \Phi_0 \) to a new orientation \( \Phi_1 \), it would be sufficient to change the innervation signal in a stepwise manner, changing its value from \( K_s \cdot \Phi_0 \) to \( K_s \cdot \Phi_1 \). However, this would produce a slow movement, with the eye orientation changing from \( \Phi_0 \) to \( \Phi_1 \) with an exponential time course (step response of a single-pole system; Fig. 3A). For any movement, at least 600 ms (3 \( T_c \)) would be needed to foveate the target. This is clearly undesirable, because retinal slip during this time could strongly degrade vision (Westheimer and McKee 1975).

Recordings in the motoneurons of the extraocular muscles show that, fortunately, the innervation signal does not change in a stepwise manner during saccades (Fuchs et al. 1988; Luschei and Fuchs 1972; Robinson 1970; Robinson and Keller 1972). In fact, the motoneurons’ activity is composed of a tonic (Step) and a phasic (Pulse) component. During periods of fixation, only the Step is present, whereas during saccades both the Step and the Pulse are present, and the movement is considerably faster (Fig. 3B). Moreover, recordings in the brain stem and anatomic studies (for a review see Hepp et al. 1989) revealed that these two components are generated in different neural structures and that they are summed together at the level of the motoneurons. Thus, as far as the saccadic system is concerned, the innervation signal can be expressed as

\[
I(t) = \text{Pulse} + \text{Step}
\]

When the eye is not moving (steady state, \( \omega = 0 \)), only the Step component is present in the motoneurons’ activity. Because both Eqs. 4 and 5 define the same signal (innervation), it follows that, in steady state

\[
\text{Step} = K_s \cdot \Phi
\]

Thus, at least in steady state, the Step encodes eye orientation (\( \Phi \)). However, the above considerations do not guarantee that the Step encodes the orientation during the movement, when \( \omega \) is not zero. In fact, Eqs. 3 and 5, which describe innervation in two different ways, guarantee only that the sum of Step and Pulse is proportional to the mechanical torque, but do not impose any constraint on the relative contribution of Pulse and Step to the innervation signal. For example, the Step could assume an arbitrary value during the movement, and its final value could be calculated directly from the desired final orientation \( \Phi_f \) (i.e., target position) using Eq. 6. Nevertheless, if the orientation of the eye at the end of the Pulse is not equal to the orientation associated with the value of the Step (which, by Eq. 6, always determines the steady-state condition), the eye would drift to \( \Phi_f \) with a time constant \( T_c \) (Fig. 3C). Such
The two signals (Pulse and Step) could be generated independently, as long as they were appropriately matched, but it would be parsimonious to generate one from the other. There is compelling physiological evidence that the Step is generated from the Pulse. For example, when saccades are interrupted in mid-flight by stimulation of the omnipause neurons, which inhibit the pulse generators, the eye does not drift toward the goal or the initial orientation, but stays still (Keller 1974). Furthermore, when the Pulse is produced by electrically stimulating the brain areas that carry the Pulse signal, no target is specified. In this case, the eye displacement is a function of the duration and intensity of the stimulation; however, when the stimulation is over, the eye does not drift but maintains its orientation (Cohen and Komatsuzaki 1972; Crawford et al. 1991; Crawford and Vilis 1992; Keller 1974). In other words, the Step is always appropriate to keep the eyes where they are, even when a Pulse is artificially generated or modified; we infer from this that the Step is calculated dynamically from the Pulse. This implies that the Step always encodes eye orientation, even during the movement, when \( \dot{v} \neq 0 \) (i.e., Eq. 6 holds all the time). This is in sharp contrast to the statement by Schnabolk and Raphan (1994a, p. 624), that the Step encodes orientation only in steady state.

Now, because the Step encodes orientation, from Eqs. 4-6 it follows that

\[
Pulse = B_s \cdot \dot{\omega}(t)
\]

Now that we have determined the value of the Pulse and the Step, we have to discover how the Step can be generated from the Pulse, i.e., we must find a function \( f \) such that

\[
Step = K_s \cdot \Phi(t) = f(Pulse) = f[B_s \cdot \dot{\omega}(t)]
\]

In the case of rotations around one axis, \( \dot{\omega}(t) \) is the derivative of \( \Phi(t) \), and the problem of determining \( f \) is trivial

\[
K_s \cdot \Phi(t) = f[B_s \cdot \dot{\Phi}(t)] = f(u) = \frac{K_s}{B_s} \int_0^t u \, dt
\]

So, the Step can be obtained by simply integrating (in the mathematical sense) the Pulse, with an appropriate gain. This automatically guarantees a Pulse-Step match, and thus the absence of postsaccadic drift (Robinson 1975).

**Effect of a Pulse-Step mismatch and estimation of the overall mismatch**

Before going on to show how the Step can be computed for rotations around arbitrary axes, it is important to see what happens when Eq. 9 is not obeyed, i.e., when an incorrect function is used to derive the Step from the Pulse. Clearly a postsaccadic drift is expected, but predicting its magnitude is not straightforward. For example, suppose that at a given point the eyes are still (i.e., the Step is appropriate to maintain eye orientation) and their orientation is \( \Phi_0 \). To make a saccade, a Pulse is generated; at the very beginning of the saccade, the Step encodes orientation by hypothesis, and, thus (Eq. 5) the Pulse must encode eye velocity. However, suppose now that, for some reason, the gain of the integrator (Eq. 9) is not appropriate, i.e.

\[
Step = k \cdot \frac{K_s}{B_s} \int (Pulse) \, dt = k \cdot K_s \int \omega(t) \, dt \neq k \cdot K_s \cdot \Phi(t)
\]
with \( k \neq 1 \). Clearly the Step no longer encodes orientation; however, regardless of the value of Pulse and Step, the total torque is always proportional to the innervation (Eqs. 1, 3, and 5), i.e.,

\[
T(t) = B \cdot \omega(t) + K \cdot \Phi(t) = S \cdot I(t) = S \cdot \text{Pulse} + S \cdot \text{Step} \tag{11}
\]

Because the Step accounts for only a fraction of the orientation (Eq. 10), the Pulse must account both for the velocity and for the remaining part of the orientation. Thus we can rewrite Eq. 11 as follows

\[
T(t) = B \cdot \omega(t) + K \cdot \Phi(t) = B \cdot \omega(t) + \gamma(t) \cdot [K \cdot \Phi(t)] + [1 - \gamma(t)] \cdot [K \cdot \Phi(t)] \tag{12}
\]

with \( \gamma(t) \neq 0 \). Now, from Eq. 12 it is clear that the Pulse does not simply encode the velocity \( \omega(t) \), but some different signal that is not proportional to \( \omega(t) \). However, if the viscous torque \( [B \cdot \omega(t)] \) is much smaller than the elastic torque \( [K \cdot \Phi(t)] \), \( B \cdot \omega(t) \approx \gamma(t) \cdot K \cdot \Phi(t) \). Thus the Pulse can be considered as proportional to \( \omega(t) \). In this case, Eq. 10 essentially holds (i.e., the Pulse always encodes velocity), and the instantaneous Pulse-Step mismatch (i.e., \( k \); it will become clear later on why the term instantaneous mismatch is used) is a good estimate of the overall Pulse-Step mismatch. For example, if \( k \) is equal to 0.9, during the movement the Step will change by only 90% of the change in orientation (Eq. 10), and thus the overall mismatch (i.e., the magnitude of the post-saccadic drift) will be 10% of the amplitude of the movement.

In contrast, if the viscous component of the torque is smaller than (or comparable with) the elastic torque (i.e., the velocity of the movement is low), Eq. 12 implies that the Pulse does not encode angular velocity (i.e., Eq. 10 does not hold anymore), and it is thus impossible to evaluate the overall Pulse-Step mismatch from the instantaneous mismatch. Nonetheless, note that when the innervation signal changes very slowly (i.e., Pulse \( \rightarrow 0 \) and \( \omega \rightarrow 0 \)), Eqs. 1 and 4 can be reduced to Eq. 6; in other words, the orientation matches the Step, and the Pulse-Step mismatch, which by definition (Bahill et al. 1975) is the difference between the orientation of the eye and the Step of innervation, is null, regardless of the value assumed by the instantaneous Pulse-Step mismatch (i.e., \( k \)).

To summarize, when \( \omega \rightarrow \infty \), the overall mismatch coincides with the instantaneous mismatch, and, when \( \omega \rightarrow 0 \), the overall mismatch is always null. For all intermediate values of \( \omega \), the overall mismatch is then smaller than the instantaneous mismatch, because part of the drift occurs during the movement. Consequently, the instantaneous mismatch provides an upper bound for the overall mismatch: if the instantaneous mismatch is small, the overall mismatch will be small, always. However, if the instantaneous mismatch is large, that does not necessarily mean that the overall mismatch will be large: if the speed of the movement is small, the overall mismatch can still be small. Nevertheless, because of the high speeds that characterize saccadic eye movements, the viscous torque is larger than the elastic torque; accordingly, when saccades are considered, the instantaneous mismatch is only slightly larger than the actual overall mismatch. In contrast, when slow movements (e.g., smooth pursuit movements) are considered, the instantaneous mismatch overestimates the overall mismatch.

**Rotations around arbitrary axes**

As we already pointed out (see Methods), the Euler representation of orientation \( (\Phi, \dot{\Phi}) \) represents the shortest path taking the eye between primary orientation and a given orientation. Thus it is reasonable to say that the restoring torque due to the stiffness \( K \) of the plant will tend to realign the visual axis with the primary position acting along the unit-length axis \( \hat{n} \), with an intensity proportional to \( \Phi \) (Schnabolk and Raphan 1994a). Accordingly, if the axis-angle form is used, expressing the torque in three dimensions is straightforward

\[
\hat{T}(t) = B \cdot \hat{\omega}(t) + K \cdot \Phi(t) \cdot \hat{n}(t) \tag{13}
\]

where \( \hat{T}(t) \) is the torque exerted by the muscles and \( \hat{\omega}(t) \) the angular velocity (both are 3-D vectors).

The torque is applied to the eyeball by appropriately innervating three pairs of muscles. Using the simplification that each pair of muscles is collapsed into an equivalent ideal muscle (see Methods), from now on we will assume that three innervational signals are generated, forming a vector of innervation \( I = [I_1 I_2 I_3]^T \). The torque exerted by the muscles can be evaluated by multiplying the vector of action of each pair of muscles, \( \hat{m}_i \) (the unit-length vector along which the globe rotates under the action of a pair of muscles), by the corresponding innervation and by the innervation/tension ratio

\[
\hat{T}(t) = S \cdot I(t) \cdot \hat{m}_i \tag{14}
\]

The total torque applied to the globe is then the sum of the three vectors obtained applying Eq. 14 to each pair of muscles

\[
\hat{T}(t) = S \cdot [I_1(t) \cdot \hat{m}_1 + I_2(t) \cdot \hat{m}_2 + I_3(t) \cdot \hat{m}_3] \tag{15}
\]

This is mathematically equivalent to multiplying the matrix that has as columns the vectors of action of the three muscles, by the vector of innervation

\[
\hat{T}(t) = S \cdot \hat{M} \cdot \hat{n} \tag{16}
\]

where both the Step and Pulse are vectors of three components. As stated in Methods, we will suppose that the three pairs of muscles act in orthogonal planes and that the matrix \( \hat{M} \) is the identity matrix.

Now, using the same line of reasoning used for the one-dimensional case, it can be shown that, to avoid a Pulse-Step mismatch, from Eqs. 13 and 16, which both define the torque vector, it follows that

\[
\text{Step} = K \cdot \Phi(t) \cdot \hat{n}(t) \tag{17}
\]

\[
\text{Pulse} = B \cdot \hat{\omega}(t) \tag{18}
\]

At this point we are again facing the problem of how to generate the Step from the Pulse

\[
\text{Step} = K \cdot \Phi(t) \cdot \hat{n}(t) = f(\text{Pulse}) = f[B \cdot \hat{\omega}(t)] \tag{19}
\]
Intuitively, the simplest thing to do to extend the model described by Eq. 9 [i.e., the Step is the integral of the Pulse, as proposed by Robinson (1975)] from one dimension to three dimensions, is to use three integrators, one for each pair of muscles. However, as pointed out in the introduction, rotations along arbitrary axes do not commute, and thus the orientation cannot be obtained simply by integrating the angular velocity, as assumed in the one-dimensional case to compute the Step from the Pulse (i.e., to derive Eq. 9 from Eq. 8).

To account for this fact, Tweed and Vilis (1987) developed a model (the quaternion model) that uses noncommutative, rotational operators to generate the Pulse and to compute the Step from the Pulse. The quaternion model is a mathematically correct extension of the Robinson model, and, if the appropriate weights are selected, it produces perfect three-dimensional movements, without any postsaccadic drift (the Pulse and the Step are perfectly matched). Although the mathematics of the model are fairly complicated, it is conceptually straightforward: a Pulse is generated and the Step is evaluated as a function of the Pulse and of the current eye orientation (i.e., of the Step itself), by means of a multiplicative feedback loop (Tweed and Vilis 1987).

In contrast, Schnabolk and Raphan (1994a) proposed that, because the innervation signals applied to the muscles produce torques, which commute, a commutative controller, in which the Step is obtained by integration of the Pulse, can be used. Now, it is true that torques commute, and thus the steady-state orientation is determined by the summation of the torques in any order. In fact, regardless of the dynamics of the movement, in steady-state (Pulse and angular velocity both null), the orientation will be determined by Eq. 17, which simply relates the orientation of the eye with the value of the Step, irrespective of past movements and innervation signals. However, the commutativity of torques guarantees only what happens in steady state, but does not enforce Pulse-Step matching. Nonetheless, using simulations, Schnabolk and Raphan showed that their model also seems to behave fairly well dynamically, at least when small movements are considered. To solve the paradox that a noncommutative plant can apparently be controlled by a commutative controller, a very simple question has to be addressed: just how large is the postsaccadic drift when a commutative controller drives the oculomotor plant?

How noncommutative is the plant, as seen by the controller?

The only information needed to decide whether a commutative controller is sufficient for a 3-D oculomotor plant is the magnitude of the Pulse-Step mismatch that occurs when a commutative neural controller is used. In fact, in normal movements small drifts, due to Pulse-Step mismatch, are sometimes present (Bahill et al. 1975); however, they are, and they must be, small.

If the plant were commutative, the integral of vectorial velocity would be orientation and thus, in analogy to Eq. 9, we could write

\[ K_S \cdot \Phi(t) \cdot \hat{n}(t) = f[B_S \cdot \omega(t)] = f(u) = \frac{K_S}{B_S} \int u \, dt \quad (20) \]

So, ignoring the scaling factor \( K/B \), the system would be commutative if and only if

\[ \Phi(t) \cdot \hat{n}(t) = \int \omega(t) \, dt \Rightarrow \omega(t) = \frac{d}{dt} [\Phi(t) \cdot \hat{n}(t)] \quad (21) \]

If Eq. 21 holds, the Step (which by Eq. 17 should encode orientation) can be computed by simply integrating the Pulse (which by Eq. 18 encodes angular velocity), with an opportune gain, and a commutative controller would be sufficient to produce movements with correct dynamics. Thus one easy way to estimate the magnitude of the postsaccadic drift is to check how inaccurate Eq. 21 is. So, if we compute

\[ \omega'(t) = \frac{d}{dt} [\Phi(t) \cdot \hat{n}(t)] \quad (22) \]

we can define the following parameter \( \Delta \)

\[ \Delta = \frac{||\omega(t) - \omega'(t)||}{||\omega(t)||} \quad (23) \]

where the operator \( || \cdot || \) indicates the Euclidean norm of a vector. We call \( \Delta \) the instantaneous Pulse-Step mismatch (or, more concisely, the instantaneous mismatch), because it represents the difference between the derivative of the orientation and the Pulse (at least when the speed of the movement is not too low, as explained earlier). If \( \Delta \) is small, the integral of the Pulse is very close to the orientation, and thus a simple integrator (i.e., a commutative controller) can be used to compute the Step from the Pulse. It can be shown (see Appendix A) that \( \Delta \) can be expressed as a function of the eccentricity \( \Phi \) and of the angle \( \alpha \) comprised between the orientation vector \( \hat{n} \) and the instantaneous velocity vector \( \omega \)

\[ \Delta(\alpha, \Phi) = |\sin(\alpha)| \cdot \sqrt{1 - \Phi^2 \cot^2 \left( \frac{\Phi}{2} \right) - \left( \frac{\Phi}{2} \right)^2} \]

\[ \approx |\sin(\alpha)| \cdot \frac{\Phi}{2} \quad (24) \]

where \( \Phi \) is expressed in radians.

As previously explained (see section entitled Effect of a Pulse-Step mismatch and estimation of the overall mismatch), \( \Delta \) is an upper bound for the overall mismatch. So, if, for example, during a movement, \( \Delta \) is always equal to 0.2, it means that the overall Pulse-Step mismatch will be smaller than 20% of the amplitude of the movement, but because of the high speed of saccades (see above), only slightly smaller.

Equation 24 shows that the instantaneous mismatch (which in this case coincides with the relative difference between the angular velocity and the derivative of orientation) increases almost linearly with the eccentricity \( \Phi \), and it is a function of the angle between orientation and angular velocity. Because \( \Delta \) is not a constant, and it varies with eccentricity, a simple change in the gain of the integrator is not sufficient to fix the problem. It is worth noting that, because \( \Delta \) is a function of eccentricity, the same movement (fixed axes rotation) executed at different eccentricities will have different Pulse-Step mismatches. When rotations around one axis are considered, \( \alpha \) is always equal to zero, the system is commutative, and \( \Delta \) is always zero.
In Fig. 4 we plot $\Delta$ as a function of the eccentricity $\Phi$ when $\alpha$ is equal to 90° (i.e., the worst case scenario for a given eccentricity), e.g., at the beginning of an upward saccade made from a rightward orientation. For small eccentricities (<15°), $\Delta < 10\%$, so the system is almost commutative. And this is exactly why the movements simulated by Schnabolk and Raphan (1994a), which had small amplitudes, were characterized by a fairly good dynamic behavior, with a limited, but not zero, Pulse-Step mismatch. However, for eccentricities >15°, $\Delta$ can become large, and large Pulse-Step mismatches are expected. And that is exactly why when Tweed et al. (1994a) simulated the model proposed by Schnabolk and Raphan using large movements and eccentricities, they obtained movements with large postsaccadic drifts, which are not observed experimentally.

These observations led Tweed and co-workers to conclude that such a model cannot be right, and that the noncommutativity of rotations (more precisely the derivative of orientation not being angular velocity) must be accounted for, either neurally or mechanically. The neural solution to the problem is to use the model developed by Tweed and Vilis (1987); as a mechanical solution, Tweed and colleagues (1994a) proposed the so-called linear plant model, in which eye orientation and its derivative, but not angular velocity, are encoded neurally (and thus one can be computed by simply integrating the other), and then the plant somehow carries out the necessary transformations. However, Tweed and colleagues did not suggest any scheme regarding the physical implementation of the "linear plant."

Straumann and colleagues (1995) made another attempt to solve the problem mechanically, using a commutative neural controller. They showed that if a second-order plant is paired with a neural controller that generates a Slide component in addition to the Step and the Pulse, the postsaccadic drift produced by Schnabolk and Raphan’s model can be reduced. However, this finding was based on a very restricted subset of simulations, and it has been recently shown (Tweed 1997b) that it does not hold for arbitrary movements.

Recently, Raphan (1997) replied to the observation of Tweed et al. (1994a), noting that the simulations by Schnabolk and Raphan assumed that the planes of action of the muscles do not change with the orientation of the eye, whereas Miller et al. (1993) showed that they do, as a consequence of passing through pulleys coupled to the orbit. Miller showed that the muscles do not change their path from their origin point to some point behind the insertion point; from there they go straight to the insertion point. This intermediate point corresponds to the location of orbital tissues that act on the muscles as pulleys, constraining their movements. As Miller and co-workers (1993) pointed out, "... orbital mechanics is fundamentally different under a pulley model. Here, the axis of rotation is determined by the center of rotation, the effective location of the pulley, and the anatomic insertion. Unlike the conventional model, the pulley model predicts that gaze movements out of the muscle plane will cause the axis of rotation to tilt with the globe..."

In Fig. 5 this concept is expressed graphically with a scale model of the human orbit (generated using anatomic data from Miller and Robinson 1984). If no pulleys were present (Fig. 5A), the muscles would be able to move freely in the orbit, and an elevation of the eyes by 45° would cause a mild backward tilt of the axis of action of the horizontal recti. This change in the vector of action (i.e., the angle around which a pair of muscles rotates the globe) is due to the change of the position in space of the insertion point of the muscles on the globe, and it has always been ignored. If pulleys are introduced (Fig. 5B), the geometry changes dramatically, and the axes of action of the muscles can change considerably with the orientation of the eyes. This enlarged effect (which cannot be ignored) is due to the reduced distance between the insertion point and the fixed point, which corresponds not to the muscle origin but to the pulley position. Thus for the same innervation, the rotation produced by the muscles varies as a function of eye orientation.

Introducing a first-order mathematical approximation for the action of the pulleys, previously only modeled qualitatively by Miller and colleagues, Raphan (1997) showed that the same movement simulated by Tweed et al. (1994a) using the original Schnabolk and Raphan model, was essentially drift-free when the action of the pulleys was accounted for. However, the effect of pulleys on arbitrary movements remained to be determined, because simulations of individual movements had previously been found to be misleading (Schnabolk and Raphan 1994a; Straumann et al. 1995). Furthermore, an analysis of how the pulleys affect the physical significance of the innervation signals was not provided, and, as a consequence, some of the conclusions drawn were inaccurate. Finally, as Crawford and Guitton (1997) pointed out, for the pulley scheme to work, the pulleys have to react differently to phasic and tonic inputs, but neither Crawford and Guitton nor Raphan have shown how such a differential effect can emerge.

**Rotations with pulley effect**

In the case described above (rotations around arbitrary axes without pulleys), it was assumed that the axes of action...
Clearly, Eq. 25 holds under the assumption that $\bar{M}$ is equal to the identity matrix when the eye is in primary position. If this condition does not hold, $\bar{M}$ is equal to the product of $R[\alpha, \hat{n}]$ and $\bar{M}_0$, the muscle matrix in primary position. We will assume that $\bar{M}_0$ is equal to the identity matrix, as done throughout the paper (see METHODS). Thus Eq. 25 holds as it is.

So, the torque applied to the globe (Eq. 16) can be rewritten as

$$\hat{T}(t) = S \cdot \bar{M}(t) \cdot \dot{\hat{I}}(t) = S \cdot \bar{M}(t) \cdot \text{Step} + S \cdot \bar{M}(t) \cdot \text{Pulse} \quad (26)$$

where both the Step and the Pulse components of the innervation are vectorial signals. With the use of this equation and the definition of the torque in terms of viscous and elastic components (Eq. 13), it is easy to show that, when the partial slip of the muscles is accounted for, the Pulse-Step mismatch would be null if and only if the Pulse and the Step are defined as follows

$$\text{Step} = K_r \cdot \Phi(t) \cdot \dot{\hat{n}}(t) \quad (27)$$

$$\text{Pulse} = B_r \cdot \bar{M}(t)^{-1} \cdot \dot{\omega}(t) \quad (28)$$

With the use of the following properties of rotation matrices ($\alpha$ and $\dot{\hat{n}}$ generic)

$$\begin{align*}
R[\alpha, \dot{\hat{n}}] \cdot \dot{\hat{n}} &= \dot{\hat{n}} \\
R[\alpha, \dot{\hat{n}}]^{-1} &= R[\alpha, \dot{\hat{n}}]^T = R[\alpha^*, \dot{\hat{n}}]
\end{align*} \quad (29)$$

and taking into account Eq. 25, the Step and the Pulse are

$$\text{Step} = K_r \cdot \Phi(t) \cdot \dot{\hat{n}}(t) \quad (30)$$

$$\text{Pulse} = B_r \cdot \bar{M}(t)^{-1} \cdot \dot{\omega}(t) \quad (31)$$

From Eqs. 30 and 31 it is clear that the pulses exert a different action on the Step and the Pulse. In particular, the Step encodes eye orientation even when the pulleys are considered. This very important finding will be discussed and illustrated in a more intuitive manner later on.

Going back to the quantification of the instantaneous mismatch, the problem is reduced to quantifying the difference between the derivative of the Step and the Pulse; if and only if this difference is small can a commutative controller be safely used. Ignoring the ratio between $K$ and $B$ as done before, we can define $\Delta$ as

$$\Delta = \frac{\|M^T(t) \cdot \dot{\omega}(t) - \frac{d}{dt} [\Phi(t) \cdot \dot{\hat{n}}(t)]\|}{\|M^T(t) \cdot \dot{\omega}(t)\|} \quad (32)$$

In this case, $\Delta$ is not equivalent to the difference between angular velocity and the derivative of eye orientation, because the Pulse does not encode angular velocity in this model (see Eq. 31).

It can be demonstrated (see APPENDIX B) that $\Delta$ can be expressed as a function of the eccentricity $\Phi$, of the angle $\alpha$ and of $\delta = K_r \cdot \Phi$

$$\Delta(\alpha, \Phi, \delta) = \left| \sin \left( \alpha \right) \right| \cdot \sqrt{1 - \frac{\Phi}{2} \cot \left( \frac{\Phi}{2} \right)^2 + \left( \frac{\Phi}{2} \right)^2 + \Phi \cot \left( \frac{\Phi}{2} \right) \cdot (1 - \cos \delta) - \Phi \cdot \sin \delta} \quad (33)$$
So, Eq. 24 can now be derived as a particular case (δ = 0) of Eq. 33.

In Fig. 6 we plot the value assumed by Δ when α is equal to 90°, as was done in Fig. 4. We plot different curves, showing the value assumed by Δ for five different values of $K_\theta$ (0, 0.25, 0.5, 0.75, and 1). It appears clear from Fig. 6 (and it can be easily confirmed by setting the derivative of Δ equal to 0) that the optimal value of $K_\theta$ is 0.5. If the pulleys are located so as to produce a 50% muscular slip ($K_\theta = 0.5$), the value of Δ always stays below 0.025. This means (see above) that the overall mismatch will always be <2.5%, regardless of the movement. Furthermore, the reader should bear in mind that the curves reported in Fig. 6 represent the worst case scenario (when angular velocity is orthogonal to orientation) for a given eccentricity. When an actual movement is considered, the value of Δ varies during a saccade, and its average tends to be <0.02.

We simulated the same eye movement (from a secondary to a tertiary position) coupling a commutative controller with two different plants, one without pulleys and one with optimally located (0.5) pulleys. In Fig. 7 we plotted the magnitude of the instantaneous Pulse-Step mismatch, i.e., the magnitude of the difference between the orientation of the eye and the orientation encoded by the Step [Mismatch = $\|\Phi(t) - \hat{n}(t) - \text{Step}(t)/K_\theta\|$]. Even though the movement is not carried out at extreme eccentricities ($\Phi$ always smaller than 28.3°), without pulleys (---) the Pulse-Step mismatch is large, definitely beyond the physiological range. In contrast, when the pulleys are optimally located (-----), the Pulse-Step mismatch is very small, well within the range of mismatches normally observed. However, even with an optimal location of the pulleys, the mismatch is not exactly zero, as indicated by the fact that Δ is not zero. When $K_\theta = 0.5$ the mismatch in the torsional plane (torsional blips) is null, but that is irrelevant to determine the suitability of a commutative oculomotor controller. What matters is the global mismatch, and, by deriving Δ mathematically we have demonstrated that the mismatch is small for any movement within the oculomotor range, and it is not restricted to the particular simulation shown here. In other words, a commutative controller is sufficient to control saccadic eye rotations, provided that the pulleys are properly placed.

To have a better idea of the range of possible mismatches associated with a generic movement (around arbitrary axes), we simulated 1,000 movements, using random initial and final orientation (uniform distributions, $\hat{n}$ completely arbitrary, $\Phi < 45°$), with the only constraint that the movement had to be >10°. We then plotted (Fig. 8) the overall Pulse-Step mismatch as a function of the average of Δ at the beginning and at the end of each movement. The value of Δ at the beginning of the movement has been calculated by using Eq. 33 with $K_\theta = 0.5$ and calculating α from the orientation and the velocity vectors as soon as the magnitude of $\omega$ exceeded 10°/s. The final Δ has been calculated using the orientation and the velocity at a time (threshold time) when the magnitude of the Pulse vector fell below an equivalent velocity of 10°/s, i.e., Pulse ≈ 10/$B_\theta$. The overall mismatch has been calculated as the difference of the orientation encoded by the Step and the actual orientation of the eye (Bahill et al. 1975) at the threshold time, divided by the displacement of the eye since the beginning of the movement. The amplitude of the movements simulated ranged from 10 to 85.5°, and the mismatches ranged from 0 to 1.53%; furthermore, 97.75% of the movements had a mismatch smaller than 1%. The maximum absolute mismatch observed was 0.53°. In describing his new model, Raphan (1997, p. 365) again postulates that the Step approximates orientation only during fixation or slow movements, whereas when the Raphan-Miller model of the plant is used, the Step
always smaller than the average saccadic drifts). Of this Pulse signal (but not of the angular velocity) is a concept that model have good dynamic behavior (very limited post- and we have demonstrated mathematically that the integral of rotation were simulated using the equations of motion from Rapahm (1997). The maximum mismatch observed is equal to 1.53% of the actual displacement of the eye since the beginning of the movement. The high correlation indicates that the instantaneous mismatch $\Delta$ can be used to estimate the overall mismatch at the end of the movement (see text).

From Fig. 8 it appears clear that the overall mismatch is always smaller than the average $\Delta$, computed as above. Two effects contribute to this result: first of all, we already pointed out that the instantaneous mismatch imposes an upper bound on the overall mismatch. However, given the high speed of saccadic eye movements, this is not the major contribution. More important is the fact that $\Delta$ represents only the amplitude of the instantaneous mismatch; if the direction of the instantaneous mismatch vectors changes during the movement, the magnitude of their sum will clearly be smaller than the sum of their magnitudes ($||\mathbf{a}|| + ||\mathbf{b}|| \geq ||\mathbf{a} + \mathbf{b}||$). Nonetheless, there is a tight correlation between these two parameters, and thus the instantaneous Pulse-Step mismatch can be safely used to estimate the magnitude of the overall Pulse-Step mismatch.

To dissipate any doubt about the criteria used to define the overall mismatch, we also checked whether changing the value of the Pulse threshold used to define the threshold time had any dramatic effect. We found little change: a value of 50°/s results in a slope of 0.65225, with a correlation ($r^2$) of 0.91684. With a threshold of 100°/s, the slope is 0.67489 and the correlation is 0.91793. With an increase in the threshold the slope gets larger, because the drift that occurs during the movement is more conspicuous at low speeds, but the change is negligible.

**Discussion**

We have demonstrated that, to produce eye movements with the correct dynamics (i.e., free of postsaccadic drift), the brain does not necessarily need to have, or to acquire through learning, any knowledge of the noncommutative mechanics of rotations. If the pulleys are well-placed, from the point of view of the dynamics of the movement, the oculomotor plant can be treated by the brain as a translational (commutative) system; $\text{Eq. 33}$ ensures a close Pulse-Step match, regardless of how the Pulse is generated. Obviously, if the Pulse is not appropriate, the target will not be foveated, but no drift will occur. The appeal of this solution is that the brain only needs to generate the Pulse, whereas the appropriate Step is computed automatically without using complex (and not easily neurally implemented) noncommutative operators. Thus this would represent an example where a biological system has evolved a relatively complex peripheral system to simplify its neural controller.

We will now explain more intuitively how this is possible and how the pulleys affect the various signals implicated in eye movement control. We will then go on to point out the implications of the results presented here.

**Effect of the pulleys on the pulse**

We have demonstrated that, if the pulleys are well-placed, the integral of the Pulse is a very good approximation of orientation. This statement is apparently at odds with the fact that rotations do not commute, and thus the integral of angular velocity is not orientation. In fact, both statements are true, and this is possible simply because in the pulley model the Pulse does not encode angular velocity. Instead, the Pulse vector is defined as the angular velocity vector $\omega$ rotated by $-\delta$ degrees around the axis $\hat{n}$ (see $\text{Eq. 31}$); and we have demonstrated mathematically that the integral of this Pulse signal (but not of the angular velocity) is a very good approximation of the eye orientation.

This concept is elucidated graphically in Fig. 9, where the direction of the Pulse (green dotted line) and the direction of the horizontal recti is vertical, and the eye is primary position (Fig. 9A). The axis of rotation of the horizontal recti is vertical, and thus the angular rotation vector (which is always collinear with the axis of rotation) does not coincide with the Pulse. Thus the Pulse does not encode angular velocity, and its integral can encode orientation.

The fact (Figs. 6 and 7) that the instantaneous mismatch is small means that the Pulse is very close to the derivative of orientation, but, even with an optimal localization of the Pulley plant model proposed by Tweed and co-workers (Tweed 1997b; Tweed et al. 1994a); the principal difference is that we have made explicit here the mechanism that underlies the effect of the plant on the neural signals. Furthermore, this finding supports and gives larger significance to other studies that modeled the Pulse as the derivative of eye orientation (Crawford 1994, 1997; Crawford and Guitton 1997).
a rotation of $\beta$ degrees around $\hat{x}$; subsequently, $\alpha(t)$ will induce a rotation of $\alpha$ degrees around a new axis $\hat{y}'$. Now, it turns out that, if the pulleys are in the right position, these two sequences of rotations result in the same final orientation. Of course, different sequences of rotations around the same axes are noncommutative. However, when different sequences of rotations are made around orientation-dependent axes (e.g., $\hat{x}$ followed by $\hat{y}'$ in one case, and $\hat{y}$ followed by $\hat{x}'$ in the other), the noncommutativity (which again refers to sequences of rotations around the same axes) does not apply. And this is why, even though rotations are noncommutative, the brain can use a simple, commutative, controller for eye rotations: the pulleys provide a mechanism that makes the plant (extraocular muscles, ocular pulleys, and eyeball) appear commutative to the controller.

Effect of the pulleys on the Step

Up to this point we have described in great detail the effect of the pulleys on the Pulse; it is, however, also interesting to note the effect of the pulleys on the Step. Equation 30 implies that the pulleys have essentially no effect on the Step, i.e., the Step represents orientation with or without the pulleys. The need for such a different effect of the pulleys on Pulse and Step was first pointed out by Crawford and Guitton (1997), but no implementation was offered.

Mathematically it is easy to explain why the Step encodes orientation even when the pulleys are considered: the Euler axis that defines the orientation is the eigenvector of the muscle matrix associated with the unitary eigenvalue (Goldstein 1980); in other words, $\mathbf{M}(t) \cdot \vec{h} = \vec{h}$ (see Eqs. 25 and 29). We now use a specific example to explain in an intuitive manner why this is possible. Suppose that the eye is in the primary position, i.e., $\text{Step} = [0 0 0]^T$. Now, if

The behavior of the model can be intuitively explained also by using the geometric definition of noncommutativity (see INTRODUCTION). Suppose that the eye is in primary position and that a Pulse $\alpha(t)$ applied to a pair of muscles produces a rotation of $\alpha$ degrees around the axis $\hat{y}$ (e.g., the vertical axis in Fig. 10). Subsequently, a Pulse $\beta(t)$ is applied to the muscles that, with the eye in primary position, act around the horizontal axis $\hat{x}$. However, because of the first rotation around $\hat{y}$, the eye is not in primary position anymore, and the Pulse $\beta(t)$ will thus produce a rotation of $\beta$ degrees around a new axis $\hat{x}'$ (see Fig. 10). Suppose now that the order in which the pulses are applied is reversed; applying $\beta(t)$ starting from the primary position will produce a rotation of $\beta$ degrees around $\hat{x}$; subsequently, $\alpha(t)$ will induce a rotation of $\alpha$ degrees around a new axis $\hat{y}'$.
the first component of the Step is set to $\alpha$, the corresponding muscles (e.g., the horizontal recti, which turn the eye around the vertical axis when the elevation is 0) will be activated and the eye will reach a new orientation, corresponding to $[\alpha 0 0]^T$ (for simplicity, we will ignore the scaling factor $K_\alpha$). Suppose now that, starting again from the primary position, the second component of the Step (which innervates the vertical recti) is set to $\beta$. In this case the eye will stabilize in the new orientation $[0 \beta 0]^T$. What happens when the Step is changed from $[\alpha 0 0]^T$ to $[\alpha \beta 0]^T$? Equation 30 implies that the orientation is also $[\alpha \beta 0]^T$, but why? The innervation applied to the vertical recti is $\beta$, as it was in the case considered previously, but now the pulling direction of the vertical recti is not the same as before, because the eye is adducted (or abducted). And the same reasoning can be applied to the first component (horizontal recti) of the Step. So, how can the orientation be $[\alpha \beta 0]^T$? When the orientation is $[\alpha 0 0]^T$, the axis of action of the horizontal muscle is $[1 0 0]^T$, and thus a Step equal to $[\alpha 0 0]^T$ is appropriate to keep the eye still. When the orientation is $[\alpha \beta 0]^T$, the axis of action of the horizontal recti becomes $[(1 - a) b c]^T$ and the axis of action of the vertical recti becomes $[d (1 - e) f]^T$ (in primary position $a - f$ would all be zero), i.e., the axes of action of both the horizontal and vertical recti are modified. This implies that the innervation $\alpha$ applied to the horizontal recti will produce a torque $[\alpha \cdot (1 - a) a \cdot b c]^T$. Similarly, the innervation $\beta$ applied to the vertical recti will produce a torque $[\beta \cdot d b \cdot (1 - e) \beta \cdot f]^T$. Now, it turns out (see APPENDIX C for a mathematical derivation) that the sum of these two torques is equal to $[\alpha \beta 0]^T$. In other words, although the horizontal recti alone do not provide a torque sufficient to have the first component of orientation equal to $\alpha$, the vertical recti provide the additional torque $[i.e., \alpha \cdot (1 - a) + \beta \cdot b \cdot c = \alpha]$. Similarly, the two pairs of muscles cooperate to guarantee that the second component of the orientation is equal to $\beta$ [i.e., $\alpha \cdot b + \beta \cdot (1 - e) = \beta$]. In contrast, the third component of the torques produced by the two pairs of muscles cancels out (i.e., $\alpha \cdot c + \beta \cdot f = 0$). This cooperation-compensation between different pairs of muscles makes it possible for the Step to encode orientation irrespective of the presence of the pulleys.

We think it is now safe to conclude that Raphan’s (1997, p. 363) statement that the introduction of the pulleys “is a refinement of the original model, leaving the structural aspects of the model unchanged” does not give due credit to the important functional role of the pulleys. Instead, introducing the pulleys has made a significantly different model, which, as we have just shown, has very interesting emergent properties.

**Implications for the saccadic system**

The organization proposed here for the saccadic system (we refer here to the simple case of head-fixed saccades) is similar to the one proposed by Hepp (Hepp 1990; Hepp et al. 1993) with the vector model and modified by Van Opstal and colleagues (1996). In this scheme, at the level of the superior colliculus (SC), which is a central structure for the generation of saccadic eye movements (for a review see Sparks and Hartwich-Young 1989; Wurtz 1996), the target is encoded as a desired displacement in 2-D oculocentric coordinates. The 3-D coordinates of the angular velocity axis are determined downstream from the SC; Hepp and colleagues (1993) proposed that the transformation from the 2-D motor displacement command to the 3-D angular velocity command is carried out either at the level of the burst generators in the brain stem or by the cerebellum. In contrast, we propose here that this transformation is performed in two steps. First, the 2-D command, which defines a desired change in orientation in a plane is converted into a 3-D Pulse vector that lies in the same plane. Second, the Pulse is converted into the appropriate angular velocity signal by the action of the pulleys on the muscles’ axes of action.

In Fig. 11 we plot a schematic representation of the system needed to generate 3-D saccades when the pulses are taken into account. When a visual target is presented to the saccadic system (retinal error not 0), the Pulse vector has to be parallel to the difference $d_{\Delta z}$ between the current value of the orientation $\Phi_z \cdot n_z$ and the value of the orientation that corresponds to the target position in space $\Phi_z \cdot n_z$. As shown by Hepp et al. (1993), the locus activated on the SC is in fact well correlated with the displacement $d_{\Delta z}$. To generate the Pulse it is thus sufficient that the SC output be a vector representing either the Pulse itself or the displacement that is then converted by a pulse generator (PG) [alternatively, the SC could output both the Pulse and the displacement, one encoded temporally and the other spatially, as recently proposed (Optican et al. 1996)]. The duration of the Pulse will then be controlled in feedback to make sure that the integral of the Pulse from the beginning of the movement, evaluated by a displacement integrator (DI), corresponds to $d_{\Delta z}$. The Pulse is also integrated to obtain the Step (NI); Eq. 33 guarantees that the target is foveated as quickly as possible and with a small post-saccadic drift. The transformation of the Pulse, which is always collinear with the displacement vector $d_{\Delta z}$ and is very close to the derivative of eye orientation, into an angular velocity signal appropriate to foveate the target, which is not necessarily collinear with $d_{\Delta z}$, is carried out mechanically because of the position of the pulleys.

Thus the major problem for the saccadic system in this scheme is to derive the signal $d_{\Delta z}$ from retinal error (i.e., position of the target on the retina) and current eye position. Recently, Crawford and colleagues (Crawford 1997; Crawford and Guittion 1997; Klier and Crawford 1997) pointed out that this problem is not trivial. However, this computation probably takes place outside the feedback loop allegedly used to control saccades and is related to the sensory-motor transformation (SMT in Fig. 11) required to convert a retinal error into a desired eye movement, and not to the execution of the movement itself. Addressing this issue is thus beyond the scope of this paper, which deals exclusively with motor execution. What must be kept in mind is that, if such a problem is not correctly addressed, the target would not be foveated, but the movement would still be dynamically correct (i.e., drift-free).

**Implications for Listing’s Law**

Donder’s Law states that, when the head is fixed, the torsional eye position component is a function of the horizontal and vertical components. In his Treatise on Physiol-
The vestibuloocular reflex (VOR) slow phases (Crawford has been observed (Misslisch et al. 1994; Tweed et al. 1990) that the static positions that the eye can assume are described by Euler axes $\hat{n}$ (see METHODS) that lie in a plane, the so-called Listing's plane.

Initially, Listing's Law was thought to hold only during static fixations, and not during eye movements. The application of accurate systems for recording 3-D eye positions led to the discovery that Listing's Law is also obeyed, to a good approximation, during smooth pursuit and saccadic eye movements (Ferman et al. 1987; Haslwanter et al. 1991; Straumann et al. 1996; Tweed and Vilis 1988).

As already pointed out by Schnabolk and Raphan (1994a,b) and Raphan (1997), the use of an integrator to derive the Step from the Pulse, which we have demonstrated is possible in general, simplifies the implementation of Listing's Law. The only constraint required to restrict the orientation of the eyes, and thus the Step, to a plane is that the Pulse be generated in that plane. As long as the Pulse lies in Listing's plane, the Step, which is the integral of the Pulse, must lie in that plane. Evidence for an alignment of static fixations, and not during eye movements. The application of accurate systems for recording 3-D eye positions led to the discovery that Listing's Law is also obeyed, to a good approximation, during smooth pursuit and saccadic eye movements (Ferman et al. 1987; Haslwanter et al. 1991; Straumann et al. 1996; Tweed and Vilis 1988).

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On the basis of phylogenetic arguments, Tweed and colleagues (1992) argued that it is more reasonable to implement Listing's Law neurally, rather than 'mechanically rig' the extraocular muscles (i.e., introduce pulleys) to yield Listing's Law. However, we propose here that the major role of the pulleys is not to simplify the neural implementation of Listing's Law. What really matters is that the pulleys make it much easier for the saccadic system, and for the ocular motor system in general, to produce eye movements with the correct dynamics. Thus the simplicity of implementation of Listing's Law is just "the frosting on the cake," and the "mechanical rig" is well worth the hassle.

**Implications for the VOR**

Whereas models that consider the muscles as fixed in the orbit could hypothesize a simple conversion of head velocity information into eye velocity information (Robinson 1982), when the pulleys are considered the picture is obviously more complex. In fact, because the axis of action of the muscles changes with eye orientation, the same Pulse signal produces rotations around different axes depending on eye orientation. Thus, if head velocity were translated directly into the Pulse signal, without accounting for eye orientation, the axis of eye rotation associated with the VOR would be a function of eye orientation, and thus it would not always align with the axis of head rotation.

Interestingly enough, given a fixed vestibular stimulation, a relation between the axis of eye rotation and eye orientation has been observed (Misslisch et al. 1994; Tweed et al. 1991; Yue et al. 1994), and to a lesser extent during saccades and smooth pursuit (Straumann et al. 1996; van Opstal et al. 1996), are generated whenever the Pulse signal does not lie in Listing's plane. To bring the eyes back in Listing's plane with a subsequent saccade (Crawford and Vilis 1991; van Opstal et al. 1996), the appropriate displacement $\hat{d}_{21}$ (in Listing's plane) has to be provided by the SMT block (Fig. 11), while the torsional component of orientation can be zeroed independently, possibly by a circuit that does not involve the SC (van Opstal et al. 1996).

On the basis of phylogenetic arguments, Tweed and colleagues (1992) argued that it is more reasonable to implement Listing's Law neurally, rather than 'mechanically rig' the extraocular muscles (i.e., introduce pulleys) to yield Listing's Law. However, we propose here that the major role of the pulleys is not to simplify the neural implementation of Listing's Law. What really matters is that the pulleys make it much easier for the saccadic system, and for the ocular motor system in general, to produce eye movements with the correct dynamics. Thus the simplicity of implementation of Listing's Law is just "the frosting on the cake," and the "mechanical rig" is well worth the hassle.
1994b): when the eye is not in primary position, the VOR does not compensate perfectly for the vestibular stimulation, i.e., eye velocity and head velocity are not aligned. Tweed and colleagues (1994b) showed that the relation between the orientation of the eye and the eye velocity vector is consistent with an attempt by the system to minimize the optical flow over the fovea (stabilization of the foveal image). In contrast, they noted that this pattern is not fully compatible with what they call the orbital mechanics hypothesis, i.e., it cannot be due only to the plant and some neural processing is required, although Raphan (1997) does not seem to agree on this issue.

What we want to stress here is that, because the VOR slow phase depends not only on head velocity but also on eye orientation, the presence of the pulleys probably does not solve the problem (Tweed 1997b) but does not introduce any complication either.

Implications for strabismus

Recently it has been shown that whereas among normal subjects the scatter in the positions of the pulleys is extremely small, in subjects affected by some types of strabismus the pulleys are grossly misplaced (Clark et al. 1997, 1998b). Furthermore, surgical destruction of pulleys can induce strabismus (Demer et al. 1996). These observations raise the possibility that the presence and location of the pulleys could have strong implications for the development and treatment of strabismus.

If strabismus is associated with a misplacement of the pulleys, a prediction of the pulley model would be that the eye movements of patients affected by strabismus are characterized by a larger postsaccadic drift than that observed in normal subjects. As shown in Fig. 6, the drift should be most prominent for movements executed at large eccentricities, and from secondary to tertiary positions. An important requirement to test this prediction is that the subjects not have a strong postsaccadic drift for movements from the primary to a secondary position (rotations around one axis), when no model predicts a drift (unless the neural gains are not appropriate). If this requirement is not met, it is impossible to distinguish between a drift due to an incorrect set of the weights in the controller (i.e., $K_s$ and $B_s$) and the inability of a commutative neural system to control, because of the misplacement of the pulleys, a noncommutative plant.

Unfortunately, as shown by Inchingolo and co-workers (1996), strabismic children show a fairly large postsaccadic drift even for rotations around a single axis (in their study the vertical axis). Clearly such subjects do not represent a good test for the pulley model, but the existence of strabismic subjects that do not present single-axis drift cannot be excluded.

Nonetheless, one conclusion that can be drawn from this study is that a lot of care should be taken before attempting to reposition the pulleys (or even to cut them loose) within a procedure for surgical correction of strabismus. In fact, if the task accomplished by the pulley is the one proposed in this paper, the effect of moving them could be disastrous, leaving the brain with the task of driving a plant that no longer appears commutative to the controller.

Do the pulleys solve the noncommutativity problem?

In a recent paper Tweed (1997b) stated that, even as far as the saccadic system is concerned, a mechanical solution of the noncommutativity problem does not really solve the problem, but just pushes it upstream. This statement was based on the consideration that a mechanical solution does not solve the problem of the SMT from retinal error to desired eye rotation (Crawford 1997). However, we disagree with the statement that the problem is pushed upstream, because we regard the velocity-position mechanism and the SMT to be completely separate processes. In fact, the problem of the SMT is always present, regardless of the presence of the pulleys, and even the quaternion model (Tweed and Vilis 1987) had to take it into account. The difference is that the quaternion model had to solve, in addition to the SMT problem (i.e., determination of the desired eye rotation), the problems of generating the Pulse and computing the Step from the Pulse (i.e., the velocity-position problem); and both these additional problems required the use of noncommutative operators.

However, the SMT problem is a static problem, it has to be solved before the movement can take place, and it can thus be addressed over a relatively long period (100-ms timescale). In contrast, the velocity-position problem is dynamic, must be solved during the movement, and whatever solution is used to solve it, it must act continuously (on a 1-ms time scale). Thus the pulleys simplify drastically the most difficult problems (i.e., generation of the Pulse and computation of the Step), and they do not push any problem upstream. Nonetheless, Tweed is certainly correct when he states that the pulleys cannot solve all the problems caused by the noncommutativity of rotations; one, albeit the simplest, problem (SMT) still has to be addressed by the saccadic system (but not by the saccadic generator, which is downstream from the SMT).

Predictions of the model

The strongest prediction of the pulley model is that the Pulse is closer to the derivative of orientation than to the angular velocity. To verify this prediction, recordings in the medium lead burst neurons (i.e., the neurons that carry the Pulse) during movements from secondary to tertiary positions are necessary. Because of the relatively large span of burst-neurons’ on-direction, to have a good estimate of the signal they carry it is important to average over a fairly large population of neurons (Quaia and Optican 1997b). Although the results of such an experiment have not been published yet, Van Opstal and colleagues (van Opstal et al. 1996) reported (p. 7294) that “... recordings from both the riMLF and the oculomotor nucleus so far indicate that saccade-related burst activity is better correlated with the rate-of-change of 3-D eye position than with eye angular velocity (our unpublished observation).” These preliminary observations strongly support the model proposed here, as well as all the studies in which it has been proposed that the Pulse encodes the derivative of eye orientation (again, this is not true in the mathematical sense, but the difference $\Delta$, quantified for the 1st time in this paper, is very small). It is especially important that similar activity was recorded in
both burst neurons and motoneurons. In this case the only place left to perform the needed conversion of the Pulse into angular velocity is the plant, as proposed here.

So, essentially all the predictions, in terms of neural activity, that are associated with the model presented here seem to have been confirmed: the SC locus activated during saccades is well correlated with the displacement $d_{31}$ (Hepp et al. 1993; van Opstal et al. 1991, 1995), and, as van Opstal and colleagues reported, the Pulse appears to be well correlated with the derivative of orientation. As already pointed out, recently a wide consensus has grown among workers in the field that the Pulse encodes the derivative of eye orientation than with angular velocity) and that the plant is responsible for somehow converting the Pulse into angular velocity (Crawford and Guitton 1997; Tweed 1997a). We have demonstrated mathematically here how the plant can carry out such a function.

**Experimental tests of the pulley model**

As we have repeatedly pointed out, what we have shown here is that, if the pulleys are correctly placed, the oculomotor plant appears to the neural controller as an approximately commutative system. However, we have presented here no proof, and we do not have any, that the pulleys are properly placed. Several tests could be devised to test the model presented here and to quantify accurately the action that the pulleys exert on the innervation signals.

A first test consists of recording the activity present in burst neurons and motoneurons during eye movements from secondary to tertiary positions. The relationship between the neural activity and the movement produced could then shed light on the axes of action of the extraocular muscles. As previously pointed out, some preliminary observations on this issue have been reported in the literature, but a full study on this subject is certainly in order.

A second test consists of stimulating the sites that contain burst neurons and motoneurons while the animal fixates different targets. This should elucidate how the axes of action of the extraocular muscles depend on orbital eye position. Studies involving stimulation in these areas have been carried out repeatedly but, to the best of our knowledge, no systematic study of the effect of stimulation as a function of eye orientation has been published. Because of the fairly complicated organization of burst neurons controlling vertical movements (e.g., see Crawford and Vilis 1992), we think it is simpler to electrically stimulate either directly the motoneurons of individual muscles or the burst neurons that control the “horizontal” muscles.

A third test for the pulley hypothesis is represented by the surgical resection of the orbital pulleys. The effect of such a procedure on the steady state and the dynamics of eye movements would certainly have a great value in evaluating the functional role of the pulleys. Demer and colleagues (1996) have shown that, even though displacement of the pulley of the medial rectus alone is probably not sufficient to cause strabismus (Clark et al. 1998a), surgical destruction of the pulleys can cause strabismus; however, the effects of such procedure on the dynamics of the movement have yet to be investigated. This test also has clinical relevance, revealing the consequences of such a procedure if carried out on strabismic subjects.

The fourth test consists of determining, with good precision, the positions of the pulleys in the orbit, and making a computer model to simulate their action. Certainly the pulleys, which have been shown to receive innervation (Demer et al. 1997), are placed anterior to the posterior pole of the eyeball, and their location has been determined in the frontal plane (Clark et al. 1997), but their exact locations have yet to be accurately described in three dimensions. Hopefully, thanks to the efforts of Miller, Demer, and colleagues, we will shortly know where they are and what value of $K_0$ is associated with their location. Unfortunately, even if the exact positions of the pulleys were known, the strength of this test is undermined by a lot of unresolved issues (e.g., the stiffness of the pulleys, the function of their innervation, etc.) that should also be addressed.

**Conclusions**

We have demonstrated that, if the pulleys are correctly placed, eye movements are dynamically correct; furthermore, the saccadic system and the neural implementation of Listing’s law are simplified, whereas the complexity of the VOR is at least unaffected. This is possible because the effect of the pulleys is to make the oculomotor plant appear essentially commutative to the neural controller. We have also shown how, thanks to the cooperation-competition between different pairs of muscles, the pulleys can act differently on the Step and on the Pulse components of innervation. We have also demonstrated mathematically that with the pulley model the Pulse encodes a signal that is very close to the derivative of eye orientation, whereas the Step encodes eye orientation. Consequently, the Raphan-Miller pulley model represents, with a good approximation, a mechanical implementation of the linear plant model proposed by Tweed and colleagues (Tweed 1997b; Tweed et al. 1994a).

**APPENDIX A**

We will derive the instantaneous Pulse-Step mismatch of the system, when the muscles are considered fixed in the orbit

$$\Delta = \frac{[\hat{\omega}](t) - \hat{\omega}^*(t)}{\|\hat{\omega}(t)\|} = \frac{[\Delta \hat{\omega}](t)}{\|\hat{\omega}(t)\|} \quad (A1)$$

From now on, we will make implicit the fact that all the symbols used vary with time, and we will avoid indicating this dependence explicitly. From Eqs. A1 and 22 it follows that

$$\Delta \hat{\omega} = \hat{\omega} - \frac{d}{dt} [\Phi \cdot \hat{n}] = \hat{\omega} - \frac{d}{dt} [\Phi \cdot \hat{n} - \Phi \frac{d}{dt} [\hat{n}]] \quad (A2)$$

Now, as Schnabolk and Raphan (1994a) showed, the derivative of $\Phi$ and $\hat{n}$ are

$$\frac{d}{dt} [\Phi] = \hat{\omega} \cdot \hat{n} = \|\omega\| \cdot \cos (\alpha) \quad (A3)$$

$$\frac{d}{dt} [\hat{n}] = \frac{\hat{\omega} \wedge \hat{n}}{2} + \hat{n} \wedge (\hat{\omega} \wedge \hat{n}) \cdot \cot \left( \frac{\Phi}{2} \right)$$

$$= \frac{\|\omega\| \cdot \sin (\alpha)}{2} \cdot \hat{\omega} + \frac{\|\omega\|}{2} \cdot \cot \left( \frac{\Phi}{2} \right) \cdot (\hat{n} \wedge \hat{\omega}) \cdot \sin (\alpha) \quad (A4)$$
where \( \hat{x} \) is a unitary vector parallel to \( \hat{\omega} \wedge \hat{n} \), and \( \alpha \) is the angle between \( \hat{\omega} \) and \( \hat{n} \). It is now easy to demonstrate that

\[
(\hat{n} \wedge \hat{x}) \sin (\alpha) = \hat{\omega} - \cos (\alpha) \cdot \hat{n}
\]

(A5)

Now, substituting Eq. A5 into Eq. A4 and then Eqs. A3 and A4 into Eq. A2 it follows that

\[
\Delta \hat{\omega} = \|\Delta \hat{\omega}(t)\| = \left| \sin (\alpha) \right| \cdot \sqrt{(1 - H)^2 + (\frac{\Phi}{2})^2}
\]

(A6)

where

\[
H = \frac{\Phi}{2} \cdot \cos \left( \frac{\Phi}{2} \right)
\]

(A7)

Now, given that the norm of a vector can be expressed as the square root of the dot product of the vector by itself, and given that

\[
\hat{\omega} \cdot \hat{n} = \cos (\alpha)
\]

\[
\hat{n} \cdot \hat{x} = 0
\]

\[
\hat{x} \cdot \hat{x} = 0
\]

it follows that

\[
\Delta = \|\Delta \hat{\omega}(t)\| = \|\Delta \hat{\omega}\| = \|\Delta \hat{\omega}(t)\| = \sqrt{(1 - H)^2 + (\frac{\Phi}{2})^2}
\]

(A9)

**Appendix B**

We will derive the instantaneous Pulse-Step mismatch of the system when a partial muscular slip, due to the presence of orbital pulleys, is introduced. \( \Delta \), as defined in Eq. 32, is determined by the ratio of the magnitude of two vectors, and thus any transformation that does not change that ratio can be applied to Eq. 32 without affecting the final result. In particular, multiplying a rotation matrix by a vector does not change its magnitude. Thus we can redefine \( \Delta \) by multiplying the vectors in the numerator and the denominator of Eq. 32 by \( \hat{M} \)

\[
\Delta = \frac{\|\Delta \hat{\omega}(t)\|}{\|\hat{\omega}\|} = \frac{\|\Delta \hat{\omega}\||\hat{\omega}|}{\|\hat{\omega}\|}
\]

where

\[
\Delta \hat{\omega} = \hat{\omega} - \hat{M} \cdot \frac{d}{dt} [\Phi] \cdot \hat{n} - \hat{M} \cdot \Phi \cdot \frac{d}{dt} [\hat{n}]
\]

(B2)

From the properties of rotation matrices defined in Eq. 29, it follows that

\[
\Delta \hat{\omega} = \hat{\omega} - \frac{d}{dt} [\Phi] \cdot \hat{n} - \hat{M} \cdot \Phi \cdot \frac{d}{dt} [\hat{n}]
\]

(B3)

Now, the rotation matrix used in Eq. 25 is defined by the equation

\[
\hat{M}(t) = R(\hat{\phi}(t), \hat{\theta}(t)) = \left[\begin{array}{ccc}
\cos \delta + n_1^2 (1 - \cos \delta) & n_1 n_2 (1 - \cos \delta) - n_2 \sin \delta & n_2 n_3 (1 - \cos \delta) + n_3 \sin \delta \\
n_1 n_2 (1 - \cos \delta) + n_2 \sin \delta & \cos \delta + n_2^2 (1 - \cos \delta) & n_2 n_3 (1 - \cos \delta) - n_3 \sin \delta \\
n_1 n_3 (1 - \cos \delta) - n_3 \sin \delta & n_2 n_3 (1 - \cos \delta) + n_3 \sin \delta & \cos \delta + n_3^2 (1 - \cos \delta)
\end{array}\right]
\]

(B4)

that can be decomposed as

\[
\hat{M} = \cos \delta \cdot \hat{I}_x + (1 - \cos \delta) \cdot \left[\begin{array}{ccc}
n_1^2 & n_1 n_2 & n_1 n_3 \\
n_1 n_2 & n_2^2 & n_2 n_3 \\
n_1 n_3 & n_2 n_3 & n_3^2
\end{array}\right]
\]

\[
+ \sin \delta \cdot \left[\begin{array}{ccc}
0 & -n_3 & n_2 \\
-n_3 & 0 & -n_1 \\
-n_2 & n_1 & 0
\end{array}\right]
\]

(B5)

where \( \hat{I}_x \) is the 3 \times 3 identity matrix.

The use of this decomposed form is important when the product of the matrix \( \hat{M} \) by a vector is considered. In fact, from Eq. B5 it follows that

\[
\hat{M} \cdot \hat{\omega} = \hat{M} \cdot \hat{\omega}
\]

\[
= \cos \delta \cdot \hat{\omega} + (1 - \cos \delta) \cdot (\hat{\omega} \cdot \hat{n}) \cdot \hat{n} + \sin \delta \cdot \hat{n} \wedge \hat{\omega}
\]

(B6)

With the use of Eqs. A3–A5, B3, and B6, it becomes trivial to show that

\[
\Delta \hat{\omega} = \|\Delta \hat{\omega}(t)\| = \left| \sin (\alpha) \right| \cdot \sqrt{(1 - H)^2 + (\frac{\Phi}{2})^2} + 2H \cdot (1 - \cos \delta) - \Phi \cdot \sin \delta
\]

(B7)

where \( H \) is defined in Eq. A7. Proceeding as in Appendix A, from Eqs. A8 and B7 it follows that

\[
\Delta = \|\Delta \hat{\omega}(t)\| = \left| \sin (\alpha) \right| \cdot \sqrt{(1 - H)^2 + (\frac{\Phi}{2})^2} + 2H \cdot (1 - \cos \delta) - \Phi \cdot \sin \delta
\]

(B8)

**Appendix C**

We will now demonstrate with a specific example why the Step is not modified by the presence of the pulleys and always encodes orientation (see Eq. 30).

Suppose that the orientation is

\[
\hat{n} = [\alpha \quad \beta \quad 0]
\]

We have to demonstrate that a vector Step equal to \( [\alpha \quad \beta \quad 0] \) is sufficient to keep the eye still at the orientation described by Eq. C1. To show this, we have to calculate the corresponding muscle matrix \( \hat{M} \), which has been defined in Eq. 25 and Eq. B4.

We now introduce the following definitions

\[
\frac{a}{\sqrt{\alpha^2 + \beta^2}} = \frac{\alpha}{\sqrt{\alpha^2 + \beta^2}}
\]

\[
\frac{b}{\sqrt{\alpha^2 + \beta^2}} = \frac{\beta}{\sqrt{\alpha^2 + \beta^2}}
\]

\[
\delta = K_\Phi \cdot \Phi = K_\Phi \cdot \sqrt{\alpha^2 + \beta^2}
\]

(C2)

These definitions allow us to define the muscle matrix as
To get the torque applied to the muscles (ignoring the constants related to the elasticity $K$ and to the tension-innervation ratio $S$), it is necessary to multiply the Step by the muscle matrix. Given that the third component of the Step is zero, the total torque is simply the sum of the first column of the muscle matrix (which represents the axis of action of the 1st pair of muscles) multiplied by $\alpha$ plus the second column of $M$ multiplied by $\beta$. Thus

$$\mathbf{T} = \alpha \cdot \begin{bmatrix} \cos \delta + a^2 \cdot (1 - \cos \delta) \\ a \cdot b \cdot (1 - \cos \delta) \\ -b \cdot \sin \delta \end{bmatrix} + \beta \cdot \begin{bmatrix} a \cdot b \cdot (1 - \cos \delta) \\ \cos \delta + b^2 \cdot (1 - \cos \delta) \\ a \cdot \sin \delta \end{bmatrix}$$

(C4)

So, the first component of the torque is

$$T_1 = \alpha \cdot \cos \delta + a^2 \cdot (1 - \cos \delta) + \beta \cdot a \cdot b \cdot (1 - \cos \delta)$$

$$= \alpha \cdot \cos \delta + \frac{a^2}{a^2 + b^2} \cdot (1 - \cos \delta) + \frac{a \cdot b}{a^2 + b^2} \cdot (1 - \cos \delta)$$

$$= \alpha$$

(C5)

Analogously, it can be easily shown that the second component of the torque is equal to $\beta$ and the third is zero. Thus the Step is appropriate to maintain eye orientation in tertiary positions even in presence of the pulleys.

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Address for reprint requests: L. M. Optican, Bldg. 49, Rm. 2A50, National Eye Institute, NIH, Bethesda, MD 20892-4435.

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CONTROLLING 3-D EYE ROTATIONS