Three-Dimensional Rotations of the Eye

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 Movements of the Eye

Each eye is controlled by six extra-ocular muscles, and has six degrees of freedom: three for rotation and three for translation. However, the amount of translation possible is very limited, approximately 2 mm along the antero-posterior axis, and 0.5 mm in the frontal plane (Carpenter, 1977). Thus, the globe can be well approximated as a spherical joint with its center fixed in the head. With this approximation we only need to consider rotations around three orthogonal axes passing through the center of the eye. These three axes define a system of coordinates for describing ocular rotations. Unfortunately, the mathematical description of rotations of solid objects is much more complicated than that for translations. The final position reached after translations along the three space axes is independent of their order (e.g., $x$-axis followed by $y$-axis movement yields the same position as $y$ followed by $x$). In contrast, the final orientation reached after a sequence of rotations around different axes depends on their order. 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. This would not be the case for translations. Thus, rotations are said to be \textit{non-commutative}. The dependence of the final orientation on the sequence of rotations makes the study of eye movements less intuitive than one might hope. However, careful attention to the definitions of eye orientation and rotation, and on the choice of mathematical tools used to quantify them, can greatly facilitate our thinking about eye rotations.

This latter element is particularly important. In fact, translations, and the resulting positions, can be described by simply specifying the three Cartesian coordinates of the center of the eye. This more familiar, Euclidean, space of translations is flat, and moving in only one direction will never result in getting back to the initial position. In contrast, rotations, and the resulting orientations, can not be described by any simple (i.e., intuitive) set of three coordinates. One of the fundamental reasons for this complexity is that the space of all rotations is curved. This can be easily noted by considering that if one keeps rotating an object around the same axis, eventually (after 360°) it will get back to
Figure 1. Non-commutativity of rotations. The image on the right of each arrow is obtained by rotating the image on its left around an axis collinear with the arrow. A. The camera first rotates $90^\circ$ around a vertical axis, and then $90^\circ$ around a horizontal axis. B. The order of rotations is reversed. The final orientation of the camera is clearly different in the two cases. (Reprinted from Quaia and Optican, 1998)

its initial orientation. To address the inherent complexity of rotations, several mathematical tools have been developed over the last 150 years, such as quaternions, sequences of rotations, rotation matrices, rotation vectors, etc. Although all these methods are equivalent (they all describe the same rotations), each method has both advantages and disadvantages in different applications (Tweed, 1997).

Quantifying Eye Rotations

The first issue that must be addressed when describing rotations or orientations of the eye is whether to consider the three orthogonal axes of rotation as fixed in space, fixed in the head, or moving with the eye. Of course, keeping the axes fixed in space would be of little help, as the eye muscles move the eye relative to the head. The other two solutions have both advantages and disadvantages; the decision of which one to use depends on the specific oculomotor task under study.
Figure 2. Demonstration of head-fixed and eye-fixed coordinate systems. Left column shows positions reached by rotations around one of the six systems of eye-fixed axes (Fick). Because these axes move with the eye (torsion axis not shown), they can be represented by a gimbal system. In the Fick system, the order of rotations is: horizontal, vertical, torsional. Middle column shows a rotation around a head-fixed axis (Euler). With an Euler axis, there is only one rotation, about an axis that is tilted appropriately. Right column shows another eye-fixed system of axes (Helmholtz). In the Helmholtz system, the order of rotations is: vertical, horizontal, torsional. Gaze angles are referred to as primary (top row, looking straight ahead), secondary (middle row, on the horizontal or vertical meridian), or tertiary (bottom row, off both the horizontal and vertical meridians). As can be seen from the middle row, a rotation around one eye-fixed axis moves the eye into a secondary position. Note: all these tertiary orientations correspond to a $45^\circ$ rotation up and to the left. In Fick coordinates, that corresponds to $(31.8^\circ, 31.8^\circ, 0^\circ)$, in Helmholtz coordinates to $(31.8^\circ, 31.8^\circ, 0^\circ)$, and in head-fixed coordinates to $(0, 1, 1)/\sqrt{2}, 45^\circ$.

Eye-Fixed Coordinates

Eye-fixed reference frames are based on consideration of a mechanical mounting system for rotations, such as for a camera. The simplest way to make a camera mount is to have one axis for panning the camera left or right (yaw or horizontal axis), one for tilting it up or down (pitch or vertical axis), and one for twisting it clockwise or counter-
clockwise about the lens’s axis (roll or torsion axis). These axes are nested, one within
the other, in a system of gimbals. (Note: the way the gimbals are nested specifies the
mathematical order of the rotations, thus the order in which the gimbals are moved is
irrelevant). Eye-fixed systems are defined by the order of their rotations (Haslwanter,
1995). There are three rotation axes so there are six possible sequences of rotations.
These eye-fixed coordinate systems are not very useful for the general treatment of
rotations, because they favor one axis over the others (the first, which is independent of
the other two). Nonetheless, two eye-fixed systems, due to Fick and Helmholtz, were
commonly used in the past, and so are briefly mentioned here. The Fick system starts with
a horizontal rotation around the vertical axis, followed by a vertical rotation around the
new horizontal axis, and finally a torsional rotation about the new line of sight. The
Helmholtz system starts with a vertical rotation around the horizontal axis, followed by a
horizontal rotation around the new vertical axis, and finally a torsional rotation about the
new line of sight. The left column of Fig. 2 shows a Fick gimbal, and the right column
shows a Helmholtz gimbal (torsional axes not shown). The movements in the eye-fixed
axis cases have been decomposed into two rotations. The first position (top row) shows
the eye looking straight ahead, in primary position. When the eye rotates from primary
position around the head-fixed horizontal or vertical axis, it is said to move into a
secondary position. This is shown in the middle row for Fick and Helmholtz gimbals.
Note that the first Fick rotation turns the eye to the left, whereas the first Helmholtz
rotation turns the eye upward. The bottom row shows the eye rotated away from the
horizontal or vertical meridian, into what is called a tertiary position.

**Head-Fixed Coordinates**

When using head-fixed axes, the description of rotations that we prefer (because it
seems to us to be the most intuitive) is the so-called axis-angle form (Fig. 2, middle
column), 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 around an axis (through the fixed point) along a unit-length vector \( \hat{n} \)
by an angle \( \Phi \) (Goldstein, 1980). Euler's theorem highlights an aspect common to all the
methods that can be used to represent rotary motion: the need to define a reference orientation. Although its choice is totally arbitrary, the one most commonly adopted in eye movement research is the orientation with the head upright and the eye looking straight ahead. The three main axes of rotation then point straight ahead (X-axis, roll or torsion rotations), straight to the left (Y-axis, pitch or vertical rotations) and straight up (Z-axis, yaw or horizontal rotations). The X, Y, and Z axes define a right-handed system of head-fixed coordinates, \((x, y, z)\), that describe, for each eye orientation, Euler's axis of
rotation, $\hat{n}$. (Note: in a right-handed coordinate system, the direction that the eye turns for a positive angle is the direction that the fingers of the right hand curl when the thumb points along the axis $\hat{n}$.) With this convention, for example, if the eye is rotated 45° to the left, its orientation is described by $\{(0, 0, 1), 45\}$, as that orientation is achieved by rotating the eye, starting from the reference orientation, by 45° around the vertical axis $(0,0,1)$ (Fig. 3A, and Fig. 2 middle column, top row; note that we are looking at the camera from the front, so the X, Y, and Z axes point out of the page, to the right, and up, respectively). Similarly, if the eye where rotated 45° up and to the left, its orientation would be $\{(0, 1, 1)/\sqrt{2}, 45\}$ (Fig. 3B, and Fig. 2 middle column, bottom row). (Note: when eye orientations are discussed in the context of Listing’s Law, a slightly different reference orientation is chosen for convenience. See below.)

**False Torsion**

The examples of rotations about different axes shown in Fig. 2 demonstrate an interesting effect of the non-commutativity of rotations. Note that all three rotations were designed to point the eye 45° up and 45° to the left. In the Euler axis case (middle column) this entails a single rotation of amplitude 45° around an axis tipped 45° from the vertical, $(0, 1, 1)/\sqrt{2}$. In the eye-fixed axes cases, this entails two rotations of magnitude $45^\circ/\sqrt{2}$ (approximately 31.8°) around the first two gimbal axes. If rotations were commutative, like translations, then the final eye orientation in each case would be the same. However, it is clear from the bottom row that the final orientations are not the same, i.e., rotations are not commutative.

Figure 4 shows the three tertiary orientations from Fig. 2 plotted together. The graph has been rotated so that you are looking directly down the line of sight of the Fick coordinate system (white cross). Note that the Fick cross is upright, i.e., rotations in the Fick coordinate system preserve the gravitational vertical on the retina (as is obvious from the gimbals in Fig. 2). The eyeball itself is drawn rotated around an Euler axis (light gray cross). In this case, we see that both the eccentricity of the eye and its torsion are slightly different from the Fick case. A voluntary eye movement to this location would have this orientation (Listing’s Laws, see below). Finally, the dark gray cross shows the
Figure 4. Non-commutativity of rotations and false torsion resulting from equivalent rotations around eye-fixed and head-fixed axes. Eye orientation is indicated by the crosses (Fick: white, Euler: light gray, Helmholtz: dark gray). In this figure, the eye has been rotated $45^\circ$ around an axis tilted $45^\circ$ ($\{0, 1, 1\}/\sqrt{2}, 45^\circ$) middle column, bottom row of Fig. 3). The view of the graph has been rotated around to Fick coordinates ($31.8^\circ, 31.8^\circ, 0^\circ$). Thus, the Fick axis appears centered and upright, which follows because Fick rotations preserve the gravitational vertical on the retina. The Euler and Helmholtz crosses are progressively displaced and twisted from the Fick cross. This indicates the non-commutativity of rotations. Under normal circumstances, the eye assumes the orientation given by the Euler rotation (Listing’s Law). The Fick cross is rotated clockwise from there (from the eye’s point of view), and the Helmholtz cross is rotated counterclockwise. In all cases, this orientation was achieved without any rotations about the torsional axes. Thus, the twists of the local reference frame are referred to as false torsions.

The final orientation reached by rotations around the Helmholtz axes. It’s cross is even further eccentric and twisted than the Euler cross. (Note: the distance between the crosses is a function of the size of the eye rotation; as the eye rotation shrinks in size, so does the difference between the eccentricity and twist of the crosses.) These twists are called false torsions, because they do not arise from rotations about a torsional axis. Obviously, the difference in eccentricity of these three crosses could be eliminated by adjusting the size of the horizontal and vertical rotations for the Fick and Helmholtz systems. However, the difference in the twists would persist, unless a non-zero torsional rotation was introduced.

The difference between true torsion and false torsion is one of the most confusing aspects of the study of eye rotations. It arises because we think about the eye in two
different ways. As a globe, we need a way to describe all of its rotations in a consistent system linked to the head. As an eye, we think of how the gravitational vertical in the visual world will be projected on the retina. When the eye rotates about an Euler axis (fixed in the head) with zero torsional component, the local vertical (which is fixed to the eye) is carried around to a new orientation. Although the twist of the local vertical is real, i.e., it does not line up with the gravitational vertical in the new orientation, it did not arise from a twist around the Euler torsional axis (X-axis). It arose because the eye-fixed axes were carried around by a rotation in a curved space, and hence the eye-fixed axes themselves changed. It was not a true torsion, i.e., a rotation around the head-fixed, torsional axis. The existence of false torsion shows that pointing the eye involves both directing the line of gaze, and choosing a final torsion (three degrees of freedom). However, the brain chooses the final orientation as a function of the horizontal and vertical rotations, in a simple but non-intuitive way, thus reduce the number of degrees of freedom of the eye from three to two.

**Listing’s Law**

Each eye has three rotational degrees of freedom, but the direction of gaze has only two degrees of freedom, because the eye can rotate about the line of sight without changing the direction of gaze. This situation is called kinematic redundancy (Crawford and Vilis, 1995), and implies that each direction of gaze corresponds to an infinite number of different eye orientations. Despite this potential redundancy, observation of actual eye orientations reveals that the brain constrains the torsion to be a function of the horizontal and vertical orientation. This reduces the number of degrees of freedom to two. Each gaze direction (achieved with saccadic or smooth pursuit movements) corresponds to a unique eye orientation, regardless of previous movements and orientations. This observation, known as *Donder's Law* (Leigh and Zee, 1999), holds when the head is kept fixed; it was further extended by Listing to actually specify the space of possible orientations. This is *Listing's Law* (Leigh and Zee, 1999), which states that if the vectors describing the eye orientations attained by a subject having his head fixed in space are plotted, they lie in or near a plane (the so-called Listing's Plane). Figure 5 shows an example of orientation measurements made from a human subject, where each point
Figure 5. Example of Listing’s plane in a human subject. Each small square represents the 3-D components of the tip of the Euler axis from one eye orientation. A. Front view, vertical and horizontal components. B. Side view, vertical and torsional components. The large gray disks represent the orientation shown in Fig. 2A, while the large gray diamonds represent the orientation shown in Fig. 2B. Note that the horizontal component is reversed, as in Fig. 2 we were looking at the vectors from the front, while here they are plotted from the camera’s point of view. (Adapted, with the permission of Cambridge University Press, from Crawford, 1998.)

indicates the orientation of the eye during a period of fixation. Fig. 5A shows the vertical and horizontal components of the Euler axis (from the subject’s point of view), whereas Fig. 5B shows their vertical and torsional components. As an example, on top of the human data we have added two symbols indicating where the Euler axis for the camera orientations shown in Fig. 3A (large circles) and 3B (large diamonds) would be in this graph (note that the horizontal component is reversed, as in Fig. 3 we were looking at the vectors from the front, and not from the camera’s point of view). It is clear that the points in Fig. 5 form a thin, pancake-like cloud, i.e., they lie near Listing’s Plane.

With the head upright, Listing’s plane is normally tilted backwards (about 20°), i.e., it is not aligned with the vertical plane (Tweed et al. 1990 show how to compute it). However, the data are usually transformed to a new coordinate system so that the torsional axis is perpendicular to Listing’s plane. This was done, for example, in Fig. 5. The major advantage of using this transformation is that Listing’s Law then simply states
that only eye orientations with zero torsion are allowed. (Note: this refers to an axis with no torsional component, which is not the same as saying that the brain sends no torsional innervation to the oblique muscles, cf. Table 1.) This lack of a torsional component of the axis of rotation should not be confused with the alignment of the retina with the local gravitational vertical, as noted above.

It must be stressed that Listing’s Law is enforced only when the head is fixed; it breaks down when the head is moving. When the head turns, the vestibuloocular reflex (VOR) counter-rotates the eye, so that the visual world is kept (approximately) stable on the retina. When this involves head motions with the eyes in an elevated or depressed position, accumulated VOR slow phases can carry the eye out of Listing's plane by as much as 30°; the saccade generator compensates for this by adding a predictive torsional component to the innervation of the preceding VOR quick phase (Crawford et al., 1999). Furthermore, when binocular orientations are considered, Listing's plane varies as a function of the depth of the target, so that Listing's plane for each eye rotates outward as the eyes rotate inward during vergence (Mok et al., 1992). This implies that Listing's Law cannot arise from a mechanical property of the oculomotor plant, but must be enforced by providing it with the appropriate innervation signals (here “plant” refers to the system being controlled by the brain, i.e., the globe, extra-ocular muscles, and orbital tissues).

**Neural Control of Ocular Orientation**

The most important issue in the study of eye rotations is thus to understand how the brain generates three-dimensional neural signals that can accurately control the orientation of the eyes, suppress ocular drift, and (when necessary) enforce Listing's Law. To address this question we have to start by identifying the innervation signals that need to be supplied to the extraocular muscles to produce realistic eye movements.

Using the biomechanical model of the eye plant developed by Robinson (Robinson, 1964; Miller and Robinson, 1984) it is possible to show that, because of the viscoelastic properties of the orbital tissues, the torque applied to the eyeball to generate an eye movement can always be interpreted as the sum of three components: a *Step* (i.e., a signal proportional to the current eye eccentricity), a *Slide* (i.e., a low-pass filtered version of the velocity profile), and a *Pulse* (i.e., a signal proportional to the velocity of the eyes).
Figure 6. Components of the innervation signal. The innervation signal is the sum of three components: a Pulse, a Slide and a Step. **A.** When the three signals are appropriately matched, the eyes move quickly to the target and stop abruptly. In this case the eye orientation follows the Step of innervation. **B.** If the components are mismatched (in this case the Pulse is too large), the eyes drift uncontrollably toward the target. The Step is no longer a faithful representation of eye orientation.

The Step compensates for the elastic forces that tend to drag the eyeball towards its resting position, whereas the Slide and the Pulse compensate for the viscosity of the muscles and orbital tissues (Fig. 6A). If the Pulse, Slide and Step are not matched to the dynamics of the oculomotor plant, a post-saccadic ocular drift ensues (Fig. 6B).

The brain controls the generation of this torque through innervation signals (Fig. 7B), but the torques are delivered to the eyeball by the extraocular muscles. Unfortunately, the muscles are not very good actuators, especially at high speeds of shortening or lengthening; consequently, the innervation signal must take the characteristics of the muscles, as well as of the globe and orbital tissues, into account. More precisely, an analysis of Robinson’s model of the plant reveals that, in the process
Figure 7. Distribution of forces between extraocular muscles and orbital tissues. A. Schematic saccadic eye movement. B. The saccadic innervation consists of a Pulse, Slide, and Step, which generate corresponding forces in the muscles. C. Most of the Pulse and the Step are used to change muscle length. Thus the muscle itself “eats up” most of the force. D. The remaining force delivered to the tendon consists of a small piece of the Pulse, the Slide, and part of the Step (Note: the forces in D are magnified about 10 times). The ratio of the Pulse dissipated by the muscle and the Pulse delivered to the tendon is about 20. The ratio of the Step dissipated to that delivered is about 3.3. (Second row shows components of innervation and force; third row shows total innervation and force; the gray area indicates saccade duration.)

of transferring the force to the tendons, each muscle absorbs both a Step and a Pulse of force. The former is proportional to the length of the muscle, while the latter is proportional to its speed of shortening (or lengthening). The muscles behave so poorly that approximately 90% of the energy produced during a saccadic eye movement is dissipated by the muscles, and only the remaining 10% is actually used to rotate the eyeball (Fig. 7C&D, Pulse). Even during periods of fixation only 23% of the innervation force is transferred to the tendons, while the remaining 77% is used to maintain the length of the muscles (Fig. 7C&D, Step). In other words, to deliver the appropriate torque to the eyeball (Fig. 7D, note tenfold gain increase for this graph), an extra, and much larger, innervation force (Fig. 7B) must be supplied to account for the loss in the extraocular muscles (Fig. 7C).

The decomposition of the innervation signal into the force absorbed by the muscles and the force delivered to the tendons, as well as the decomposition of these
forces into their basic components, follows from the properties of the eye plant, and thus holds for any movement, regardless of its dynamics or of the innervation pattern. It cannot be stressed enough that the only signal that must exist in the brain is the overall innervation command, which is carried by the motoneurons. In contrast, the various signals described above (Pulse, Slide, and Step for the orbital tissues, and Pulse and Step for the muscles) are the result of an objective, but artificial, decomposition that we have applied to the overall command; these components do not need to exist as separate signals in the brain. However, since each of these signals compensates for different forces, their adaptation requirements are very different. Accordingly, the only reasonable way to guarantee that they are always appropriate is to compute them separately, and then to sum them together, with adaptable weights, at the level of the motoneurons.

However, this does not imply that these signals have to be computed independently from each other. In fact, because they are associated with physical signals that are related to each other (e.g., eye velocity and orientation are related, as the latter is a function of the history of the former), these neural signals must also be related to each other (i.e., they must be matched). This matching is very important, because the purpose of eye movements is to serve vision and any mismatch in these signals causes the eyes to drift uncontrollably (Fig. 6B), degrading vision (Westheimer and McKee, 1975). The simplest way to guarantee accurate control is to generate one of the three signals, and then compute the other two from that signal.

Robinson recognized this matching problem almost 30 years ago, and proposed a solution for the one-dimensional case, i.e., for rotations around a single axis. In this simplified case, there is a direct proportionality between muscle length and eye orientation, and between eye velocity and rate of change of muscle length. This implies that the Step component relative to the eye muscles is always directly proportional to the Step component relative to the orbital tissues, and they can be lumped together into a single Step; the same holds true for the Pulse components, so that the overall innervation force can then be seen simply as the sum of a Pulse, a Slide, and a Step. Robinson proposed that in this case the Step of innervation could be computed by simply integrating (in the mathematical sense) the Pulse (Robinson, 1973). Similarly, the Slide
can be computed by low-pass filtering the Pulse. This works well because, for rotations around one axis, the orientation (associated, when matching is perfect, with the Step component) is equal to the integral of angular velocity (associated, also under matching conditions, with the Pulse component).

Unfortunately, in three dimensions, when rotations around arbitrary axes must be considered, things get far more complicated. First, in the general case there is no direct proportionality between muscle length and eye orientation; accordingly, the Step signals relative to the orbital tissues (StepOT) and to the muscles (StepM) cannot be lumped together. On the other hand, the two Pulse signals are still both proportional to the rate of change of muscle length, and may still be lumped together. Thus, the overall innervation command can now be seen as a 3-D composite of four signals: Pulse-Slide-StepOT-StepM.

Second, and more important, in three-dimensions the derivative of eye orientation is not equal to eye angular velocity (Goldstein, 1980). This inequality, which is true for any rigid body rotating around a point fixed in space, is due to the non-commutativity of rotations (cf. Fig. 1).

The non-commutativity of rotations has several consequences, but one of the most important (and least intuitive) for oculomotor control is that, to keep the vectors describing the instantaneous orientation of the eye in a plane (e.g., Listing's plane) as it moves, the angular velocity vector about which the eye is spinning must tilt out of that plane (Tweed and Vilis, 1987). This applies to all rotations where the gaze does not go through a great circle on the eye centered on primary position (e.g., no tilt of the angular velocity axis for a rotation from up and left 45° to down and right 45°, which goes through primary position, but a tilt is needed for a rotation from up and left 45° to down and left 45°). This tilt of the angular velocity axis is given by the so-called half-angle rule (Tweed and Vilis, 1990), i.e., if the eyes are elevated 45° up, and you want to rotate the eyes from, say, left 10° to right 10°, the axis of angular velocity must be tipped back from the vertical by 22.5° for the orientation axis to stay in Listing’s plane (Fig. 8B, dashed line). In other words, to ensure that the orientation vector (as well as its derivative) has no torsional component during the movement, the angular velocity vector must have a torsional component whose amplitude is a function of the orientation of the eyes.
How does all this influence the task of generating the innervation command appropriate to rotate the eyes in 3-D? If the Pulse of innervation has to encode the angular velocity of the eyes, then the implications are straightforward: first, the brain will have to generate a Pulse encoding the appropriate angular velocity signal, tipped out of Listing's Plane if orientation has to be confined to that plane. Second, and more important, the step component relative to the orbital tissues ($\text{Step}_{\text{OT}}$) must be computed by passing the Pulse through some rotational operator; simply integrating it won't produce the desired signal, because angular velocity is not the derivative of orientation (Tweed and Vilis, 1987). In contrast, the Slide and the muscle’s step component ($\text{Step}_{\text{M}}$) can still be computed as in the one-dimensional case. Finally, the four components must be summed together in the correct proportions at the level of the motoneurons.

**Orbital Mechanics Can Simplify Neural Control: Extraocular Pulleys**

The abstract discussions of muscles and rotations can now be linked by considering how the orbital geometry of muscles determines the axis of rotation of the eye. Classically, the muscle actions were described in terms of how much they rotated the eye around each of the head-fixed axes, when the eye was in primary position (cf. Table 1). A more accurate analysis considers that each muscle tends to turn the eye around a specific axis, called the axis of action of the muscle. By definition, the axis of action is the unit length vector that is perpendicular to the plane determined by the three points: center of the eye, origin of the muscle, and insertion of the muscle.

The solution we have outlined above for generating the Pulse, Slide and Step is based on the assumption that the axes of action of the muscles are fixed in the orbit (i.e., the axes do not change when the eye moves). In that case there would be a one-to-one correspondence between shortening velocity of the muscle and angular velocity of the eye. However, it has been demonstrated that the axes of action of the extraocular muscle are not fixed in the orbit (Miller, 1989). Instead, they vary as a function of the orientation of the eye. The reason for this dependency is that the muscle’s path, which determines its axis of action, is constrained so that the belly of the muscle moves very little during eye rotations (Simonsz et al., 1985; Miller and Robins, 1987; Miller, 1989). Recent anatomical studies (Demer et al., 1995; Demer et al., 1997) have shed light on the
Table 1. Classic description of muscle actions with the eye in primary position. The axis of action is perpendicular to the plane formed by the center of the eye and the (functional) origin and insertion of the muscle. Each axis has some orientation, which can be described with head-fixed coordinates. The head-fixed axis where most of the force is generated by the muscle gives rise to its primary action. The axis with the next most force gives rise to the secondary action, and the axis with the least force projection gives rise to the tertiary action. Note that muscles work in pairs. From primary position, the lateral and medial recti move the eye horizontally, the superior rectus and the inferior oblique elevate the eye, the inferior rectus and the superior oblique depress the eye, and the superior oblique and the inferior oblique twist the eye. This classification is difficult to maintain once the eye moves away from primary position, because the functional origin of the muscles is changed by the pulleys.

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Primary</th>
<th>Secondary</th>
<th>Tertiary</th>
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<tr>
<td>Lateral Rectus</td>
<td>Abduction</td>
<td>none</td>
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</tr>
<tr>
<td>Medial Rectus</td>
<td>Adduction</td>
<td>none</td>
<td>none</td>
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<tr>
<td>Superior Rectus</td>
<td>Elevation</td>
<td>Intorsion</td>
<td>Adduction</td>
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<td>Inferior Oblique</td>
<td>Extorsion</td>
<td>Elevation</td>
<td>Abduction</td>
</tr>
<tr>
<td>Inferior Rectus</td>
<td>Depression</td>
<td>Extorsion</td>
<td>Adduction</td>
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<tr>
<td>Superior Oblique</td>
<td>Intorsion</td>
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underlying mechanism, showing that each rectus muscle passes through a ring or sleeve near the equator of the globe. The ring is made of collagen (Porter et al., 1996) and is linked to Tenon’s fascia, adjacent muscles, and the wall of the orbit by bands consisting of collagen, elastin and smooth muscle. This anatomical structure thus forms a functional pulley (Demer et al., 1996).

How does the presence of these pulleys affect oculomotor control? The mechanical effect of the pulleys is to make the axes of action of the extraocular muscles vary dramatically as a function of the orientation of the eye. Before the discovery of the pulleys it was assumed that the axis of action of each rectus muscle was perpendicular to the plane formed by its origin on the annulus of Zinn, its insertion, and the center of the globe. Under these conditions (see Figure 8A), changing the orientation of the eye (e.g., from straight ahead to 45° up) would only minimally affect the axis of action of the other muscles (in this case the horizontal recti). However, with orbital pulleys (Figure 8B), the axis of action of each muscle is now perpendicular to the plane formed by the location of its pulley, its insertion on the globe, and the center of the globe. In other words, the pulley
Figure 8. Axis of action of the horizontal recti for two different models of orbital mechanics. The schematics are a scaled version of an actual human orbit (Miller and Robinson, 1984). A. If the muscles can move freely in the orbit, the muscular path does not change much whether the eye is in primary position (black solid line) or elevated by 45° (gray solid line). Correspondingly, the axis of action (black dotted and gray dashed lines) is approximately fixed in the orbit. B. If the path of the muscles through the orbit is constrained by pulleys (hatched oval), the muscular path from the origin to the pulleys is essentially constant in the orbit, regardless of the orientation in the eye. However, the axis of action of the muscles changes dramatically with orientation; the magnitude of this change is clearly a function of the position of the pulleys. (Note: the axis of action is collinear with the angular velocity vector about which the eye would spin if moved by that pair of muscles.) (Adapted from Quaia and Optican, 1998)

acts as the functional point of origin of the muscle. If we now consider what happens when the eye is elevated, we see that the axes of action of the muscles change considerably (Fig. 8B).

Quantitatively it can be shown (Quaia and Optican, 1998) that, if the orbital pulleys are properly located, the velocity of contraction of the muscles (which, as we pointed out previously, is associated with the viscous force that must be compensated by
the Pulse of innervation) closely approximates the derivative of eye orientation, and not eye angular velocity. The derivative of the eye orientation signal, unlike angular velocity, is confined to Listing’s Plane whenever the orientation is. Accordingly, it becomes much easier to implement Listing’s Law: all that is needed to keep the orientation of the eye in Listing’s plane is to generate the Pulse of innervation in that plane. Furthermore, if both Step components of innervation are computed by integrating the Pulse, the resulting movement will have very small post-saccadic drifts, certainly small enough not to impede vision.

Thanks to the presence of the pulleys, it becomes much easier to compute all the components of the innervation signal. However, this simplification must not be confused with a mechanical implementation of Listing’s law. If the brain sends a Pulse of innervation that has a non-zero torsional component (i.e., an Euler axis that is not in Listing’s Plane), the eye will rotate out of Listing’s Plane. Indeed, during head-free gaze shifts, the vestibuloocular reflex (VOR) rotates the eyes opposite to any head rotation. If the head rotates out of Listing’s plane, the VOR will be constantly violating Listing’s Law, and the saccade generator will need to compute torsional components to compensate for this (Crawford et al., 1999). Thus, Listing’s Law must be implemented in the brain, although the pulleys make the required computations much simpler than they would be if the muscle axes were fixed in the orbit.

This neural simplification requires not only a proper placement of the pulleys (they have to be located between the equator and the posterior pole of the globe, in the position that causes the angular velocity vector to tilt half as much as the change in elevation, i.e., to generate the half-angle rule). As the eye turns, the pulleys must also move. More precisely, as a muscle contracts its pulley must be pulled backwards, so that the distance between the location of the pulley and the insertion point of the muscle on the globe is approximately constant. This behavior was indeed found by Demer and colleagues with high-resolution MRI studies of the human orbit (Demer et al., 2000).

The mechanism proposed to achieve such a dynamic relocation of the pulleys turns out to be quite simple, albeit surprising. It has been known for a long time that the fibers that make up each extraocular muscle can be histologically differentiated into two
groups: the global fibers and the orbital fibers (Leigh and Zee, 1999). It turns out that whereas the global fibers of the rectus muscles go through the pulley and insert anterior to the globe’s equator, the orbital fibers insert directly on the pulley (Demer et al., 2000). Thus, when the whole muscle contracts, part of its tension will be delivered to the globe, and part will be delivered to the pulley itself, moving it as required.

Summary

The brain faces a difficult problem when controlling rotations of the eye, because ocular drift suppresses vision, gaze direction has only two degrees of freedom whereas the eye has three, and angular velocity is not the derivative of orientation (i.e., rotations are non-commutative). The extraocular muscles and the orbital pulleys form a mechanism for rotating the eye in three-dimensions. The advantage of this configuration is that, if the pulleys are in the right place, generating the innervation signals appropriate to control ocular rotations without ocular drift, and to enforce Listing’s Law, becomes easier (Quaia and Optican, 1998). This neural simplification requires a more complex orbital mechanism: the pulleys must change the axes of action of the extraocular muscles as a function of eye orientation. However, it appears to be simpler, and perhaps more reliable, to control the location of the pulleys rather than to implement neural circuitry to perform non-commutative operations. The overall complexity of the system is thereby reduced.

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