

61 Neural Mechanisms of Eye Movements: Three-Dimensional Control and Perceptual Consequences

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Most body parts (the head, torso, arms, and legs) move in three dimensions (3-D). However, the third dimension is often ignored when it comes to movements of the eye. For example, we know that our eyes move horizontally and vertically, but we are unaware that they also rotate in a third, torsional dimension, which closely corresponds to movement around the line of sight (i.e., gaze) when looking straight ahead. Although these torsional components are of smaller amplitude than their horizontal and vertical counterparts, the brain possess torsion-specific nuclei and muscles, and their control leads to well-defined, torsionally constrained behaviors. Moreover, a complete description of 3-D rotations involves motion control properties and perceptual consequences that disappear when one applies only abstract descriptions based on the mathematical properties of two-dimensional translations. Thus it is worth spending some time examining the neural control of 3-D eye and gaze (combined eye and head) movements.

BEHAVIOR

Measuring 3-D Eye Movements, Listing's Law and the Half-Angle Rule

Understanding 3-D kinematics first involves describing how one measures these movements. Rather than describing eye positions in Cartesian or polar coordinates (e.g., 10° to the left), 3-D eye movement researchers have found it useful to describe eye orientation as an axis of rotation that takes the eye from some reference position (e.g., straight ahead) to its current location (see figure 61.1A). The pointing direction of the axis describes the direction of rotation according to the right hand rule (i.e., align the thumb with the axis and the fingers curl in the direction of eye rotation), and the length of the axis describes the amplitude of rotation. Together, these define an orientation vector.

Interestingly, when the head is upright and motionless, all these orientation vectors lie in a plane—here, that plane corresponds to the paper on which the figure is drawn. If one looks at these same vectors from a different perspective—a side view—one can appreciate its relative thinness (see figure 61.1B). This plane is known as Listing's plane, and eye movements that adhere to it obey Listing's law. Note that the eye is mechanically capable of rotating about the line of sight at any position, and this could produce systematic or variable distortions of Listing's plane without affecting gaze direction. However, the brain chooses not to do this. Thus Listing's law is one particular solution to the “degrees of freedom” problem, as it is called in motor control studies.

To apply these conventions to real eye movements, scientists place a 3-D eye coil (a contact lens with embedded conductive wire) on the eye and ask subjects to move their eyes randomly while seated inside a set of three magnetic fields. Using the rotation vectors described above and, for simplicity, only indicating the tip of each vector, each possible eye position can be seen to lie in this plane (figure 61.1C—behind view; figure 61.1D—side view), which is typically ~1° in thickness (Straumann et al., 1995; Tweed & Vilis, 1990), and the line of site perpendicular to it is called primary position. Note that primary position is typically different from straight ahead eye position as its location depends on the orientation of Listing's plane in the head.

In its simplest form, Listing's law states that each and every horizontal/vertical gaze direction (e.g., 10° right and 5° up) is associated with one unique torsional component, and that component is zero (Helmholtz, 1867; Westheimer, 1957). This formulation holds under two conditions: (1) Eye positions must be described using the conventions described above, and (2) torsion is defined as rotation about a head-fixed axis parallel to

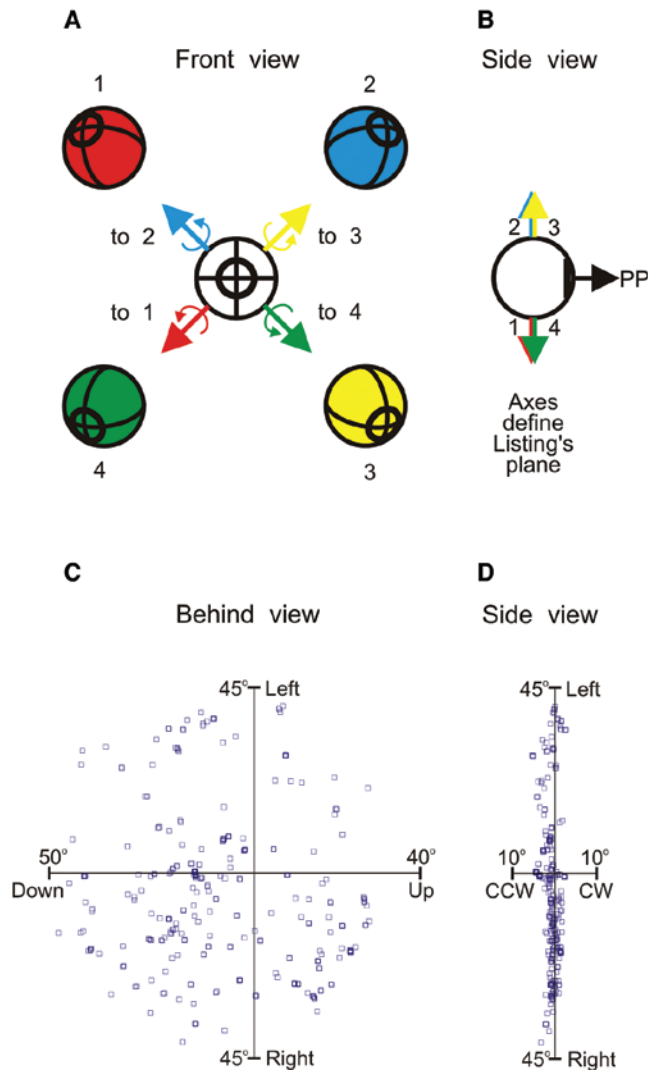


FIGURE 61.1 Measuring 3-D eye movements and Listing's law. (A) Eye orientations are described by axes of rotation (arrows) that take the eye from primary position (center eye) to any other position (1–4). The orientation of each axis describes the direction of rotation according to the right hand rule (align right thumb with the arrow and right fingers curl in the direction of rotation), and the length of the axis describes the amplitude of rotation. (B) A side view of these vectors reveals that they all lie in one plane which is perpendicular to primary position. (A and B adapted with permission from Crawford and Vilis, 1995.) (C) A behind view of real human data, in which only the tips of the rotation vectors are shown (squares). (D) A side view of the data points in (C) illustrate how these data points are confined to Listing's plane. (C and D adapted with permission from Klier and Crawford, 1998.)

primary position. This turns out to be a remarkable and tightly controlled motor phenomenon that holds for fixations, saccades, and pursuit eye movements (Ferman, Collewijn, & Van den Berg, 1987). Incidentally, other

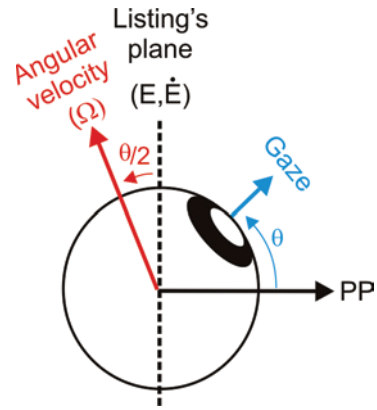


FIGURE 61.2 The half-angle rule. In order for eye position to remain in Listing's plane, angular eye velocity (Ω) must tilt out of Listing's plane by half the amount of gaze eccentricity from primary position (θ). Note that the derivative of eye position ($\dot{E} = dE/dt$) remains in Listing's plane (dashed vertical line), but \dot{E} does not correctly describe the velocity of rotating objects (see text).

body parts like the head and arm obey a similar, more general version of Listing's law known as Donders' law (head—Radau, Tweed, & Vilis, 1994; arm—Hore, Watts, & Vilis, 1992). Donders' law states that when a body part points in particular direction, it will always assume the same torsional component (although not necessarily zero) (Donders, 1848).

While Listing's law describes how eye orientation vectors lie in Listing's plane, the rotation vectors that take the eye from one orientation to another tilt out of Listing's plane. Seemingly counterintuitive at first, this becomes clear when examining the underlying mathematics of rotations. Because rotations are noncommutative (rotation A then B \neq rotation B then A), one cannot simply subtract orientation vectors to obtain the relative rotation. Consequently, the rotation axis (measurable instantaneously as the angular velocity vector) must tilt out of Listing's plane by half the (orthogonal) angle between current gaze and primary position (see figure 61.2). For example, a horizontal saccade made at a gaze elevation of 10° requires that the velocity vector tilt out of Listing's plane by 5°. This is known as the half-angle rule (Tweed & Vilis, 1987). Without this rule, a sequence of two or more rotations about axes in Listing's plane would lead to eye orientations with torsional components out of Listing's plane. Thus the half-angle rule provides the proper compensation of torsional axis tilts to keep eye orientations in Listing's plane throughout a saccade or pursuit eye movement.

Listing's Law Modifications during Vergence and Static Head Tilt

Listing's law, or some variant, is obeyed by all movements that redirect gaze from one object to another. Vergence movements do this for objects in depth and require that both eyes move in opposite directions (converging for nearer objects or diverging for farther objects). A variation of Listing's law, called L2, states that while Listing's plane is frontoparallel when the two eyes are parallel, the planes of the two eyes tilt outwards (like saloon doors) when the two eyes converge (Mok et al., 1992; Van Rijn & Van den Berg, 1993). Thus as both eyes look nasally, Listing's plane of the right eye rotates clockwise and Listing's plane of the left eye rotates counterclockwise (from an above view).

Listing's law is obeyed by eye movements when the head is fixed. However, if the head is fixed and tilted, Listing's plane is still realized, but it exhibits a torsional offset (Crawford & Vilis, 1991; Haslwanter et al., 1992). If the head is rotated clockwise (i.e., right ear down), Listing's plane shifts in a counterclockwise direction (i.e., an offset to the left in figure 61.1D), and vice versa. This shift is due to ocular counterroll which causes a ~10% counterrotation of the eyes whenever the head is rolled (Collewijn et al., 1985).

Violations of Listing's Law during VOR and OKR

Other eye movements are accompanied by head movements and/or involve movements whose goal is to keep the image of the object stable on the retina. To attain these goals, these movements must violate Listing's law and allow the eyes to assume nonzero torsional components. The vestibular-ocular reflex (VOR) is one such example (Crawford & Vilis, 1991; Fetter et al., 1992). This simple reflex causes the eyes to rotate in an equal and opposite direction to head rotation. Thus, torsional head movements (e.g., right ear down to the right shoulder) obviously cause violations of Listing's law. However, even horizontal and vertical VOR movements do not follow the half-angle rule, so they also cause position-dependent violations of Listing's law. Similarly, the optokinetic reflex (OKR) stabilizes the images of moving objects on the retina. Thus if an image is moving in a circular pattern in the frontoparallel plane, the eyes will also rotate torsionally (for as long as possible before resetting with a nystagmus-like quick phase). As a rule of thumb, eye movements engaged in visual tasks that do not specify the required torsion (e.g., saccades, pursuit, vergence) obey Listing's law whereas eye movements where torsion is required for the visual task (e.g., visual stabilization during head rotation; VOR, OKR)

do not obey Listing's law (Crawford, Tweed, & Vilis, 2003).

Listing's Law during Head-Free Movements

When the head is free to move, as is the case in everyday life, torsional constraints are complicated because more parameters need to be controlled. The eyes move in the head, the head moves in space, and both of these contribute to eye motion in space (i.e., gaze). Listing's law is obeyed by the eye-in-head at the end of each movement. In contrast, the head-in-space obeys Donders' law in a specific way known as the Fick strategy (see figure 61.3) (Glenn & Vilis, 1992; Radau et al., 1994). Here, instead of orientation vectors maintaining zero torsion on a flat plane, they form a twisted surface, with torsion at the corners (i.e., clockwise [CW] when up/left and down/right, and counterclockwise [CCW] when up/right and down/left). This is how it looks when torsion is defined using the conventions in figure 61.1 (if Fick

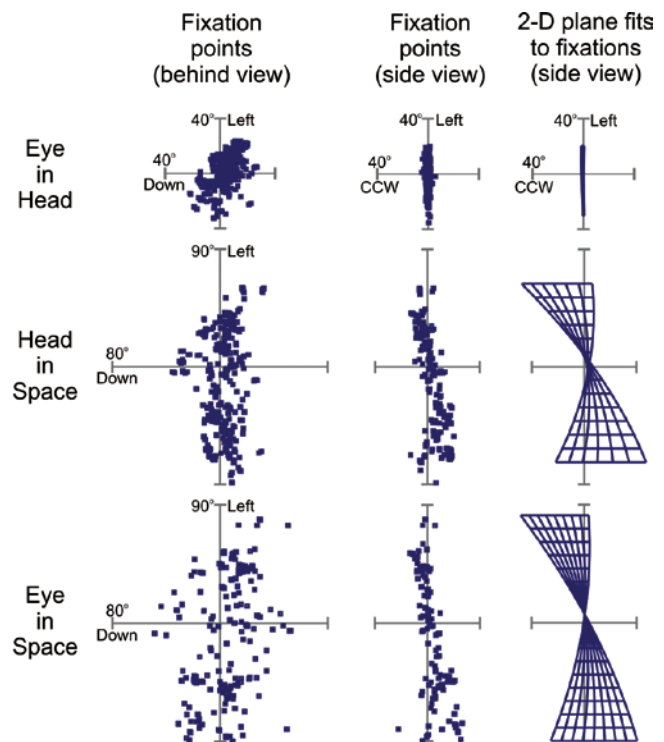


FIGURE 61.3 Three-dimensional behavior of the eyes and head. Tips of rotation vectors of the eye-in-head (top row), head-in-space (middle row), and eye-in-space (bottom row) are illustrated from a behind view (left column) and side view (center column). A 3-D plane is fit to the side view data in the right column that better illustrates the 3-D shape of these data. Notice that the eye-in-head data are planar (Listing's plane) whereas the head- and eye-in-space data look like a twisted plane known as a Fick surface. CCW, counterclockwise. (Adapted with permission from Klier et al., 2003.)

coordinates are used, i.e., where the vertical axis is fixed in the body and the horizontal axis is fixed in the head, then the data would again resemble a zero-torsion plane). The eye-in-space also obeys Donders' law using this Fick strategy. It is thought that the Fick strategy is implemented by the head-in-space and that the eye-in-space follows suit because of the way eye and head rotations naturally combine (Crawford et al., 1999; Glenn & Vilis, 1992).

At the end of a head-free gaze shift, the eye-in-head lands in Listing's plane, but this is not the case during the movement. These movements can be divided into two distinct parts (see figure 61.4A). The first phase (1) begins with the initiation of a gaze shift and ends when the eye-in-space reaches its intended target. For most of this phase, gaze is carried by the eye-in-head and there is little head movement. Here one might expect Listing's law to be obeyed, but it is not for the time being. Instead, the oculomotor system adds a systematic torsional component out of Listing's plane. To understand why, we look to the second phase (2). It begins when the eye-in-space lands on target and the head, now in motion, rotates toward the target until the eyes become centered in the orbits. Due to head motion in this latter phase, and because the eye-in-space must remain on target, the eye-in-head counter rotates according to the VOR. Consequently, Listing's law cannot be obeyed in this second phase. Thus, the oculomotor system must first add torsion to the saccade, in an anticipatory fashion, so that saccade (1) and VOR (2) torsion cancel and movements end up back in Listing's plane (Crawford et al., 1999). The following section describes the physiological implementation of these 3-D rules.

NEURAL AND MECHANICAL CONTROL

Cortical, 2-D Signals

Voluntary gaze shifts (eye only or eye + head) are programmed in the cortex and superior colliculus (SC) and subsequently transmitted to the brain stem for processing and to the oculomotor plant (i.e., the eye and its surrounding muscles and tissues) for execution. The vast majority of oculomotor cortical areas encode only the horizontal and vertical components of desired gaze direction. This has been demonstrated in two ways. First, cortical eye fields, like the frontal and supplementary eye fields, were artificially stimulated with an electrical pulse with the head free to move. This pulse generates a command that is transmitted downstream until an eye-head gaze shift is made. If each cortical site encodes one, unique, nonzero torsional value, then repeated stimulations should elicit gaze shifts with the

same, unique, nonzero torsional eye-in-head component. This would lead to violations of Listing's and Donders' laws since final eye and head positions would lie out of their respective surfaces. On the other hand, if each site encodes only a 2-D command and the torsional component is added on downstream, then repeated stimulations should elicit gaze shifts that end on their respective 3-D surfaces, much like normally elicited eye and head movements. The latter was the case (supplementary eye field: Martinez-Trujillo, Wang, & Crawford, 2003; frontal eye field: Monteon et al., 2010). Stimulation of parietal cortex did produce eye movements with inappropriate torsion, but this was because the normal, phase (2) head movements were not produced (Constantin et al., 2009).

Second, a number of experiments have shown that the SC, the gateway for cortical gaze signals to the brain stem, also carries 2-D commands. Stimulation of the SC also produced normally coordinated eye and head movements that landed in Listing's and Fick planes (Klier, Wang, & Crawford, 2003). Again, this implies that 3-D commands are added on downstream. Other stimulation studies have also backed up the finding that the SC has a 2-D motor map (Hepp et al., 1993; Van Opstal et al., 1991). In addition, bilateral inactivation of the SC does not result in violations of Listing's law during fixations or saccades, and this inactivation does not affect the torsional components of VOR fast phases (Hepp et al., 1993).

The fact that the cortex and SC encode gaze in 2-D makes sense since higher cortical functions are more concerned with redirecting the line of site to a particular location and less concerned about the correct torsional geometry once that 2-D gaze location is reached. However, torsional eye-in-head orientations must be added on somewhere because of the unique 3-D behavior observed during head-free movements and the VOR. Also, a 3-D signal is necessary to move the six extraocular muscles which rotate the eye horizontally, vertically, and torsionally. Thus the SC's 2-D, spatial code must be translated into a 3-D, temporal code. This transformation could be accomplished either neurally, by adding a 3-D signal onto the 2-D command, or by mechanical factors like the anatomical arrangement of the ocular plant. Both these factors are at play.

Brain Stem, 3-D Signal

Output of the SC reaches the burst generators, which produce a 3-D, temporal velocity signal that drives the eye from one location to the next. Interestingly, there are separate burst generators for the horizontal components of eye movements and the vertical/torsional

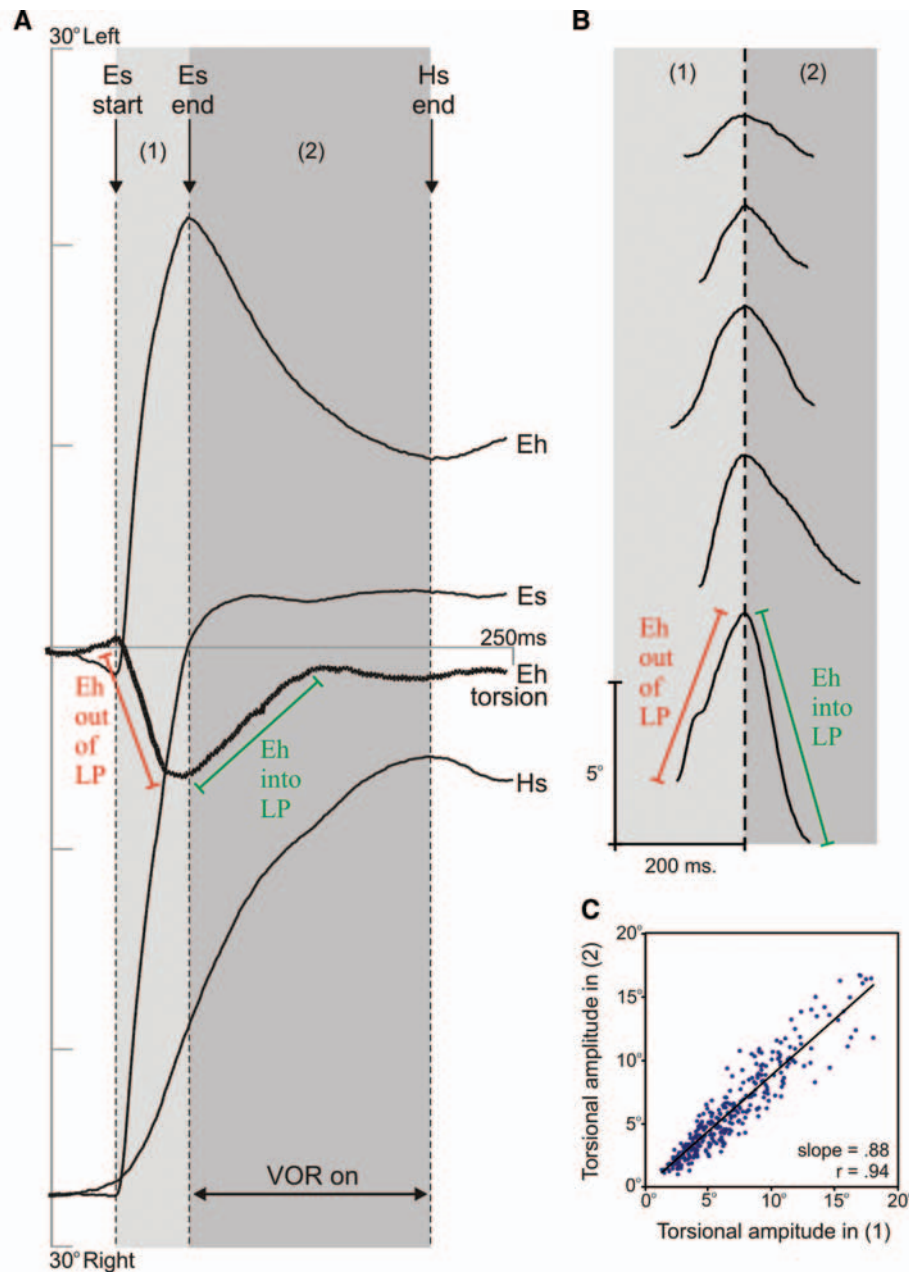


FIGURE 61.4 Torsion during a gaze shift. (A) A plot of eye-in-head (Eh), eye-in-space (Es), and head-in-space (Hs) position as a function of time. In phase 1 (light gray), gaze (Es) is carried to the target by the eye (Eh) while the head (Hs) is mostly stationary. In phase 2 (dark gray), the head (Hs) has overcome inertia and begins to move while gaze (Es) remains steadily fixed on target via the vestibular-ocular reflex (VOR), which rotates the eye (Eh) in an equal and opposite direction to the head (Hs). Eh torsion relative to 0° torsion (abscissa) is superimposed on the same plot. Eh torsion goes out of Listing's plane (LP) in phase 1 in a predictive manner such that it is returned to ~0° torsion in phase 2. Thus the net torsion on the eye (Eh) is zero. (B) Five examples of Eh torsion during gaze shifts of increasing amplitude. The torsional amplitudes in phases 1 and 2 appear to be the same. (C) Quantification of Eh torsional amplitude during phase 1 versus phase 2 for multiple gaze shifts (circles). The amount of torsion in both phases is comparable. (Adapted with permission from Klier et al., 2003.)

components. The former are found in the paramedian pontine reticular formation (PPRF) (Luschei & Fuchs, 1972) while the latter are located in the rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF) (Büttner, Büttner-Ennever, & Henn, 1977;

King & Fuchs, 1979). These velocity signals are sufficient to drive the eyes, but once at their new location, a second, position command is necessary to hold them there (otherwise the eyes would drift back toward a more central, resting position). This position signal is

K2

generated by groups of cells known as neural integrators that perform the mathematical equivalent of integration (i.e., converting velocity to position). Again, the horizontal neural integrator, located in the nucleus prepositus hypoglossi (NPH) (Canon & Robinson, 1987), is found separately from the vertical/torsional integrators, which are located in the interstitial nucleus of Cajal (INC) (Crawford, Cadena, & Vilis, 1991). Finally, all these four brain stem structures project to the oculomotor neurons (cranial nerves III, IV, and VI) that drive the eye muscles. The classic outline of the brain stem saccade generator is shown in figure 61.5A

(Robinson, 1981), and the anatomical locations of the burst neurons and neural integrators are shown in figure 61.5B.

Note that the division of labor between horizontal and vertical/torsional components found in the brain stem mimics the division of labor found in the eye muscles themselves, where the lateral and medial recti control horizontal components of eye movements while the superior and inferior oblique muscles and the superior and inferior recti muscles control vertical/torsional components. Interestingly, a similar division is also found in the semicircular canals that detect head

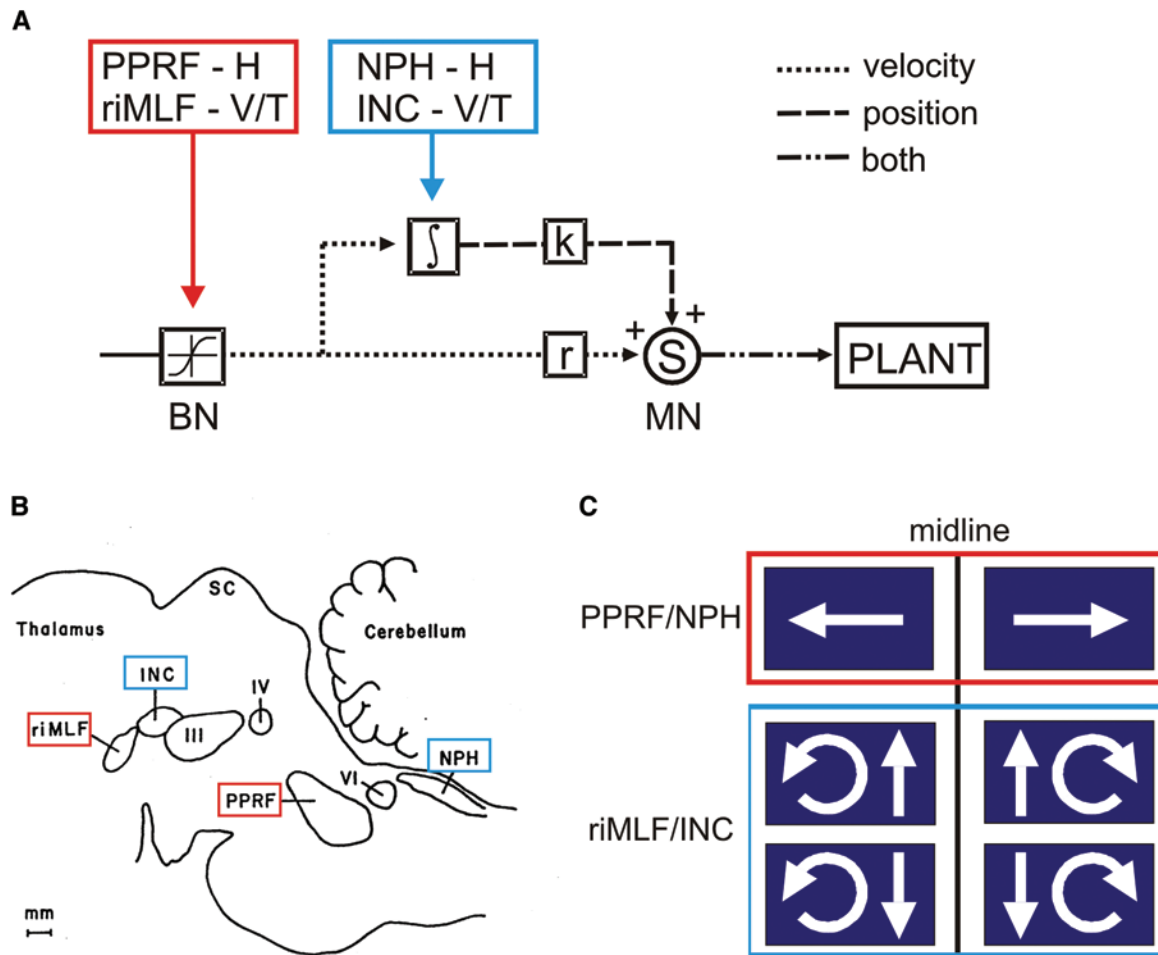


FIGURE 61.5 The three-dimensional, brain stem saccade generator. (A) The Robinson (1981) model of the brain stem saccade generator. Burst neurons (BN) output a velocity command (dotted line) that overcomes the eye's viscosity (r) and is sent to the motoneurons (MN). This velocity command is also sent to the neural integrators (\int) that output a position command (dashed line), which counters the eye's elasticity (k), and is also sent to the MNs. Thus the MNs send both position and velocity commands to the oculomotor plant. Horizontal (H) BNs are located in the paramedian pontine reticular formation (PPRF), and vertical/torsional (V/T) BNs are found in the rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF). Horizontal \int s are located in the nucleus prepositus hypoglossi (NPH), and vertical/torsional \int s are found in the interstitial nucleus of Cajal (INC; see text). (B) A midsagittal section through the primate brain stem reveals the anatomical locations of the components of the brain stem saccade generator. Adapted with permission from Henn, Hepp, and Büttner-Ennever (1982). (C) Three-dimensional control of the torsional, vertical, and horizontal components of gaze shifts across the midline. (Adapted with permission from Crawford and Vilis, 1992.)

acceleration (the horizontal canals detect motion about the yaw axis, while the left/right-anterior and left/right-posterior canals detect motion about the pitch/roll axes).

Furthermore, directional segregation has been examined within the neural integrators (NPH and INC). The right NPH encodes rightward eye positions, and the left NPH encodes leftward eye positions. The right INC encodes clockwise torsional eye positions, and the left INC encodes counterclockwise torsional eye positions, but upward and downward neuron pools are present bilaterally (Crawford et al., 1991; Crawford & Vilis, 1992). With this unique setup (see figure 61.5C), obeying Listing's law (i.e., zero torsion) can be done by balancing torsional INC neuron pools on either side of the brain. And movements that do not obey Listing's law, like those associated with the VOR and head-free gaze shifts, can be accomplished by activating one side of the INC more than the other (Crawford et al., 1991; Crawford & Vilis, 1992). Also, because these nuclei encode both eye and head movements, disorders such as the ocular tilt reaction and torticollis may be caused by an imbalance in INC activity across the midline (Klier et al., 2002).

Mechanical Factors

Evidence also exists for a role of the oculomotor plant in implementing Listing's law (Demer et al., 1995; Demer, Oh, & Poukens, 2000; Quaia & Optican, 1998). Anatomical and imaging studies have shown that eye muscles are segregated into two distinct layers: global and orbital. The former inserts onto the eyeball while the latter passes through adjacent orbital tissue and acts as a pulley, effectively changing the eye's pulling direction. The placement of the pulleys, and their own differential innervations, influences the eye's axis of rotation to implement Listing's law and the half-angle rule. These observations, made in static preparations, have been successfully modeled and explain eye movements that obey Listing's law. However, they have yet to be realized in dynamic, *in vivo* preparations, and these mechanical properties would need to be undone neurally in order to produce an ideal VOR (Smith & Crawford, 1998).

Additional evidence supporting a role for the eye plant in 3-D control comes from neural recordings of torsionally related oculomotor neurons. They only appear to encode the derivative of eye position (i.e., changes in eye orientation divided by time) rather than the angular eye velocity axes illustrated in figure 61.2 (Ghasia & Angelaki, 2005). Furthermore, stimulation of the abducens nerve produces eye movements that obey

Listing's law (Klier, Meng, & Angelaki, 2006). Since stimulation so late in the oculomotor pathway bypasses the brain, this finding supports the idea that the plant alone can generate the half-angle rule. However, similar stimulation results are found when the monkey is statically tilted (Klier, Meng, & Angelaki, 2011) and dynamically rotated sinusoidally in the roll plane (Klier, Meng, & Angelaki, 2012), indicating that the plant is obligated to implement the half-angle rule no matter what the situation.

So how can such a plant provide all the behaviors described above? It can still give any 3-D oculomotor behavior if it receives the right inputs. For example, theoretical simulations have shown that the plant can still give an ideal VOR if angular velocity signals from the vestibular system are converted into eye position derivatives, effectively compensating for the half-angle rule in the plant (Smith & Crawford, 1998). Conversely such a plant only provides Listing's law if it receives orientation and derivative vector commands that align with Listing's plane (Crawford & Guitton 1997; Quaia, Lefevre, & Optican, 1999). Finally, violations of Listing's law, like ocular counterroll or the transient torsion observed during head-free gaze shifts, require torsional orientation and derivative commands orthogonal to Listing's plane. Thus, the plant is ideally coupled to the neural mechanisms described above.

Two-Dimensional to Three-Dimensional Transformation

Where does the 2-D signal transform into a 3-D command to drive the eye muscles? Note that this question does not ask about the mechanism responsible for tilting saccade axes out of Listing's plane in a position-dependent manner, as that seems to be largely done by orbital mechanics (Demer et al., 1995, 2000). Instead, the question asks how is zero torsion in Listing's or Donders' coordinates selected? And how is the position range modified for behaviors that follow variations of Donders' law? Finally, how does the brain generate torsional eye-in-head commands that predict and nullify VOR-related, torsional components of head-free gaze shifts?

The 2-D to 3-D transformations must happen downstream of the SC and upstream of the burst neurons. It is possible that there is a direct mapping from the SC onto the burst neurons in such a way that CW and CCW signals on either side of the brain cancel, leading to zero torsion (figure 61.5C—activate the riMLF/INC bilaterally). However, this cannot explain how torsional strategies are modified or how these ranges are maintained after necessary violations of Listing's law (like

those associated with head-free gaze shifts). To accomplish this, the system must have a modifiable set point or, more appropriately, a set surface, and a comparator. For example, when the head is tilted torsionally, the eye and corresponding Listing surface tilts in the opposite direction and thus the set surface is changed via vestibular inputs (Bockisch & Haslwanter, 2001; Haslwanter et al., 1992). Similarly, when the INC is inactivated unilaterally, Listing's plane is shifted toward the unaffected side and saccades are still generated in the direction of the shifted plane (even though final eye positions cannot be held in that plane) (Crawford et al., 2003). Here this set surface appears to be maintained by the saccade generator.

Returning to anatomy, neural activity in the nucleus reticularis tegmenti pontis (NRTP) has been correlated with the small corrective movements that are sometimes necessary to bring saccades back into Listing's plane (Van Opstal, Hepp, Suzuki, & Henn, 1996). The NRTP is a nucleus that inputs to the cerebellum, and patients with cerebellar damage show an increase in the thickness of Listing's plane and torsional offsets of the plane (Briar & Dieterich, 2009; Straumann, Zee, & Solomon, 2000). Also, the cerebellar flocculus and paraflocculus have been implicated in contributing an inhibitory torsional eye velocity component to the vestibular nuclei (Ghasia, Meng, & Angelaki, 2008). Finally, the central mesencephalic reticular formation has been implicated in the control of torsional head movements (Pathmanathan et al., 2006).

VISUAL CONSEQUENCES OF 3-D EYE (AND HEAD) MOVEMENTS

The patterns of 3-D eye movement described above have an enormous impact on monocular and binocular vision for action and perception. In addition, they also build and update accurate internal representations of the external world. It has been argued that Listing's law and its variants optimize motor and perceptual factors (Tweed, 1997a). However, while Listing's law may simplify eye movement control and aid binocular vision, it does not trivialize the brain's interpretation of visual signals. The brain must still account for the actual 3-D orientation of the eyes for both perception and action.

Simple Geometry Effects

When the eyes and head move to explore the visual environment, the resulting retinal images change. This might seem trivial, but the way retinal projections change across eye movements is not intuitive. These changes will be illustrated based on the "cyclopean eye,"

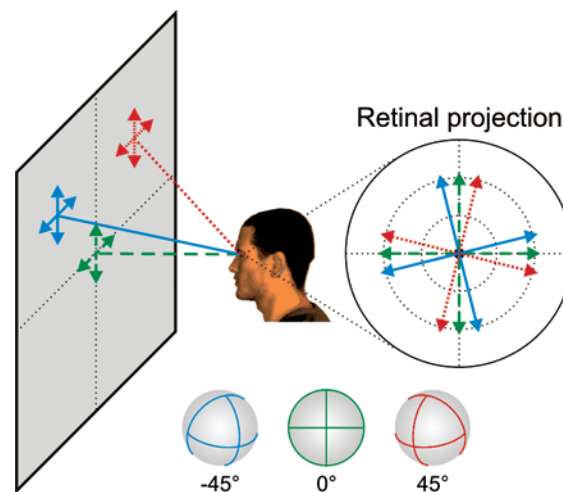


FIGURE 61.6 Retinal-spatial misalignment for oblique eye orientations. Single-axis eye rotations as described by Listing's law result in retinal orientations that are not aligned with space. For example, 45° left-up rotations (blue) result in a misalignment of the retinal axes relative to space so that spatial horizontal and vertical axes are projected onto the retina in a tilted way, that is, tilted counterclockwise relative to when the eyes are straight (green). Same argument hold for right-up fixations with clockwise rotated retinal projections (red). (Adapted with permission from Blohm and Lefevre, 2010.)

that is, a single representation of visual eccentricity based on the combination (e.g., averaging) of both retinal images (Ding & Sperling, 2006; Ono, Mapp, & Howard, 2002). For example, with the head straight, oblique eye movements result in a misalignment of the cyclopean retinal and spatial axes, partly due to eye tilt about the line of sight (Crawford & Guitton, 1997; Henriques & Crawford, 2000). Figure 61.6 shows how the retinal projections change across oblique eye movements. This happens due to the geometry of 3-D rotations, even in the absence of any net torsional eye movement component, because the eyes rotate around a single axis of rotation, which can cause a twist of the retinal axes relative to space. The misalignment angle can reach 15° when the eyes are in eccentric oblique positions (e.g., 45° up and right). And although this seems like a small effect, moving a hammer in the wrong direction by a few degrees can have undesirable consequences. Therefore, the brain must take this retinal-spatial misalignment into account when generating motor commands from visual inputs (Blohm & Crawford, 2007).

The geometry of retinal projections becomes more complex once the head is involved. Now the net rotation of the eye-in-space is determined by both 3-D eye-in-space and 3-D head-in-space orientation (Blohm &

Crawford, 2007; Tweed, 1997a). One simple consequence of head movements on retinal projection geometry can be illustrated for ocular counterroll. Here, the retinal projection pattern is rotated relative to space by the sum of head roll and (negative) ocular torsion. This is important for the visual system because correct interpretation of the visual inputs requires the brain to incorporate knowledge about ocular torsion (or head movements using an internal model of ocular counterroll) into the visual signals (Blohm & Crawford, 2007; Crawford, Henriques, & Medendorp, 2011). Head movements around other axes also influence ocular torsion because these movements alter Listing's plane. Therefore both eye and head orientations are important factors determining the retinal-spatial misalignment.

Moreover, even without torsion, properties of 3-D rotational geometry can produce large mismatches between target displacements in visual and motor coordinates, for example, every time the movement and eye orientation have orthogonal components (Blohm & Crawford 2007; Crawford & Guitton, 1997). In the head-free range, the resulting mismatch between retinal direction and directions in body coordinates can result in huge gaze shift or arm pointing errors. For example, a target that appears 90° left on the retina simply requires a leftward movement from straight ahead, but if gaze and the hand are pointing straight up, the same retinal stimulus requires motion that is equally left and down (Crawford & Guitton, 1997; Klier, Wang, & Crawford, 2001). Moreover, depth and direction become conflated when sensory information relative to the eye must be converted into motor commands relative to the body (Blohm & Crawford, 2007; Crawford et al., 2011). In practice, all these effects interact with the torsional effects described above, and the brain must account for these eye and head orientations (see below).

Consequences for Binocular Vision

Another important consequence of 3-D eye (and head) movements concerns binocular vision, in particular, stereopsis (i.e., depth perception from binocular vision). Stereopsis requires neurons to respond to small differences between both retinal images. And while no binocular orientation strategy results in perfect binocular retinal correspondence (Van Rijn & Van den Berg, 1993), L2 (described above) minimizes overall eye rotation and simultaneously aligns images within the visual plane by adjusting ocular torsion (Tweed, 1997b). Therefore, L2 may have evolved to maximize retinal correspondence and consequently binocularity across 3-D eye movements, thus narrowing the range of

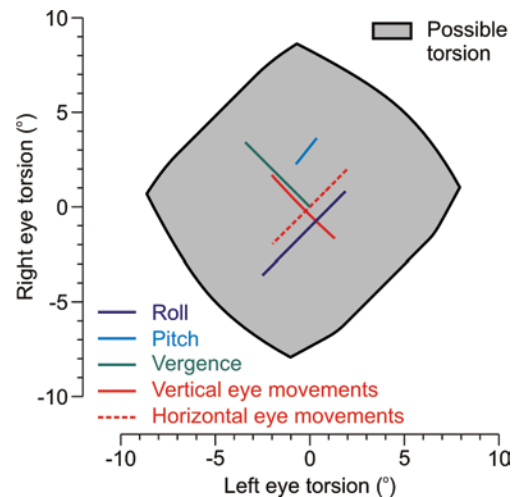


FIGURE 61.7 Possible binocular torsion states. The range of left (x-axis) and right (y-axis) eye torsion is shown across different static head orientations and vergence angles. This range increases dramatically once the head is moved dynamically. The effect of horizontal/vertical eye orientations, ocular vergence, and head roll/pitch on the torsional states is illustrated. For example, changing vergence angles has an opposite effect on left and right eye torsion as shown by the negative slope of the green line. Each eye's torsion here is the 3-D rotational component along the depth axis that brings the eyes from primary position to a given orientation. (Adapted with permission from Blohm et al., 2008.)

disparities that must be handled by striate cortex neurons.

For different ocular vergence angles, both eyes move differently as determined both by the vergence angle and by the head movement (Tweed, 1997b), and both have an interaction effect on Listing's plane (Bockisch & Haslwanter, 2001; Tweed, 1997b). The range of different right and left eye torsion combinations is shown in figure 61.7 and depicts how different eye and head movements influence the combination of both eyes' torsional states. The difference between both eyes' 3-D orientations in space yields two slightly different retinal images. This difference—called retinal disparity—is crucial to depth vision because it informs the brain about the distance of an object relative to the fixation distance, as determined by the vergence angle. Therefore, the way the eyes move has important consequences for depth vision (Blohm et al., 2008; Schreiber, Tweed, & Schor, 2006).

Figure 61.8 illustrates some of the effects eye movements can have on the retinal projection pattern of nonfoveated objects. When the eyes look straight ahead and the head is upright, objects in the visual field have a certain horizontal and vertical disparity (figure 61.8B).

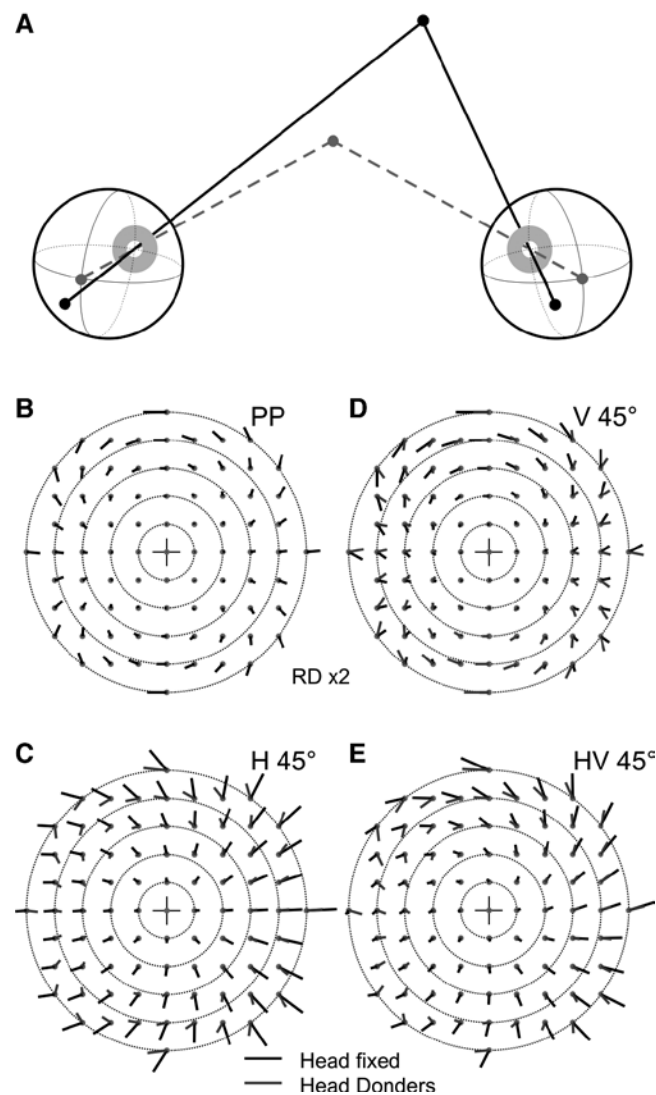


FIGURE 61.8 Consequence of L2 on retinal disparity. (A) Schematic showing the retinal projection geometry. Fixation (gray, dashed lines) and object projection lines (black) are shown. (B) Retinal projection pattern for primary position (PP) at 50-cm distance. Gray dots correspond to different cyclopean-eye-fixed targets (in 10° horizontal and vertical intervals arranged on a hemisphere at 50-cm distance), and the bars attached to them correspond to the disparity of the right and left eye's retinal images. The black bars show the direction and amplitude (length) of the retinal disparity (RD) associated with the cyclopean retinal target positions to which the bars are attached (magnified by a factor 2 for visibility). Target and fixation distance from the cyclopean eye was always 50 cm. Dotted circles are 10° intervals of retinal eccentricity. The central cross indicates the fixation position and fovea. Note that even at primary position, the interocular distance and natural tilt of Listing's law generates a nonzero retinal disparity pattern for targets on an isodistant sphere. (C) Retinal projection pattern when gaze is directed 45° horizontally (rightward), either with the head straight (black bars) or when the head accompanies the eyes in a natural fashion (gray bars), as described by Donders's law. (D) Same for the eyes oriented 45° vertically (up). (E) Same for 45° oblique eye orientations (up-right). Note that the retinal disparity pattern changes dramatically across eye and head orientations. (Adapted with permission from Blohm et al., 2008.)

When the eyes move, this pattern changes dramatically (figure 61.8C–E, black bars). Furthermore, this change depends on the contribution of the head (figure 61.8C–E, gray bars—for simplicity, only one example head orientation is shown). However, all these objects are located at the same distance from the cyclopean eye. Therefore, the brain must interpret these different

binocular retinal inputs in an eye/head orientation-dependent fashion.

Which 3-D eye (and head) orientation signals does the brain need to uniquely compute object depth from retinal images? Indeed, it has previously been shown that the same binocular retinal stimulation can result from objects being located at different distances (Blohm

et al., 2008). So how does the brain determine the object's true distance? Theoretically, the 3-D orientations of both eyes are needed to reconstruct 3-D location from binocular retinal inputs, in the case of a single, small, isolated object in darkness (Blohm et al., 2008). Vision of extended objects can provide additional (visual) information about the 3-D orientation of both eyes that are mathematically sufficient to estimate object depth (Horn, 1990). However, Blohm et al. (2008) have shown that 3-D eye or head signals are also used. Since there is no evidence that the brain has direct knowledge about both eyes' torsional angles (Banks, Hooge, & Backus, 2001), the brain must estimate these from other extraretinal signals (Schreiber et al., 2001; van Ee & van Dam, 2003), such as 2-D eye orientations, vergence and 3-D head orientation, as well as an internal model of L2 (Blohm et al., 2008).

Accounting for 3-D Eye Orientation in Vision, Memory, and Movement

To use spatial relationships of objects for perception and action, the brain creates internal representations of relevant locations. This can be seen as a type of internal working memory. Spatial updating is the process of adjusting internal representations of target location to reflect intervening eye, head, or body motion (reviewed in Klier & Angelaki, 2008). Much research has been devoted to uncovering the code (or reference frame) used by the brain during working memory (reviewed in Buneo & Andersen, 2006; Crawford et al., 2011). Early visual striate and extrastriate areas code visual information in a retinal frame of reference. This picture becomes slightly less clear for parietal areas, which are dominated by retinal codes (e.g., Batista et al., 1999; Khan et al., 2005) but include other coding schemes, for example, relative to the head (Battaglia-Mayer et al., 2001, 2003). In prefrontal and frontal areas there seem to be a wide variety of overlapping coding schemes for visual working memory (Martinez-Trujillo et al., 2004). This is important because any nonretinal code has to be generated by integrating retinal information with eye/head (or other) orientation signals. Thus knowledge about what these orientations are is critical. The advantage of these codes is that they may be independent of current gaze, which makes them robust to intervening movements.

Then what happens to the retinal codes in visual, parietal, and other areas when intervening movements of the eyes, head, and so forth occur? These codes must actively account for changes in gaze and remap (or update) the memory accordingly so that it remains in spatial register with the world. These time absolute

orientations of the eyes, head, and so forth are not required, but only changes in orientation and 3-D updating have been shown to account for changes in torsion during active (Medendorp et al., 2002) or passive (Klier, Angelaki, & Hess, 2005) head roll paradigms. Here however, the brain must also deal with the noncommutativity of rotations, which is indeed the case for eye (Smith & Crawford, 2001) and whole body (Klier, Angelaki, & Hess, 2007) movements. Finally, visual motion signals for saccades and perception are also updated across head roll (Ruiz-Ruiz & Martinez-Trujillo, 2008). Therefore, for action planning, updating has been shown to incorporate 3-D eye movement control signals, including ocular torsion.

Further, during movement execution, the brain must account for eye and head orientation to compensate for the geometric effects described above. The brain implements reference frame transformations to compute the correct depth and direction of gaze and reach movements from any initial eye and head orientation (Blohm & Crawford, 2007; Klier & Crawford, 1998). The neural mechanisms for these transformations can be theorized via neural network models that tend to develop appropriate "gain fields" for this purpose (e.g., Blohm & Lefevre, 2010), but few experiments have tested these models. For the gaze control system, some of these signals are present at the level of the SC (DeSouza et al., 2011), but otherwise the signals and the movements evoked by SC stimulation suggest that it simply uses a retinal code and leaves much of the transformation for later stages (Klier Wang, & Crawford, 2001).

Less is known about neural mechanisms that account for 3-D eye orientation for perception. For example, there are varied findings concerning the brain's ability to account for ocular torsion. As described above, sensory-to-motor transformations tend to account for 3-D eye orientation when programming saccades (Klier & Crawford, 1998; Medendorp et al., 2002), reaches (Blohm & Crawford, 2007; Medendorp et al., 2002), and smooth pursuit eye movements (Blohm & Lefevre, 2010). However, perceptual experiments have provided mixed results (Wade & Curthoys, 1997). Some have shown that ocular torsion is not accounted for when judging subjective visual verticality (Baier, Bense, & Dieterich, 2008; Brandt, Dieterich, & Danek, 1994), although intersubject differences are large (Clemens et al., 2011; De Vrijer, Medendorp, & Van Gisbergen, 2009). Other studies report that the perceptual system has access to ocular torsion under certain circumstances when judging line orientation under different eye and head orientations (Haustein, 1992; Poljac, Lankheet, & Van Den Berg, 2005). It remains unclear why different perceptual and motor systems may or may not have

access to 3-D eye orientation signals, and with very few exceptions (e.g., DeSouza et al., 2011), almost no neurophysiological investigations have even attempted to account for this.

SUMMARY

The central nervous system and peripheral anatomy have evolved with 3-D rotations in mind. Both the brain and body have adapted to restrict eye and head positions to Listing's and Donders' surfaces, respectively, and to implement the eye-in-head choreography necessary to exit and reenter Listing's plane with each and every gaze shift. And while the properties of 3-D eye rotation may seem subtle, they allow one to distinguish between fundamentally different models of neural and mechanical control. In addition, 3-D eye movements are not just a control problem, as they have important consequences on monocular and binocular vision as well as the way we remember and update memorized locations. Three-dimensional eye movement strategies such as Listing's law aid vision by restricting torsional possibilities, but still, these 3-D eye and head movements must be accurately accounted for to perform actions and perceive the external world. Much remains to be understood about the neural mechanisms and perceptual consequences of Listing's law and its variants.

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