Neural control of three-dimensional eye and head movements

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Although the eyes and head can potentially rotate about any three-dimensional axis during orienting gaze shifts, behavioral recordings have shown that certain lawful strategies — such as Listing's law and Donders' law — determine which axis is used for a particular sensory input. Here, we review recent advances in understanding the neuromuscular mechanisms for these laws, the neural mechanisms that control three-dimensional head posture, and the neural mechanisms that coordinate three-dimensional eye orientation with head motion. Finally, we consider how the brain copes with the perceptual consequences of these motor acts.

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Abbreviations
3-D	three-dimensional
INC	interstitial nucleus of Cajal
L2	extended Listing's law for two eyes
LL	Listing's law
LP	Listing's plane
OKN	optokinetic nystagmus
VOR	vestibulo-ocular reflex

Introduction
We live in a three-dimensional (3-D) world, so of course all of our movements are 3-D. However, there are some aspects of motion in 3-D space that pose particular problems for neural control. In the gaze control system, these are primarily issues of rotational control, with translational motion playing a lesser although significant role. Here, we review recent work in this field, focusing on the period of 2001 to present.

Most of what we know about 3-D rotatory control comes from the study of oculomotor kinematics. The principles of 3-D eye rotation are somewhat difficult to intuit, but they require some review in order for one to appreciate the current issues in this field. First, Donders' law. In theory, the eye could assume an infinite number of orientations for a given gaze direction by rotating 'torsionally' (where torsion means that the upper and lower part of the eye shift in opposite directions around the visual gaze axis). However, Donders' law states that each time the eye looks in a particular direction, it only assumes one 3-D orientation (i.e. there is just one torsional value for a given horizontal and vertical gaze angle) [1].

Listing's law (LL) further states exactly what those torsional values are [2,3]. If one describes eye orientations as shown in Figure 1 and if we redefine torsion as rotation about the head-fixed axis parallel to the primary gaze direction, then LL says that torsion is always zero, and thus eye orientation vectors fall within a horizontal-vertical range known as Listing's plane (LP).

The following may sound paradoxical, but to keep eye orientation in LP, the eye must rotate about axes that tilt torsionally out of LP in the direction of, but by half the angle of, current gaze direction (Figure 2). This is known as the 'half angle rule' and is related to the non-commutative (order dependent) aspects of rotational kinematics [4]. In general, for any two rotations A and B, rotation A followed by B does not give the same final orientation as B then A. As a result, rotations do not sum linearly. One unusual consequence of this is that two sequential eye rotations about two different axes within LP will result in an eye orientation with a torsional component out of LP. The half angle rule thus provides the compensatory torsional axis tilts required to keep eye orientation in LP throughout the saccade [3].

It turns out that the eyes obey LL (or some variant) under normal behavioral conditions whenever the head is immobilized. Thus, saccadic eye movements and smooth pursuit movements obey LL [2,3,5•,6•]. Saccades with different levels of binocular convergence obey a variant of LL called L2: when the gaze lines of the two eyes are parallel, the eyes both form a fronto-parallel LP, but when the eyes are converged, the planes of the two eyes tilt outwards, opposite to each other [7,8•].

By contrast, during head rotations, perfect stabilization of a distant visual target requires the vestibulo-ocular reflex (VOR) and optokinetic nystagmus (OKN) to rotate the eye in the opposite direction [9–11] — clearly this violates LL when the head rotates torsionally (because the eye then rotates in the opposite torsional direction). However, the VOR also causes subtle position-dependent torsional violations of LL during horizontal and vertical head movements, because here there is no longer a half-angle

Figure 1
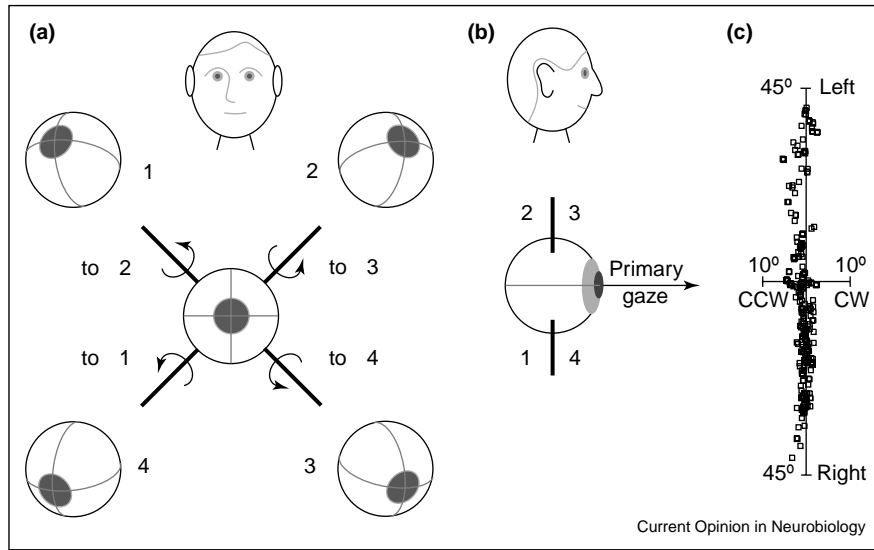
3-D eye orientation vectors and Listing's law. Head caricatures indicate the perspective used to view these vectors. Note that horizontal rotations occur about the vertical axis and vertical rotations occur about the horizontal axis. **(a)** Eccentric eye orientations (e.g. 1, 2, 3, or 4) can be described by the axes (thick lines) giving their rotation from the central primary position. These axes become 'eye orientation vectors' when we give them a direction according to the right hand rule (i.e., directed like the right hand thumb while the fingers are positioned to curl in the direction of rotation) and make the length of this vector proportional to the angle of rotation. For movements that obey Listing's law, these vectors lie in the plane of the page in this view. **(b)** The same vectors viewed edge-on from the side view. Here the torsional axis is defined as aligning with gaze direction at primary position, and the orthogonal horizontal and vertical axes are aligned in Listing's plane. **(c)** Data collected from a human subject. Data represent the tips of 3-D eye orientation vectors emanating from the origin (primary position), as explained in panels (a) and (b). Abbreviations: CW, clockwise; CCW, counter-clockwise.

rule. Furthermore, when the head is held at a constantly tilted torsional orientation (e.g. with the ear towards the shoulder) LP remains mainly intact but shifts slightly in the opposite torsional direction — so called ocular counterroll [12,13]. However, not all head movements alter LL. Angelaki and co-workers [14,15••] have recently shown that the translational VOR — the vestibular-driven eye rotation that compensates for translational head movement — does obey LL.

These and other 3-D eye control rules are summarized in Table 1. To remember them, one can apply a rule of thumb: during eye movements in which the task does not specify the required amount of torsion (saccades, pursuit, fixation, vergence), torsion is specified by LL or some variant of LL. The translational VOR fits into this cate-

gory because it only tries to stabilize the retinal image at the fovea [14]. However, when the required torsional rotation is dictated by the task — as in the rotational VOR or OKN, which need torsional rotation to stabilize the retinal image — LL is violated.

In comparison, during head-unrestrained gaze shifts the head obeys Donders' law (albeit with less precision than the eye), but not LL [16]. Instead of obeying LL, the head obeys a rule called the Fick strategy (Figure 3). This strategy gives rise to the non-planar range of orientations shown in Figure 3c. However, it has recently been shown that the head range can sometimes be flattened out like LP in a task-dependent manner [17], perhaps providing clues that these constraints are primarily in place to optimize motor performance. As a result of the head's

Table 1

Which eye movements obey Listing's law?

Eye movements that obey Listing's law	Eye movements that obey a modified Listing's law	Eye movements that don't obey Listing's law
Saccades (head fixed)	Saccades during constant vergence (L2)	Rotational VOR and OKN
Smooth pursuit	Saccades and pursuit during tonic head tilt	Saccades (head free)
Translational VOR		Pathological eye movements, particularly after
Final end-points of head-free gaze shifts		brainstem damage
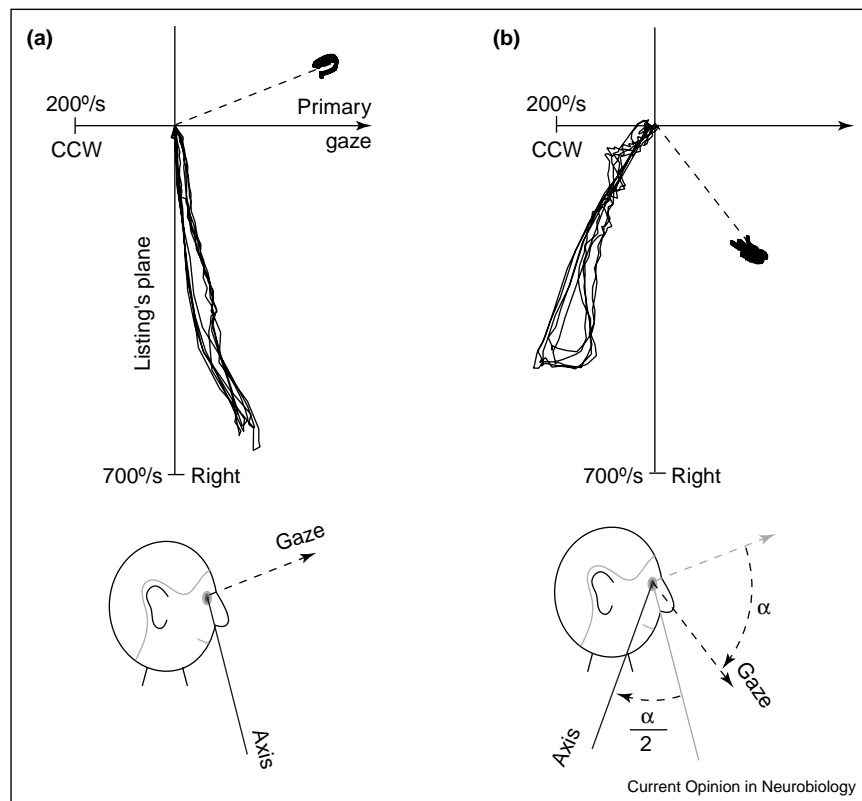
Figure 2

Half angle rule for Listing's law. The data are plotted in the same Listing's coordinates — viewed from the side as in the previous figure — but now showing gaze direction vectors (at the ends of the dashed lines) and angular velocity vectors (narrow loops starting and returning to the origin). Each point on the latter velocity loops gives a vector that is parallel to the axis of eye rotation at that moment, directed according to the right-hand rule, and scaled lengthwise as a function of angular speed. 60° rightward saccades are shown at two vertical levels: **(a)** around 30° above primary gaze direction, and **(b)** around 50° below primary gaze direction. The axis of rotation for saccades tilts with gaze direction but only by about half the angle (α), as shown in the caricatures below the data.

Fick strategy and the LL of the eye, the eye in space ends up obeying a more Fick-like range of orientations.

The importance of these rules is that they dictate the axes of rotation generated by the motor system, the sensory consequences of these rotations (visual, proprioceptive, and vestibular), and thus the complete sensorimotor input–output relations of the neural control system. Next, we review recent advances in understanding these control issues.

Neural versus mechanical factors in Listing's law

One issue crops up in almost every recent study of 3-D eye movements: which aspects of LL are implemented neurally and which mechanically? Recently, Demer and co-workers [18•] have shown that the soft tissues surrounding the eye muscles near their insertion points on the globe act like 'pulleys', potentially changing the effective pulling directions of the muscles as a function of eye orientation. Anatomic evidence is consistent with

the idea that these muscular eye position-dependencies cause saccade axes to tilt torsionally in the direction required by the half angle rule (Figure 2) observed in Listing's law [19••]. Moreover, Demer [20] has suggested that differential neural activation of the orbital (close to the skull) sub-population of eye muscle fibers could influence the mechanical properties of the pulleys themselves, that is, changing the eye-position dependencies of the eye muscles.

These observations have led to widespread speculation about the role of such mechanics in implementing Listing's law and its variants [20–22]. Theoretical simulations of 3-D saccades show that the pulleys can be rigged so that a horizontal–vertical saccade command will result in the half-angle axis rule required to keep eye orientation in LP [23]. It has been speculated that active control of the pulleys could account for other aspects of 3-D ocular kinematics, although probably not the complete eye position-independence required for an ideal angular VOR [21]. With this in mind, the various tilts and wobbles

Figure 3
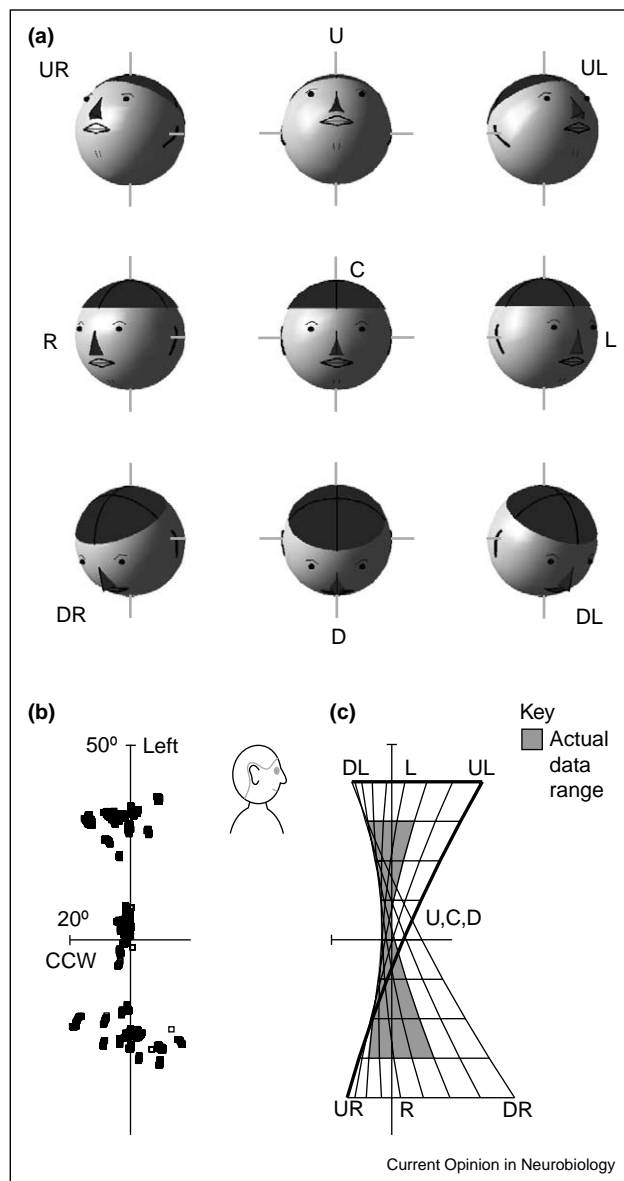
The Fick strategy and Donders' law for head movements.
(a) Simulated head orientation during fixation of nine different targets (center (C), up (U), down (D), left (L), right (R) and the combinations RU, LU, RD, LD). In the Fick pattern, purely horizontal rotations occur about the illustrated torso-fixed vertical axis, and purely vertical rotations about the illustrated head-fixed horizontal axis.
(b) Side view (see caricature) of 3-D head orientation vectors for a human subject looking in directions corresponding to those shown in panel (a). **(c)** Two dimensional surfaces fit to the data in panel (b). Each grid indicates 10 deg horizontal/vertical across the surface, with a 40 deg × 40 deg limit. The shaded area reflects the actual data range (i.e. data range of (b)). Thickened lines correspond to the upper and leftward edges of the fit (DL, down-left; UL, up-left; DR, down-right; UR, up-right, according to gaze direction). CCW: counter-clockwise torsion. Modified from data shown in Ceylan *et al.* [17].

in angular VOR axes and their dependency on eye orientation have been closely scrutinized, sometimes revealing trends consistent with the pulley hypothesis, and sometimes not [24–27]. Such observations have led to a general consensus that the eye muscles are probably rigged in a way that is advantageous for eye movements that obey LL, but perhaps less so for other movements like the rotational VOR. However, this current consensus primarily arises from theoretical simulations that in turn are formed on the basis of static eye muscle anatomy rather than direct physiological evidence.

Another way to answer this question is to look at the neural signals that drive the muscles. Recordings from the paramedian pontine reticular formation burst neurons that drive horizontal saccades show relationships between firing rate and torsional eye position that could be consistent with the effects of pulleys [28•]. However, neural signals in the rostral vestibular nucleus that code the direction of smooth pursuit (which also obeys LL) show modulations with eye orientation consistent with a neural coding of the torsional axis tilts required for LL [29••]. Thus, the direct physiological evidence is not as consistent as is often assumed — some neural signals seem appropriate to drive a pulley-rigged muscle system optimized for LL [28•], whereas others do not [29••].

If one takes a broader view, it is well established that the constraint of eye orientation to LP is fundamentally neural in origin. The eye can rotate about any axis, sometimes in violation of LL, in a task dependent manner [21]. Violations of LL produced by neural and muscular damage reveal the delicate dependence of LL on correct neural function [30–33]. In addition, the normal rules of 3-D kinematics are subject to a range of factors including state of arousal [7], age [34], visual adaptation [35,36], and even lighting conditions [37]. Clearly LL is under neural control. However, it is also clear that these control signals must be matched to the properties of the eye muscles, which in turn could influence which behavioral strategy is optimal. Moreover, it appears that neural signals may adjust the mechanical properties of the muscles [20]. In light of this, questions about what is mechanical and what is neural are ill-posed — every motor behavior is both mechanical and neural.

To make further progress in understanding these neuromuscular relationships we will need direct physiological recordings of the position-dependent torques generated by muscles during eye movements, and more direct 3-D recordings of the signals that drive these muscles.

3-D head control
Compared to the oculomotor system, much less is known about neural circuits for head control [38], but there are some hints that they may follow principles similar to those used in oculomotor control. In particular, it may be that

similar to the oculomotor system, the head control system utilizes a 3-D 'neural integrator' to convert velocity-like movement commands into the tonic signals that hold posture. It was recently shown that unilateral microstimulation of the midbrain interstitial nucleus of Cajal (INC) in the monkey produces torsional head (and eye) movements that can hold their final orientation as if the stimulus had been mathematically integrated (as in calculus) [39••]. Similarly, pharmacological damage to the INC produces drifting movements of torsional and vertical head (and eye) orientation consistent with degraded integration of 3-D velocity commands. Moreover, following prolonged unilateral inactivation of this 'head integrator', head posture settles into a tilted orientation consistent with the symptoms of cervical dystonia (spastic torticollis) [40]. This suggests that there is a 3-D neural integrator for head orientation in the midbrain and that it may be implicated in clinical disorders of head posture.

Ocular counterroll

Normally when the head has a tilted posture the eyes show a slight torsional tilt in the opposite direction [41–44]. This 'counterroll' is preserved across both saccades and smooth pursuit eye movements [45•], which perhaps suggests that it represents a general recalculation of the internal coordinates for LP [45•]. It has recently been recognized that counterroll – like other eye movements driven by the otolith organs of the inner ear — uses a more complex neural path than previously suspected, probably acting through the neural integrator that holds eye orientation between movements [46•]. This was confirmed by the observation that damaging the torsional parts of the neural integrator in the INC causes the eye to drift toward a non-counterrolled orientation [47•]. The investigation by Crawford *et al.* [47•] speculates that counterroll is not a vestigial righting reflex, but rather is part of a more complex 3-D eye–head coordination system for head-unrestrained gaze shifts.

Eye–head control in 3-D gaze shifts

Recording 3-D gaze shifts in the head-unrestrained monkey provides an ideal experimental model for studying issues in 3-D control. One reason for this is that the greater range of motion magnifies the non-linear position-dependent aspects of 3-D rotational geometry [48]. Conversely, standard 2-D linear approximations of orientation and velocity accrue alarmingly large errors in the range of head-free gaze shifts. For example, vector displacements defined in the eye, head, or body reference frame appear to be equivalent in the abstract 2-D representations that are often used to describe rotations, but in real 3-D rotations they are not equivalent. Eye-fixed vector displacements diverge from head-fixed displacements as a non-linear function of eye orientation. This fact was recently used to show that stimulation of the superior colliculus in the head-unrestrained monkey produces fixed vector gaze displacements in an eye-centered frame [48,49•].

Another reason that head-free movements are useful for studying 3-D control issues is that it is only here that one sees the full coordinated combination of saccades, VOR, and other types of eye movement as they occur in real life. For example, to land eye orientation in LP at the end of a head-free gaze shift, the initial saccade-like eye movement must include an actively produced torsional movement that is equal and opposite to the ensuing torsional component that is produced by the VOR phase of the movement. This level of torsional control is beyond the scope of eye mechanics alone. We have recently found that gaze shifts evoked by stimulating the supplementary eye fields [50] and superior colliculus [51••] in the monkey preserve this pattern — as well as Donders' law of the head — which suggests that the neural mechanisms for these default 3-D coordination strategies are implemented quite far downstream in the gaze control system, presumably involving the brainstem reticular formation.

Perceptual consequences of 3-D eye rotations

The study of the perceptual consequences of LL and its family of motor constraints has a long and rich history, dating back to Donders [1] and von Helmholtz [2]. Recent, more direct measurements have illustrated how LL determines the pattern of retinal stimulation during eye movements, requiring motor systems to account for eye orientation when programming visually guided movements [52]. Also, it is well known that the saccade generator takes into account other eye movements that intervene between seeing a target and then looking at it; a process known as 'spatial updating'. Recent experiments have shown that this updating process accounts for the 3-D aspects of intervening gaze movements, including the non-commutative aspects of eye rotation [53], torsional eye and head rotations [54•], and 3-D aspects of translational head movement [55•]. To do this, the cortex must receive multidimensional feedback about eye and head movements, and incorporate the non-linear geometry of rotations.

Vision researchers have also realized the important implications of L2 for the problems of binocular correspondence and depth vision. Torsion, even when conjugate (same for both eyes), tends to disrupt binocular image fusion, particularly during vergence movements towards near targets. Hess and co-workers have recently shown that convergent eye movements to near targets override counterroll, which demonstrates that the needs of the visual system outweigh the gravitational reflex [56•]. Moreover, Schor and co-workers, Zee and co-workers, and others [6•,57•,58•] have shown that adaptation to consistent visual disparities can produce adjustments in

L2 — including disconjugate tilts of LP and constant cyclovergence (binocular torsional adjustments made to fuse the visual image) — as required to reduce the overall level of binocular visual disparities.

Why are these binocular motor control strategies so important for vision, when in principle the brain could solve the binocular visual correspondence problem by using 3-D feedback signals for the orientation of both eyes? Tweed and co-workers [59•] have recently shown that rather than doing this, the visual system searches for corresponding image features within small retina-fixed search zones, relying on the fact that L2 is upheld. This simplifies depth perception at the cost of sub-optimal perception at some eye orientations, apparently because the motor system prefers to hang onto a modified version of LL rather than rotating the eyes to the orientations that would completely eradicate cyclodisparity. This topic provides an elegant demonstration of the intimate relations between vision and movement in the 3-D gaze control system.

Conclusions

Measuring 3-D orientations of the eye and head is an attractive prospect because it brings the gaze control investigator closer to reality — albeit a reality that often turns out to be quite strange — and opens up important new questions. With the advent of technology for the accurate measurement of 3-D axes of rotation, the 1990s saw a rush to describe the 'rules' of 3-D kinematics. In the current decade the search for these lawful relationships seems to be all but completed, and yet we still know very little about how they arise from developmental and environmental factors. What is evident, is that Listing's law and its family of motor rules are shaped to optimize both motor and perceptual factors. The motor factors because they determine the pattern of muscular activity for any given movement, and the perceptual factors because the resulting eye and head orientations profoundly influence spatial vision.

The search for the neural control mechanisms for LL has been more elusive. It has become clear that in the motor control of gaze, high level structures in the cortex and the superior colliculus do not ordinarily concern themselves with the details of 3-D implementation — just the goal of gaze direction [48]. However, we still do not know how those details, for example, the transformation of a 2-D gaze command into 3-D eye and head commands, are implemented. Simple 'Listing's law box' conceptions of this process fail, not because it's all done in the muscles as once suspected, but rather because 3-D control subsumes all aspects of gaze control. If there are Listing's or Donders' boxes, they are embedded and distributed throughout the entire brainstem neural control system [60]. If we are to sort out the workings of this system, we will need more 3-D recordings of the brainstem control

signals, more models of the neural control system that account for real 3-D geometry, and a firm understanding of the eye muscle mechanics that these signals command.

Update

Demer and co-workers [61•] have recently imaged the paths of the extra-ocular muscles during different states of binocular convergence. They found that vergence-related shifts in the eye muscle pulleys were inconsistent with a mechanical implementation of L2, instead suggesting that L2 is under central neural control [7,8•,56•–59•]. These results highlight the current complexity of understanding the neuromuscular implementation of 3-D ocular kinematics.

Acknowledgements

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In this study, the midbrain INC nucleus of the monkey was microstimulated and then injected with muscimol (an inhibitory mimic of GABA) while the experimenters recorded 3-D eye and head orientation. Unilateral stimulation of the INC produced torsional head (and eye) rotations that transiently held their final position, as if a 'neural integrator' had been charged up. Conversely, the initial effect of muscimol injection included a failure to hold torsional and vertical head (and eye) positions consistent with damage to a neural integrator. The head finally settled into a position that looked like spastic torticollis.

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41. Angelaki DE, Newlands SD, Dickman JD: **Inactivation of semicircular canals causes adaptive increases in otolith-driven tilt responses**. *J Neurophysiol* 2002, **87**:1635-1640.

42. Kori AA, Schmid-Priscoveanu A, Straumann D: **Vertical divergence and counterroll eye movements evoked by whole-body position steps about the roll axis of the head in humans**. *J Neurophysiol* 2001, **85**:671-678.

43. Moore ST, Clement G, Raphan T, Cohen B: **Ocular counterrolling induced by centrifugation during orbital space flight**. *Exp Brain Res* 2001, **137**:323-335.

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45. Hess BJM, Angelaki DE: **Gravity modulates Listing's plane**
•   **orientation during both pursuit and saccades**. *J Neurophysiol* 2003, **90**:1340-1345.
Previously counterroll was measured during fixation or saccades — this paper shows that the same principles hold during smooth pursuit movements.

46. Glasauer S, Dieterich M, Brandt T: **Central positional nystagmus**
•   **simulated by a mathematical ocular motor model of otolith-dependent modification of Listing's plane**. *J Neurophysiol* 2001, **86**:1546-1554.
This theoretical study shows how the ocular counterroll reflex could be implemented through a 'leaky' 3-D neural integrator for eye position, requiring adjustments to the torsional set point for the saccadic input to this integrator plus a tonic input.

47. Crawford JD, Tweed DB, Vilis T: **Static ocular counterroll**
•   **is implemented through the 3-D neural integrator**. *J Neurophysiol* 2003, **90**:2777-2784.
This study tested a model similar to Glasauer's [46•] by measuring ocular counterroll and saccades following inactivation of the torsional neural integrator in the monkey. As predicted, the monkeys could not hold counterrolled positions between saccades.

48. Martinez-Trujillo JC, Klier EM, Wang H, Crawford JD: **Contribution of head movement to gaze command coding in monkey frontal cortex and superior colliculus**. *J Neurophysiol* 2003, **90**:2770-2776.

49. Klier EM, Wang H, Crawford JD: **The superior colliculus encodes**
•   **gaze commands in retinal coordinates**. *Nat Neurosci* 2001, **4**:627-632.
The authors of this study demonstrate the importance of recording in 3-D in order to answer more general questions, for example, those about spatial reference frames.

50. Martinez-Trujillo JC, Wang H, Crawford JD: **Electrical stimulation of the supplementary eye fields in the head-free macaque evokes kinematically normal gaze shifts**. *J Neurophysiol* 2003, **89**:2961-2974.

51. Klier EM, Wang H, Crawford JD: **Three-dimensional**
•• **eye-head coordination is implemented downstream from the superior colliculus**. *J Neurophysiol* 2003, **89**:2839-2853.
In this study the monkey superior colliculus was stimulated while 3-D eye and head orientations were recorded. Stimulation elicited gaze shifts that included all of the 3-D eye and head kinematics observed in normal movements, including torsional eye rotations out and back into Listing's plane and Donders' law of the head.

52. Klier EM, Henriques DYP, Crawford JD: **Visual-motor transformations account for 3-D eye orientation**. *Arch Ital Biol* 2002, **140**:193-201.

53. Smith MA, Crawford JD: **Implications of ocular kinematics for the internal updating of visual space**. *J Neurophysiol* 2001, **86**:2112-2117.

54. Medendorp WP, Smith MA, Tweed DB, Crawford JD: **Rotational**
•   **remapping in human spatial memory during eye and head motion**. *J Neurosci* 2002, **22**:RC196.
This was the first study to show that human subjects can remember targets for saccades after an intervening torsional eye and head movement.

55. Medendorp WP, Tweed DB, Crawford JD: **Motion parallax**
•   **is computed in the updating of human spatial memory**. *J Neurosci* 2003, **23**:8135-8142.
This study shows that human subjects can remember target directions and depths for saccades after intervening translational eye and head movements. It provides a model, also incorporating the results from Smith and Crawford [53] and Medendorp *et al.* [54•], showing the multidimensional efference copy feedback, non-linear geometry, and intrinsic circuits that the cortex has to incorporate in order to provide this behavior.

56. Misslisch H, Tweed D, Hess BJ: **Stereopsis outweighs gravity in**
•   **the control of the eyes**. *J Neurosci* 2001, **21**:RC126.
Conjugate ocular counterroll is bad for vision because it disrupts the matching process between points on the two retinas required for stereovision. In other words, it is at odds with the 'L2'. These authors tested vergence movements with the head tilted and found that the vergence system overrides counterroll to optimize stereo matching.

57. Steffen H, Walker M, Zee DS: **Changes in Listing's plane after**
•   **sustained vertical fusion**. *Invest Ophthalmol Vis Sci* 2002, **43**:668-672.
This was the first study to examine LP in both eyes after long-term (72 hours) adaptation to optical prisms that produced a vertical deviation between the two eyes. After training the two LPs were deviated in the same way (opposite to each other), even during monocular viewing, consistent with the visuomotor system trying to minimize cyclodisparity.

58. Schor CM, Maxwell JS, Graf EW: **Plasticity of convergence-**
•   **dependent variations of cyclovergence with vertical gaze**. *Vision Res* 2001, **41**:3353-3369.
The authors found that visual adaptation could induce subjects to reduce or increase the amount of outward tilting of the two LPs (L2) as a function of vergence.

59. Schreiber K, Crawford JD, Fetter M, Tweed D: **The motor side**
•   **of depth vision**. *Nature* 2001, **410**:819-822.
In this study, human subjects viewed stereograms at different eye elevations. The ability to perceive depth was position dependent, consistent with the visual system matching the two images by looking for correspondence with eye-fixed search zones. L2 reduces the necessary size of these search zones, but as it is not the theoretically ideal solution it may pose a compromise between these perceptual factors and other motor factors.

60. Smith MA, Crawford JD: **Self-organizing task-modules and explicit coordinate systems in a neural network model for 3-D saccades**. *J Comput Neurosci* 2001, **10**:127-150.

61. Demer JL, Kono R, Wright W: **Magnetic resonance imaging of**
•   **human extraocular muscles in convergence**. *J Neurophysiol* 2003, **89**:2072-2085.
The authors measured extraocular muscle paths using tri-planar, contrast-enhanced magnetic resonance imaging of the orbits during binocular fixation of a target observed at 15 or 800 cm distance. They found that in the torsional direction 'rectus pulley shift in convergence is inconsistent with the reconfiguration predicted to explain the temporal tilting of Listing's planes, instead suggesting that this temporal tilting is due to variations in oblique extraocular innervation'. In other words, it looks like modifications of LL for binocular convergence (L2) are under central neural control.