

Mechanics of Eye Movements: Implications of the “Orbital Revolution”

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ABSTRACT: Our understanding of the functional structure of extraocular muscles has undergone a profound change: while these muscles used to be represented by strings running straight from their origin in the posterior orbita to their insertion on the globe, we now know that their paths and pulling directions are dominated by fibromuscular pulley structures, keeping them close to the orbital wall for most of their path. An overview is presented of recent models that have been developed to understand the implications of muscle pulleys for the neural control of eye movements and the applications of such models to the interpretation of experimental data.

KEYWORDS: muscle pulleys; modeling; extraocular muscles; orbital plane; Listing’s plane; Listing’s law; orbit

THE “ORBITAL REVOLUTION”

The first “golden age” of oculomotor research, around 1860, profoundly changed our understanding of the eye, its movements and its mechanics. The experiments by Listing, Donders, and Helmholtz shaped the subsequent understanding of the kinematics of eye movements. At the same time, Volkmann’s anatomical measurements of the ventral origin of the extraocular muscles (EOMs), and of their insertion points on the globe, provided the basics of the understanding of the mechanics of the oculomotor plant.¹ This picture of EOMs as strings running straight from their origin to the insertion on the globe dominated the view of the orbital mechanics for a long time. About 100 years later, a combination of modeling^{2,3} and imaging work^{4–6} sparked off the “orbital revolution”: researchers realized that the EOMs do not run freely in the orbit, but for most of their path stay close to the orbital wall. Initially attributed to a combination of retrobulbar pressure on the fat tissues behind the orbit⁷ and attachments of the EOMs to the orbital wall by connective tissue,⁸ the EOM paths are now thought to be dominated by pulley-like sleeves, which consist of connective tissue as well as smooth muscles.⁹ Ample evidence now also exists that these muscle pulleys are actively innervated¹⁰ (Demer, this volume). In this paper I will refer to these fibromuscular structures simply as “pulleys.” Imaging work has shown that irregularities in these pulleys can lead to incomitant strabismus¹¹ and that their

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locations in turn are affected by muscle palsies.¹² Nevertheless, the detailed implications of these pulleys for the control of eye movements are still controversial.

IMPLICATIONS OF THE “ORBITAL REVOLUTION”

The experimental data that have revolutionized our understanding of the anatomy and physiology of the EOMs have been provided mainly by the work of Demer, Miller, and co-workers (Demer, this volume, and references therein). To understand the implications of these findings for the control signals required to move and hold the eye in eccentric positions, a number of models have been developed. Two types of models can be distinguished:

- (1) Models with a simplified plant that focus on the information processing and control aspects under idealized conditions. By simplifying the mechanics of the oculomotor plant, these models can investigate static as well as dynamic situations.
- (2) Biomechanically correct models that incorporate all known anatomical and physiological details of the oculomotor plant. Because such models include many measured parameters, they are usually quite complex. This has restricted them so far to the simulations of fixations only.

I will present an overview of the most important models and their applications to experimental data.

IDEALIZED-PLANT MODELS AND THEIR IMPLICATIONS

“Idealized-plant models” dramatically simplify the mechanical and physiological properties of the oculomotor plant, in order to better simulate its effects on the control of eye movements. These models commonly assume three idealized muscle pairs (*horizontal*, *vertical*, and *torsional*), which are perfectly orthogonal to each other. The forces generated by these muscle pairs are strictly linear to their innervation. In these models, the location of the pulleys is usually described by a free, adjustable parameter.

The first such model that used the mechanical properties of the oculomotor plant to explain experimental findings was by Schnabolk and Raphan.¹³ Using an oculomotor plant without pulleys but with idealized EOMs, they showed that a two-dimensional horizontal-vertical torque command to the oculomotor plant would nicely explain Listing’s law. (Note that we talk about “torque” here and not about “force,” because a torque is necessary to cause a rotation. In all idealized-plant models, only rotational movements of the eye are considered.) Listing’s law states that for static subjects all rotation vectors describing the eye rotation from the primary position to any eye position align along a plane. Using this plane to determine the coordinate system in which data are described, this can be rephrased as “all eye positions have zero torsion.”¹⁴ In an idealized plant the elastic-restoring torque T , exert-

ed by the elasticity of the EOMs and the orbital tissue onto the eye, is related to the rotation vector \vec{rot} describing the current eye position by

$$\vec{T} = -a^* \vec{rot}. \quad (1)$$

Therefore, a zero torsional component in \vec{rot} automatically implies a zero torsional component in the corresponding torque vector \vec{T} . In other words, in this model a two-dimensional, horizontal–two-dimensional torque command is sufficient to generate all eye positions in Listing’s plane.

Tweed *et al.* quickly pointed out that such a model predicts “blips” in the torsional eye position during eccentric saccadic eye movements, which are not found experimentally.¹⁵ (A later study by Straumann *et al.* did find small but consistent torsional position blips for eccentric horizontal eye movements.¹⁶ But they were much smaller than the ones predicted by Schnabolk and Raphan, and had idiosyncratic directions for vertical eye movements.) The reason for these torsional blips lies in the noncommutativity of rotations.

This noncommutativity entails a paradox: eye *positions* in Listing’s plane have zero torsion, but eye *movements* require a nonzero torsional velocity to stay in Listing’s plane.¹⁴ FIGURE 1 shows this effect graphically: the circles at the center of each surface mark a starting position, and the surrounding surfaces show the amount of torsion that is necessary to move to an adjacent position in Listing’s plane. For example, starting from the primary position (0/0), any surrounding position in Listing’s plane can be reached with no torsion (FIG. 1, flat surface lower left). Also, a purely vertical movement from a vertical starting position requires no torsion (upper left surface, moving “in the groove”). However, a horizontal eye movement from the same starting position needs a torsional component proportional to the size of the movement in order to stay in Listing’s plane (upper left surface, moving perpendicular to the groove).

The change of the surface shape with eye position shows that an eye position–dependent torsional eye-velocity component is necessary to keep the eye in Listing’s plane. This torsional *velocity* component was absent from the Schnabolk/Raphan model, which caused the torsional *position* blips during saccades. Raphan corrected for this by suggesting that pulleys on the EOMs might implement the necessary eye position–dependent torsion during eye movements. FIGURE 2 illustrates the idea: for a horizontal rectus muscle (lateral or medial rectus), a pulley located exactly on the horizontal rotation axis would lead to an axis of eye velocity that tilts with the eye (FIG. 2, top and left). In contrast, if there were no pulleys, the axis of eye velocity would always be (almost) earth-vertical, independent of the eye position (FIG. 2, bottom and left).

Parametrizing these extremes with $k = 1$ (for eye-fixed rotation axes, FIG. 2 top) and $k = 0$ (for head-fixed rotation axis, FIG. 2 bottom), Raphan showed that a value of $k = 0.5$ would correctly implement Listing’s law for fixations as well as for saccades.¹⁷ This is not too surprising because it had been pointed out previously that Listing’s law entails the “half-angle rule” for eye velocity: the axis of eye velocity has to lie halfway between a head-fixed and an eye-fixed axis in order to follow Listing’s law.¹⁸ Quaia and Optican generalized this result for all eye movements, and showed mathematically that EOM pulleys have a different effect on the pulse and on the step components of saccadic innervation.¹⁹ The innervation step generates the

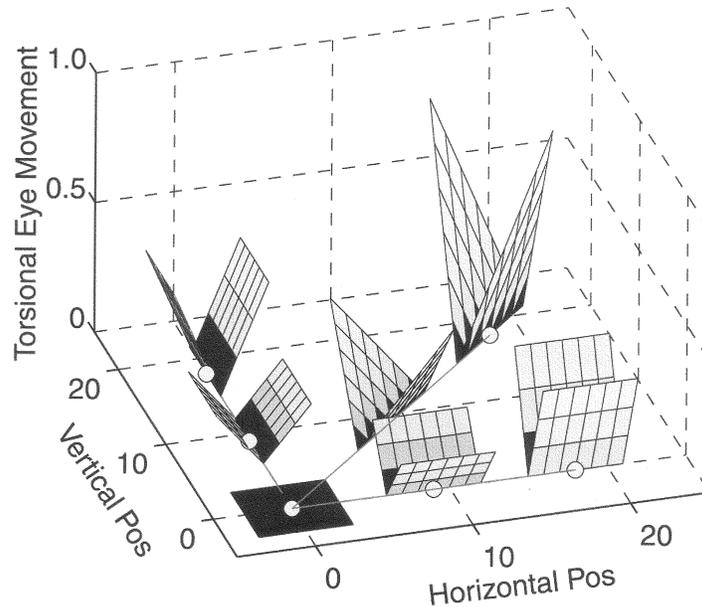


FIGURE 1. The paradox of Listing's plane and torsional eye movements: for different starting points in Listing's plane (*circles at the center of each surface*), a position-dependent, nonzero amount of torsional eye movement is required to move the eye to adjacent horizontal/vertical eye positions in Listing's plane (i.e., with zero torsion!). All eye positions are in Listing's plane, and the angles are in degrees.

torque that keeps the eye in an eccentric eye position by compensating for the elastic restoring forces of the oculomotor plant that pull the eye back toward the straight-ahead position. This torque, which corresponds to the torque \vec{T} in Eq. 1, is independent of muscle pulleys. In contrast, the saccadic pulse is necessary to move the eye and must compensate for the torque generated by the viscous force induced by the eye movement. This torque is proportional to the angular eye velocity, which—as illustrated in FIGURE 2—depends on the pulley locations. Quaia and Optican also showed that with “correctly” located pulleys ($k=0.5$) the saccadic step is almost exactly the same as the mathematical integral of the saccadic pulse. This allows a simple online computation of the saccadic step from the pulse signal, and solves the problem of the 3-dimensional (3-D) velocity–position transformation, without encountering the noncommutativity of 3-D rotations. Such an arrangement would explain, for example, the lack of torsional eye movement signals in the superior colliculus^{20,21} and shows the importance of ocular plant mechanics for the understanding of the neural control of eye movements. However, as Quaia pointed out, more experiments are needed to test the predictions of these models.¹⁹

The discussion about the implications of EOM pulleys sometimes gets mixed up with the controversy about commutativity or noncommutativity in the control of eye

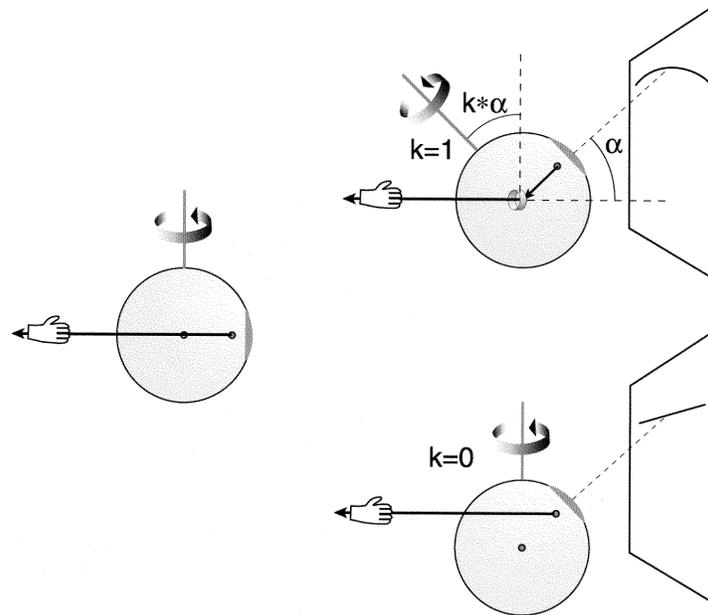


FIGURE 2. Sketch of the effect of a muscle pulley. (*Left*) Pulling on a horizontal rectus muscle exerts a torque about an earth-vertical axis. (*Top right*) If the pulley for the horizontal muscle were located at the center of the globe, the torque that rotates the eye: would always be perpendicular to the line of sight: an eye elevation of α would lead to a tilt of the eye velocity axis of $k*\alpha$, with $k = 1$. (*Bottom right*) If there were no pulley, the torque would always be about an earth-vertical axis, independent of the vertical eye position ($k = 0$, assuming a very long muscle).

movements. A “commutative controller” means that the neural command for a horizontal eye movement is independent of the vertical eye position, and vice versa. The models described above have shown that such commutative controllers, which only use a horizontal-vertical but no torsional eye position signal, can implement Listing’s law, if the EOM pulleys are properly located.

Contrary to a widely held opinion, many researchers who believe in a *non*-commutative, 3-D controller for eye movements do not deny the implications of pulleys, and sometimes also incorporate muscle pulleys in their models.²² However, they have shown that under dynamic conditions (VOR or combined eye-head movements) the torsional component of eye position is actively controlled, something that would not be possible with a horizontal-vertical control system.^{22,23} The proposed noncommutative control systems that can explain these observations are not necessarily complex and can be implemented in a simple, plausible way.²² Furthermore, the visuomotor transformation from retinal information into kinematically correct eye movements requires accurate control over horizontal, vertical, *and* torsional eye position.²⁴ Therefore, the often heated argument about commutativity or noncommutativity in the control of eye movements is not about pulleys, but about whether

the central nervous system uses a 2-D (horizontal/vertical) or a 3-D (horizontal/vertical/torsional) controller for eye movements.

PULLEY MODELS AND EXPERIMENTAL DATA

Models that simplify the mechanics of the orbital plant have also been used to interpret experimental data. For example, Thurtell *et al.* found intriguing differences between active and passive rapid horizontal head movements.²⁵ To investigate whether EOM pulleys could be responsible for these differences, they applied the model by Raphan¹⁷ to the vestibulo-ocular reflex.²⁶ They found that to reproduce the eye movements during the first 50 ms of active head impulses, their model required a pulley coefficient k of 0.5. In contrast, fitting eye movements during passive head impulses led to a pulley coefficient closer to zero (0.2). However, it is arguable how much this reveals about pulleys: it simply shows that during active movements the eye stays in Listing's plane ($k = 0.5$), whereas for passive movements—where the central nervous system does not know about the upcoming head rotation—the central nervous system makes a compromise between Listing's plane ($k = 0.5$) and optimal retinal image stabilization ($k = 0$). No pulleys would be necessary to implement such a control system.

EOM pulleys play a role in all experiments in which the pulling direction of the EOMs is critical for the interpretation of the experimental data. For example, Rambold *et al.* wanted to determine which muscle groups are involved in the generation of nystagmus after lesions in the interstitial nucleus of Cajal. Using a geometric muscle model that accounts for the change of the EOM pulling directions by pulleys, their data suggested a co-activation of eye muscles similar to the effects of electrical stimulation of the anterior canal nerve.²⁷

The recent finding that the locations of EOM pulleys are not constant but can be actively changed by innervation of the global layers of the EOMs has been used to explain changes in the orientation of Listing's plane, such as the lateral tilt of Listing's plane during convergence (Demer, this volume). This mechanism has also been invoked to motivate the lateral tilt of Listing's plane during light sleep.²⁸

Single-cell recordings in the paramedian pontine reticular formation (PPRF) have suggested that during torsional movements of the eye, pulleys may also change their location in the coronal plane. Scherberger *et al.* determined the preferred on-direction of neurons in the PPRF while orienting the monkey in different roll positions, and showed that these on-directions are consistent with pulleys moving in the coronal plane by half the amount of the eye movement.²⁹

BIOMECHANICAL MODELS

All models mentioned so far dramatically idealize the orbital plant. They do not take into consideration the functional differences between the individual EOMs. For example, although the functional origin of the rectus muscles is determined by EOM pulleys that can change their location,¹⁰ the functional origin of the superior oblique is fixed by the trochlea. In addition, idealized-plant models use two gross simplifications. For one thing, they assume that the tension in the muscles is linearly propor-

tional to the innervation. In contrast, the force exerted by real EOMs has a complicated, nonlinear length-tension relationship,³⁰ which is ignored by these models. The second simplification is the assumption of three perfectly aligned push-pull muscle pairs. This assumption avoids the complication of an overdetermined system, which is present in the real oculomotor plant: for each eye we have six EOMs, but only three rotational degrees of freedom. To investigate the actual effects of the individual components of the oculomotor plant, *biomechanical models* incorporating our current knowledge about the anatomical and physiological properties of the orbital plant are indispensable.

The first biomechanical model by Robinson—which also inspired all subsequent modeling efforts—already indicated that the EOMs could not run in a straight line from their origin to their insertion.² This would cause too much “bridle” effect (horizontal rectus muscles becoming elevators in up-gaze, for instance), and too much twist of the muscle at the insertion. Imaging work then indicated that the EOMs in fact stay close to the orbital wall for most of their path.^{4–6} This finding was included in two independent models, both based on the original Robinson model. Simonsz developed a program that was optimized for a handheld computer, aimed at assisting in complicated strabismus surgeries.⁷ In parallel, Miller refined his SQUINT model of binocular alignment³ and made it commercially available as *Orbit*. While Simonsz tried to make his model as straightforward as possible, Miller’s model was characterized by the anatomical accuracy, a user-friendly interface, and superb graphics. *Orbit* now also includes passive pulleys and allows simulation of a number of ophthalmologic pathologies (e.g., muscle palsies, Duane’s retraction syndrome) through modification of parameters characterizing the anatomic and physiologic properties of the orbital plant.

Most recent developments of biomechanical models are related to *Orbit*. Since the source code of *Orbit* is proprietary, Porrill *et al.* implemented many *Orbit* ideas in the MATLAB model *EyeLab*.³¹ Parameters were thereby chosen such that the behavior approximated that of *Orbit*. While the idealized-plant models mentioned above only indicated that properly placed pulleys would *facilitate* the implementation of a commutative controller for eye movements, *EyeLab* demonstrated that the actual structure of the orbital plant is in fact such that commutative horizontal-vertical control signals would implement Listing’s law.³¹

OUTLOOK

Because of the computational complications arising from an overdetermined system (six EOMs, but only three degrees of freedom), current biomechanical models are restricted to the investigation of fixations only. They also cannot easily incorporate recent anatomical findings like the active-pulley hypothesis with its layered view of the EOMs, or additional orbital structures like Lockwood’s ligament (coupling between the inferior oblique and the inferior rectus pulley). To incorporate these elements, the development of a new, strongly object-oriented model of the oculomotor plant is necessary and is currently under development by Miller and co-workers. Also, an extension of biomechanical models to include eye movement dynamics is desirable. This requires a better understanding of the force development in

EOMs during actual eye movements³² and inclusion of the complex properties of muscle force generation.^{33,34}

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