Interstitial Nucleus of Cajal Encodes Three-Dimensional Head Orientations in Fick-Like Coordinates

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Klier EM, Wang H, Crawford JD. Interstitial nucleus of Cajal encodes three-dimensional head orientations in Fick-like coordinates. J Neurophysiol 97: 604–617, 2007. First published November 1, 2006; doi:10.1152/jn.00379.2006. Two central, related questions in motor control are 1) how the brain represents movement directions of various effectors like the eyes and head and 2) how it constrains their redundant degrees of freedom. The interstitial nucleus of Cajal (INC) integrates velocity commands from the gaze control system into position signals for three-dimensional eye and head posture. It has been shown that the right INC encodes clockwise (CW)-up and CW-down eye and head components, whereas the left INC encodes counterclockwise (CCW)-up and CCW-down components, similar to the sensitivity directions of the vertical semicircular canals. For the eyes, these canal-like coordinates align with Listing’s plane (a behavioral strategy limiting torsion about the gaze axis). By analogy, we predicted that the INC also encodes head orientation in canal-like coordinates, but instead, aligned with the coordinate axes for the Fick strategy (which constrains head torsion). Unilateral stimulation (50 μA, 300 Hz, 200 ms) evoked CW head rotations from the right INC and CCW rotations from the left INC, with variable vertical components. The observed axes of head rotation were consistent with a canal-like coordinate system. Moreover, as predicted, these axes remained fixed in the head, rotating with initial head orientation like the horizontal and torsional axes of a Fick coordinate system. This suggests that the head is ordinarily constrained to zero torsion in Fick coordinates by equally activating CW/CCW populations of neurons in the right/left INC. These data support a simple mechanism for controlling head orientation through the alignment of brain stem neural coordinates with natural behavioral constraints.

INTRODUCTION

The goals of this study were 1) to determine the coordinate system used by the brain to control head orientation during gaze shifts and 2) to establish the relationship between these coordinates and the neural strategies used to constrain the redundant degrees of freedom observed in head movement. Coordinate systems, and the reference frames in which they operate, are crucial to representing and understanding the locations and movements of objects (Crawford 1994; Simpson and Graf 1985; Soechting and Flanders 1992). For example, any three-dimensional (3D) orientation or rotation can be described as a vector composed of components along three coordinate axes (normally horizontal, vertical, and torsional), where the latter roughly corresponds to rotation about the line of sight (Crawford 1994; Simpson and Graf 1985). Experimentally, such coordinate systems can be defined with respect to arbitrary frames of reference such as the eye, head, or body (Martinez-Trujillo et al. 2004; Schlag and Schlag-Rey 1987).

How the brain represents different directions of movement and how it constrains these directions when it has more degrees of freedom than necessary constitute a far more complex and controversial topic. For example, in the gaze control system, visual stimulus direction is initially encoded with respect to an eye-fixed, two-dimensional (2D) retina, whereas the final motor output is encoded in 3D eye and head muscle coordinates, embedded in the head and body frames, respectively. Thus the sensory input specifies only a desired 2D gaze direction and not the required amount of torsion. However, Donders’ law states that only one 3D eye orientation is used for each of these gaze directions (Donders 1848; Haslwanter 1995; Helmholtz 1867; Straumann et al. 1991; Tweed and Vilis 1990). Thus the dual question: what intermediate representations are used to code eye and head movement directions and what is their role in the implementation of Donders’ law?

Most of what we know about this topic comes from studies of the oculomotor system with the head fixed (i.e., immobilized). Such studies showed that horizontal burst neurons [located in the paramedian pontine reticular formation (PPRF)] (Hepp and Henn 1983; Lüscher and Fuchs 1972) are found separate from torsional/vertical burst neurons [located in rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF)] (Crawford and Vilis 1992; Henri et al. 1991; King and Fuchs 1979; Moschovakis 1997). Similarly, the horizontal neural integrator [located in the nucleus prepositus hypoglossi (NPH)] (Cannon and Robinson 1987; Cheron and Godaux 1987) is separate from the torsional/vertical integrator [located in the interstitial nucleus of Cajal (INC)] (Crawford et al. 1991; Dalezios et al. 1998; Fukushima 1991; Helmchen et al. 1998; Moschovakis 1997).

For the horizontal component of the oculomotor system, rightward movements are elicited by stimulating nuclei to the right of the midline, whereas leftward movements are elicited by stimulating nuclei to the left of the midline (Cohen and Komatsuzaki 1972; Gandhi and Sparks 2000). For the vertical system, nuclei on the right of the midline encode clockwise (CW)-up and CW-down eye movements, whereas nuclei on the left encode counterclockwise (CCW)-up and CCW-down eye movements (Crawford et al. 1991; Vilis et al. 1989). This framework agrees with both physical eye muscle anatomy and the anatomy of the semicircular canals that formed the basis of the phylogenetically older eye movement system—the vestibuloocular reflex (VOR). These canal/muscle-like coordinates...

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are 3D, orthogonal, and symmetric across the sagittal plane (Crawford and Vilis 1992; Robinson 1985; Simpson and Graf 1985).

At first glance, these coordinates do not appear to correspond well with the 3D behavioral constraints observed in visually guided eye movements. Saccades and smooth pursuit obey a form of Donders’ law called Listing’s law (Ferman et al. 1987; Hastlwander et al. 1991; Tweed et al. 1992). Listing’s law determines torsion by constraining the eye to only those orientations that can be reached from a central primary position by rotations about axes that lie in a head-fixed Listing’s plane (Haslwander et al. 1991; Helmholtz 1867; Mok et al. 1992; Tweed and Vilis 1990; van Rijn and van den Berg 1993). Put simply, Listing’s law does not allow torsion around the head-fixed torsional axis aligned with the primary gaze direction (Westheimer 1957). Clearly, the saccade generator has the capacity to violate Listing’s law because electrical stimulation of the riMLF and INC produces ocular torsion (Crawford and Vilis 1992; Crawford et al. 1991) that is corrected only by the next endogenous eye movement (Crawford and Guittion 1997). Moreover, in head-unrestrained conditions, the saccade generator produces finite torsional components to counterbalance the torsional components of the VOR (Crawford and Vilis 1991; Crawford et al. 1999; Klier et al. 2003; Tweed 1997). So how is it then that these structures normally implement Listing’s law?

The answer appears to be that, although the riMLF and INC use a muscle/canal-like coordinate system, their coordinates do not consistently align with head-fixed anatomical landmarks. Instead, the axes align with Listing’s plane in the sense that the vertical axis of rotation aligns with Listing’s plane and the axes for torsional–vertical rotation are symmetric about Listing’s plane (Crawford 1994; Crawford and Vilis 1992; Suzuki et al. 1995). Because the clockwise and counterclockwise components of torsional control are separated across the left and right sides of the brain stem, coactivation of the INC on each side would allow these components to cancel out and give zero torsion in Listing’s plane. This becomes more complex during head movements, in which case a bilateral imbalance is required to provide saccades with torsional components (Klier et al. 2002). However, when the head is motionless, this organization provides a simple implementation of Listing’s law.

In comparison, far less is known about the neural control of head movements, i.e., the neural coordinate systems for head control and their relationship to the behavioral constraints observed in head movement during gaze shifts (Cornel and Elsley 2005; Cornel et al. 2002; Flanders 1988; Freedman and Sparks 1997; Guittion 1992; Guittion et al. 2003; Keshner and Peterson 1988; Klier et al. 2002; Martinez-Trujillo et al. 2004; Peterson 2004; Sparks et al. 2002; Waitzman et al. 2002). Like eye movements, 2D gaze commands do not constrain the amount of torsion required in head orientation. However, head movements obey another form of Donders’ law called the Fick strategy (i.e., the observed head torsion is zero when measured in Fick coordinates) where the vertical axis (for horizontal rotation) remains fixed upright in the body but the torsional and horizontal axes (for torsional and vertical rotations, respectively) rotate with the head (Glenn and Vilis 1992; Radeau et al. 1994). This constraint does not appear to be mechanical in origin because it can be voluntarily violated (i.e., by rolling the head) or adapted to suit different task requirements (Ceylan et al. 2000). Gaze-shifts evoked by stimulation of the superior colliculus (Klier et al. 2003) and frontal cortex (Martinez-Trujillo et al. 2003) include head movements that obey the Fick constraint, so presumably it is implemented at the level of the brain stem, although nothing more is known about its physiological origin.

It was recently shown that electrical microstimulation of such brain stem areas as the PPRF (Sparks et al. 2002) and nucleus reticularis gigantocellularis (Quessy and Freedman 2004) produce ramplike horizontal head rotations, much like the effect of stimulating the horizontal brain stem system for eye movements. In contrast it has long been known that electrical stimulation of the midbrain regions in and around the riMLF and INC produces torsional (i.e., roll) movements of the head (Hassler 1972; Hassler and Hess 1954) and that these areas project to the spinal cord centers for head movement control through the interstitiospinal tract (Fukushima 1987).

Moreover, it was recently suggested that the INC is part of the head integrator for torsional/vertical head positions, similar to its role as an integrator for eye positions (Klier et al. 2002). Right INC inactivation causes drift of head posture toward a counterclockwise shifted range, whereas left INC inactivation causes drift toward a clockwise shifted range, similar to the clinical symptoms of torticollis (Klier et al. 2002; Medendorp et al. 1999). These findings suggest that the INC may perform a function for the head similar to that for the eyes.

Based on these findings, we hypothesize that the INC controls head movements using a canal-like coordinate system, as it does for the eye, with CW-vertical components controlled on the right brain and CCW-vertical components controlled on the left. In addition, we propose that, by analogy with the oculomotor system, the head’s neural integrator would use a coordinate system that aligns with the behavioral constraint of the head (i.e., Fick coordinates). If this is the case, then electrical stimulation of the INC should produce torsional/vertical rotations of the head—CW on the right side and CCW on the left side—about axes that rotate with the orientation of the head.

METHODS

Surgery and equipment

Four monkeys (Macaca fascicularis) underwent aseptic surgery under general anesthesia (isoflurane, 0.8–1.2%) during which they were each fitted with 1) an acrylic skullcap; 2) a stainless steel chamber (centered at 5 anterior and 0 lateral in stereotaxic coordinates) that allowed access to the brain; and 3) a stainless steel cylinder, used in combination with a bolt and screw, to immobilize the head when required. 3D eye movement recordings were made possible by implanting two 5-mm-diameter scleral search coils in one eye of each animal (one coil was placed in the nasal-superior quadrant, whereas the second was located in the nasal-inferior quadrant, such that the two were not parallel). 3D head movements were recorded by two orthogonal coils mounted on a plastic base. The base was then screwed onto a plastic platform on the skullcap during each experiment. Animals were given analgesic medication and prophylactic antibiotic treatment during the postsurgical period and experiments commenced after 2 wk of postoperative care. These protocols were in accordance with the Canadian Council on Animal Care guidelines on the use of laboratory animals and preapproved by the York University Animal Care Committee.

The primate chair was placed such that each monkey’s head was at the center of three mutually orthogonal magnetic fields (90, 125, and
250 kHz), each 1 m in diameter. During each experiment, the monkey sat in a modified Crist Instruments primate chair such that its head and neck were free to move as desired. Specifically, the top plate was removed and replaced by canvas cloth that buckled snugly at the back. The upper body (to the shoulders) was prevented from rotating in the yaw direction (i.e., movement around an earth-vertical axis) by the use of plastic molding over the shoulders. Finally, each monkey also wore a primate jacket (Lomir Biomedical) outfitted with four metal hoops on the backside. Restraints running through these hoops and through holes in the back of the primate chair further secured the upper body.

Experimental procedures

Before each experiment, the three magnetic fields were calibrated using 1) an eye coil similar to the two implanted in the monkey’s eye and 2) the same orthogonal coils that were later fixed to the monkey’s head during the experiment (using a plastic base). During calibration, these coils were mounted in the center of a Fick gimbals and rotated to the cardinal positions in all three fields. The gains and biases of the coils’ outputs were then adjusted such that maximum 8-V signals were generated at these positions (Tweed et al. 1990).

At the beginning of each experiment, with the head fixed, a tungsten microelectrode (0.5–1.5 MΩ impedance; FH) was slowly lowered down a preselected track with the use of a hydraulic microdrive (Narishige model MO-99S). Neuronal activity was output on an audio monitor. We first identified burst neurons in the superior colliculus as a landmark (Klier et al. 2001) and subsequently moved our electrodes anteriorly to the stereotaxic coordinates corresponding to the INC. If burst-activity was modulated along with corresponding vertical/torsional eye movements then the site was deemed to be a potential INC site. Putative INC sites were further confirmed by observing eye movements elicited after head-fixed stimulation. If conjugate, ipsilateral eye movements, with mainly vertical and/or torsional components, were elicited by stimulation then we classified the site as an INC site (Crawford et al. 1991).

With the head free, the electrode would then be lowered through the same track in which head-fixed recording and stimulation indicated INC activity. Every 0.5 mm, stimulations with 200-ms pulse trains (50 μA, 300 Hz) were delivered automatically every 3.3 s (by Grass Instruments model S88) in dim light. Outputs from the eye and head coils were simultaneously viewed on-line in an adjacent room as well as recorded at 100 Hz for further off-line analysis (see Tweed et al. 1990). It should be noted that after each stimulation experiment, an inactivation experiment was conducted in which muscimol was injected into the most responsive INC site. The results of the inactivation experiments are reported elsewhere (Klier et al. 2002).

The monkeys were untrained with respect to making gaze shifts and were never required to make saccades with the head fixed for extended periods of time. As the stimulations were delivered, the monkeys simply moved their eyes and heads freely and naturally. Some of these movements were self-initiated, whereas others were encouraged. One experimenter always stood hidden behind a hemispherical dome (barrier paradigm; Guitton et al. 1990) and motivated the monkeys to use their entire eye/head motor ranges by presenting the monkeys with novel visual objects and sounds. A second experimenter viewed the eye/head movements on-line and provided verbal feedback about the range of initial positions obtained. This was done to obtain the large range of initial eye and head position necessary for the quantifications described below.

As a control to the INC stimulation data, a “random” control paradigm was run at the beginning of each head-free experiment. In this paradigm, the monkeys were again required to look around freely and encouraged to maximize their ocular and head motor ranges in the same way described above. However, no stimulations were delivered during these controls.

Of the 80 putative sites tested, 65 qualified to be included in this study on the basis that head movements were evoked in >50% of the stimulations. The remaining sites were located on the outer edges of the INC and produced inconsistent eye and head movements (possibly resulting from current spread to the INC or other midbrain structures). In M1 (monkey 1), six sites were examined in the right INC; in M2, eight sites were investigated in the right INC and three sites in the left INC; in M3, 2 sites were investigated in the right INC and five sites in the left INC; and in M4, 28 sites were examined in the right INC and 13 sites in the left INC. Postmortem, these sites were confirmed histologically.

Data analysis

QUANTIFICATION OF COIL SIGNALS. At the beginning of each head-free experiment, each monkey was required to fixate its own image, for 5–10 s, in a 5 × 3-cm mirror. The mirror was located 0.75 m directly in front of the monkey’s head and thus the head was oriented directly straight ahead along the forward-pointing magnetic field. This straight-ahead measure was sufficiently accurate for quantitative comparisons between controls and data recorded within a given experiment. Coil signals were measured at this position and were used as the initial reference position for the head in space coordinates. This reference position was then used to compute quaternions using a method described previously (Tweed et al. 1990). The quaternions were also transformed into linear angular measures of 3D head position (Crawford and Guitton 1997) for statistical analysis. In this way, any final head orientation could be described as a rotation vector from the initial reference eye position.

COORDINATE SYSTEMS. The raw head coil data were initially represented in an earth-fixed orthogonal coordinate system defined by the magnetic fields that we call “space” coordinates. Quaternions calculated from these signals represent head orientations in space.

Next, head velocities were computed using the following formula

\[ \omega_{\text{head}} = \frac{1}{12} q_{\text{head}} \cdot \omega_{\text{space}} \cdot q_{\text{head}}^{-1} \]

where \( \omega_{\text{space}} \) is angular head velocity relative to space, \( q \) is the head quaternion, and \( q_{\text{tot}} = (q_{\text{old}} - q_{\text{new}})/\text{(time interval between q}_{\text{old}} \text{ and } q_{\text{new}}) \).

To put these head-in-space velocities into head coordinates, the following formula was used

\[ \omega_{\text{head}} = \frac{1}{12} q_{\text{head}} \cdot \omega_{\text{space}} \cdot q_{\text{head}}^{-1} \]

Here, \( q_{\text{head}} \) is the head-in-space quaternion, \( q_{\text{head}}^{-1} \) is its inverse, \( \omega_{\text{space}} \) describes instantaneous head velocity relative to space, and the operation between the variables is quaternion multiplication. This is a coordinate system transformation that rotates velocities from a space-fixed frame into a head-fixed frame. For example, if one were standing upright and oscillating about the yaw axis at a constant frequency, the head’s axis of rotation is purely vertical and aligns with the vertical axis in space. If one were then to nod one’s head forward by 45°, then the head-fixed and space-fixed vertical axes would no longer be aligned. Computing the head’s new velocity would require the use of this formula (i.e., a coordinate system transformation) to convert the velocity of rotation from space coordinates into head coordinates, where the vertical axis of rotation is now off space vertical by 45°.

SELECTION OF HEAD TRAJECTORIES. Each stimulation-induced head movement produced a stereotyped movement of the head. Because we were stimulating the INC, the elicited movements consisted of fairly obvious abnormal torsional deviations (Klier et al. 2002). Thus the beginning and end of each head movement was chosen manually by viewing quaternion versus time traces of the head in space. This method was also found to be more reliable than automatic-selection algorithms that work well on natural gaze shifts.

COMPUTING THE CHARACTERISTIC VECTOR. The characteristic vector for each stimulation site represents the theoretical movement...
trajectory that would be elicited at a given site if the monkey was looking straight ahead (i.e., 0° torsional, 0° horizontal, 0° vertical) when the stimulation train was delivered. Individual characteristic vectors for the eye-in-space (Es), head-in-space (Hs), and the eye-in-head (Eh) can be obtained by 1) selecting the 3D starting and ending points of the eye and head trajectories; 2) computing the displacement of each movement in the torsional, vertical, and horizontal dimensions; and 3) performing a multiple linear regression on the stimulation-induced displacements of Es, Hs, and Eh as a function of their initial starting positions. This calculation, which takes into account between 30 and 60 stimulations per site, results in three vectors (Es, Hs, and Eh), which have their tail ends at the origin and extend to the site-specific amplitude. This analysis was done so that one could compare the stimulation-induced movements across different INC sites.

RESULTS

The Fick strategy in normal gaze behavior

Our first goal was to confirm that our monkeys normally obey the Fick constraint on head orientation during gaze shifts. The details of Listing’s law and the Fick constraint during head-free gaze shifts were previously described for some of the same monkeys elsewhere (Crawford et al. 1999; Klier et al. 2002, 2003), so here we will only summarize the directly relevant head movement data. The boxed panels in Fig. 1 (top left) show head orientations (●) extracted from the random control paradigm (see METHODS), using only those orientations during head fixation (i.e., head positions with velocities of <10°/s) in a typical trial. These data are plotted in right-handed coordinates (standard in previous studies on this topic), such that a line joining the origin to each point provides a vector parallel to the axis of rotation that would take the head from its reference position to the actual plotted orientation. When the right-hand thumb points along this vector, the fingers curl in the direction of rotation. These vectors are plotted as they would be viewed looking down from above (left panels) and from the right side of the animal (right panels). Second-order surfaces were fit to these fixation points (see METHODS) and superimposed on the data (see Glenn and Vilis 1992). Similar surface fits are shown for the remaining animals in the other panels of the figure based on similar control head-fixation data (not shown).

The torsional variance of such data is normally quantified as the SD of torsion (in degrees) relative to the surface of best fit.
On average, across animals, this was 5.54 ± 1.52, showing that head torsion was relatively (compared with horizontal and vertical position), although not perfectly, constrained to zero. In addition, the surfaces of best fit to each of the animal’s control data sets showed a characteristic bow tie–like twist. It was previously shown that such a twist results from rotating an object in Fick coordinates where Fick torsion is held at zero (Glenn and Vilis 1992; Radau et al. 1994). These planes can be quantified by the so-called twist score, where an ideal Fick twist score is −1. In our monkeys the average twist score was −0.78 ± 0.16. All of these observations agree qualitatively and quantitatively with previous measurements in the human (Glenn and Vilis 1992; Radau et al. 1994) and in the monkey (Crawford et al. 1999; Klier et al. 2003; Martinez-Trujillo et al. 2003).

Violations of the Fick strategy during INC stimulation

The trajectories plotted in the remaining panels of Fig. 1 show the typical trajectories of head movement evoked by stimulation of the left INC (left columns) and right INC (right columns) in each animal (except for animal 1, where we were unable to explore the left INC before the animal’s untimely demise). For reference, these trajectories are superimposed on the Fick surfaces fit to the control data of each animal. Left INC stimulation (first and second columns) caused consistent CCW head movements (downward trajectories in above views and leftward trajectories in side views). In contrast, right INC stimulation (third and fourth columns) resulted in consistent CW head movements (upward trajectories in above views and rightward trajectories in side views). These trajectories resulted in dramatic violations of the Fick strategy, often producing transient head roll (or torticollis) in excess of 45°. In every case, the range of final head orientations at the end of the stimulus was significantly deviated along the torsional dimension from the normal Fick range of head orientations (paired t-test, \( P < 0.05 \)).

Stimulation-induced movements had variable vertical components (e.g., downward movements in M2, upward movements in M4, and upward/downward vertical movements in M3). The horizontal components of these movements were generally the smallest. Both of these components also showed a variable position-dependent pattern. Sometimes stimulations at one site produced movements with consistent horizontal components (e.g., rightward movements in M4), whereas other sites produced trajectories with small, position-dependent horizontal components (e.g., M3: the trajectories had rightward components when the monkey’s initial head position was left and leftward components when the monkey’s initial head position was right). These position dependencies will be explained in a later section after we determine the INC’s intrinsic coordinate system.

We summarized the different directions of head rotation produced by left and right INC stimulation by examining the velocities of the elicited head movements in all trials from each animal. We first averaged the mean stimulation-induced velocities, component by component, at each site tested. We then normalized these velocities by the mean speed at each site. This produced a range of values, between 1 and −1, from which we could compare the relative effects of stimulation on head velocities across the three components of head movements and across animals (Fig. 2). For right INC stimulation (Fig. 2, top panel), it is evident that the most consistent head velocities were directed CW. In contrast, left INC stimulation (Fig. 2, bottom panel), produced consistent head velocities in the CCW direction. The vertical and horizontal velocity components were generally smaller than the torsional component and—more important—these two components were variable across sites. (Note that this is what the data look like when plotted in arbitrary “space” or “magnetic field” coordinates; a detailed site-by-site quantification of stimulus evoked amplitudes and directions will be provided below when we return to this topic in the context of coordinate systems.) Thus as shown previously for the oculomotor system (Crawford et al. 1991), right INC stimulation consistently produced primarily CW torsional deviations of the head, whereas left INC stimulation produced mainly CCW head rotations.

Following the large torsional violations of Donders’ law illustrated in Figs. 1 and 2, animals corrected most of this torsion as part of the next endogenous gaze shift. Examples of these corrective movements are illustrated in Fig. 3 for both the left (top panels) and right (bottom panels) INC [notice that final head positions (○) lie on or near the surface]. This behavior is similar to eye movements induced by INC stimulation where their torsional position returns to Listing’s plane. For the head, however, it cannot be determined with certainty how much of these movements were passive and how much were active (i.e., knowingly generated by the animal on finding its head in an unusual, torted position) because we do not know enough about the mechanical time constants of torsional head rotation to make such estimates. However, because these torsional movements coincided with horizontal and vertical movements, and because they followed similar time courses to these other components (Fig. 3), it appears that they were at least partially composed of active components. The final ranges formed by the endpoints of these corrective movements, after both left and right INC stimulation, showed a significantly reduced torsional offset than the poststimulation ranges (the reduction in torsional variance was from 7.95 to 4.98° in M1, 11.40 to 7.58° in M2, 10.22 to 6.33° in M3, and 10.17 to 6.36° in M4; paired t-tests across all animals, \( P < 0.01 \)), on average reducing the torsional offset by 39.8%. However, their final torsional positions were still significantly different from the normal torsional ranges (Fig. 1, boxed panels) (paired t-test, \( P < 0.05 \)), suggesting that one or more subsequent movements were required to completely return the head to its normal torsional operating range.

Neural coordinate systems

To quantify and compare the induced movements at all of the stimulation sites, we first computed the characteristic vector of each site (see METHODS). This measure represents the predicted head movement that would result from stimulation at one site if the head was pointing directly straight ahead at the time of stimulation (i.e., if head position was 0° torsional, 0° vertical, and 0° horizontal when the stimulation was delivered). This measure, one value per site, allowed us to compare the effects of stimulation across INC sites.

The characteristic vectors for all sites, from all four monkeys, are shown in Fig. 4 (right INC sites are shown in gray; left INC sites are shown in black). The above view (Fig. 4A),
plots torsional displacements in head positions (ordinate) as a function of vertical displacements of head positions (abscissa), i.e., as one would view the axes for these components of rotation from above. The characteristic vectors generally consisted of a combination of vertical and torsional components, where in most cases the torsional component was equal to or greater than the vertical component. CV amplitudes were generally <30°, but individual movements could be much larger. Again, the torsional components were always consistent for right or left INC stimulation, whereas systematic vertical components were more variable.

With respect to the oculomotor system, the riMLF and INC appear to equally intermingle canal/muscle-like up-torsional and down-torsional signals on each side of the brain (Crawford et al. 1991; Fukushima 1991; Henn et al. 1991). As a result, unilateral stimulation of the midbrain produces nearly pure torsional eye movements (Crawford and Vilis 1992). If this were the case for head control, one would also expect unilateral INC stimulation to produce purely torsional eye rotations and fall along the ordinate in Fig. 4A. In contrast, if the INC encoded head rotations using anatomically segregated canal coordinates, one would expect the axes of stimulus-evoked head movements to align with the individual vertical canal axes, like the “X” superimposed in Fig. 4A. The data fall between these two extremes, suggesting a partial anatomical segregation between up and down signals with the INC. Unfortunately, we were not able to fully map the INC with electrode penetrations in enough animals to confidently answer whether this partial segregation has some consistent anatomic basis, nor can we exclude that possibility.

The side view (Fig. 4B), which plots horizontal head positions (ordinate) as a function of torsional head positions (abscissa), again shows that head characteristic vectors from right versus left INC stimulations are clearly segregated on either side of the ordinate (CW movements to the right and CCW movements to the left). In contrast, the horizontal components were not generally elicited and, even when they were, they were not very large. Five outliers (circled group) were col-
monkeys (Crawford et al. 1999) and is illustrated schematically in Fig. 5, A and B. The colored vectors (rectangles connected to the origin by solid lines) show different pointing directions of the head, whereas the dotted/dashed loops (in matching colors) show corresponding angular velocity loops for the head. These velocity loops are composed of vectors that obey the right-hand rule, but are scaled (distance from origin) by the speed of rotation.

In Fig. 5B, head direction (viewed from the side) is set at different vertical positions (e.g., red = head pointing down; green = center; purple = up) while the head makes either leftward (dotted loops) or rightward (dashed loops) gaze shifts. (The velocity loops have different magnitudes for illustrative purposes.)

Again, our hypothesis was that the INC head controller uses a canal-like coordinate system that aligns with the intrinsic coordinates observed in head behavior (i.e., the Fick constraint), which is equivalent to setting torsion to zero in Fick coordinates. The observation that the axes of head rotation during INC stimulation tend to align orthogonally to the vertical axis of the Fick surface (Fig. 4) is a necessary, but insufficient, condition to conclude that the INC encodes head movements in a Fick-like coordinate system. The more important test is to see how the stimulation-evoked head movement axes depend on head orientation.

In a Fick coordinate system, similar to a telescope mount, the horizontal axis (for vertical rotations) is nested in the vertical axis, but the vertical axis (for horizontal rotations) is fixed in space. One consequence for head control is that the horizontal axis of rotation is dependent on position, whereas the vertical axis of rotation is completely independent of position. This was previously shown for head rotations in
purposes.) Here, the head rotates about a fixed vertical axis independent of its vertical position, i.e., the velocity loops overlap (Crawford et al. 1999).

In contrast, the horizontal axis (for vertical rotations) is completely dependent on horizontal head orientation. As shown in Fig. 5A, when the pointing direction of the head (viewed here from above) steps from the left (purple vector) to the right (red vector), the corresponding velocity loops for vertical head rotations remain orthogonal to the head vectors, i.e., they also step from left to right. (Here dashed loops represent downward rotations and dotted loops represent upward rotations.) Notice that the angle between each gaze direction and its correspondingly colored velocity loop remains constant. All of these observations were previously confirmed in behavioral data (Crawford et al. 1999). What cannot be shown in normal behavioral data is that the torsional axis of rotation in a Fick coordinate system is dependent on both vertical and horizontal head orientation, so it would tilt horizontally with the head similar to the horizontal axes shown in Fig. 5A, but unlike the axes in Fig. 5B, it would also tilt vertically with the head. In other words, the torsional axis in a Fick coordinate system should be fixed in the head.

This gives rise to two experimental predictions, one of which we can test here. The first is that activation of the horizontal centers for head rotation (Sparks et al. 2002) should produce head rotations about a fixed vertical axis that is independent of head elevation. The second, which we can test, is that the primarily torsional axes of rotation produced by INC stimulation should remain head fixed at different head orientations.

The latter prediction is confirmed in Fig. 5, C and D and in Fig. 6. In Fig. 5C we show the head’s instantaneous axis of rotation (squiggly traces) and the head’s gaze direction (i.e., head’s pointing direction) during five left INC stimulations, using the same conventions as in Fig. 5A, but now showing real data. Here, the direction of head rotation is CCW about a mainly torsional axis, but notice that it does not remain fixed in space. Instead, as the pointing direction of the head moves from right to left (red to purple), the axes of rotation also move in the same direction by roughly the same amount. Thus the angle between the two appears to remain constant, suggesting that the torsional axis of head rotation is fixed in the head. Figure 5D depicts the same effect for right INC stimulation. Here the axis of rotation is equally torsional and horizontal when the head looks straight ahead (green velocity trace), but it rotates horizontally with the head so that it can range from nearly pure CW (blue velocity trace) to nearly pure CCW (red velocity trace) in space coordinates.
In Fig. 6 we show how this pattern was quantified across all sites and across all animals. First, Fig. 6, A and B describes how the torsional axis of rotation is dependent on the horizontal position of the head. The abscissa describes the head’s horizontal gaze direction, during stimulation, with the following conventions: if the head is pointing over the left shoulder, then its gaze direction is 0°; if the head is pointing straight ahead, then its head gaze direction is 90°; and if the head is pointing over the right shoulder, then its gaze direction is 180°. The ordinate uses this same convention to describe the corresponding axes of head rotation during stimulation. This convention was chosen because both the head gaze directions and the axes of rotations used by the head do not appear at the 0°/360° mark and therefore do not produce discontinuities when plotting.

In Fig. 6A, data from two INC sites in one monkey are shown. The top cluster (□) is from a left INC site (i.e., CCW head rotation), whereas the bottom cluster (■) is from a right INC site (i.e., CW head rotations). Each square represents the position of the head’s axis of rotation (ordinate) plotted as a function of the head’s average horizontal pointing direction (abscissa) during one stimulation. A regression line was then fit to all the data from that one site. Figure 6B depicts all the regression lines from all the sites tested in one monkey. A slope of zero would indicate that the head’s axis of rotation is independent of the horizontal position of the head and thus independent of the vertical axis of head rotation. In contrast, a slope of one would imply that the head’s axis of rotation is completely dependent on the vertical axis of head rotation and therefore fits with a Fick strategy. The average slopes (± SE), computed for all four animals, were 1.123 ± 0.037 (M1), 0.961 ± 0.095 (M2), 0.932 ± 0.066 (M3), and 0.976 ± 0.061 (M4).

Figure 6, C and D is similar to Fig. 6, A and B, except for describing how the torsional axis of rotations is dependent on the vertical position of the head. Here, the abscissa describes the head’s vertical gaze direction, during stimulation, with the following conventions: if the head is pointing directly down, then its gaze direction is 180°; if the head is pointing straight ahead, then head gaze direction is 270°; and if the head is pointing directly up, then its gaze direction is 360°. Again, this convention was chosen because both the head gaze-directions and the axes of rotations used by the head do not appear at the 360°/0° mark and therefore do not produce discontinuities when plotting.

Once again, Fig. 6C depicts two clusters of data, one for a left INC site (□, CCW head rotations) and one for a right INC site (■, CW head rotations). This time, each square represents the position of the head’s axis of rotation (ordinate) plotted as a function of the head’s average vertical pointing direction (abscissa). Again, regression lines were fit to all the stimulation data from each site, and Fig. 6D shows all the regression lines from all sites in one monkey. The average slopes (± SE), computed for all four animals, were 1.017 ± 0.128 (M1), 0.875 ± 0.238 (M2), 0.698 ± 0.158 (M3), and 0.751 ± 0.099 (M4). These slopes, which gather around a slope of one, indicate that the head’s axis of rotation was dependent on the vertical position of the head. Together, these results confirm that the torsional axes of head rotation produced by unilateral INC stimulation are head fixed. This complements the behavioral data (shown schematically in Fig. 5, A and B) to show that the head truly uses a Fick-like controller.

**Relationship between coordinate systems and position trajectories**

Finally, because the axes of head rotation appear to obey a Fick strategy, it is useful to directly illustrate that these axes are fixed relative to the head and use this to explain the seemingly complex position-dependent patterns in head-position trajectories that were observed in Fig. 1. Figure 7 first shows above views of mean head velocities for a right INC site (top row) and a left INC site (bottom row) in two different coordinate frames: head (A and B) and space (C and D). If one draws a line from each average velocity point to the origin, then that line represents the average axis of rotation of the head, whereas the length of the line determines the average speed of the movement and the direction of rotation is determined by the right-hand rule (i.e., align the thumb of the right hand with the line and the fingers of the right hand curl in the direction of head rotation). Although the directions of head movement are as

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**FIG. 6.** Evidence for a Fick strategy. Top row: torsional axis of head rotation and horizontal head position. A: for one CW INC site (■) and one CCW INC site (□), the orientation of the head’s axis of rotation is plotted as a function of the head’s pointing direction in the horizontal plane for each stimulation-induced movement (see text for angle conventions). A regression line was then fit through the data whose slope indicates how the head’s axis of rotation changes with changes in horizontal head gaze. B: all regression lines from all INC sites in one animal (see text for quantification of slopes in all animals). Bottom row: like top row, but abscissa now indicates vertical changes in head gaze. C: data from the same 2 sites as in A, D: regression lines are shorter because animals had a narrower vertical head position range (as compared with the larger horizontal head-position range in B).

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previously discussed (CW for right INC stimulation; CCW for left INC stimulation), notice how these mean velocities (which represent the head’s axis of rotation) change when plotted in head coordinates (A and B) versus space coordinates (C and D). The axes of rotation appear to be fixed in the former (i.e., the dots seem to gather and lie along one line), but show more variance in the latter. This is because the axes depend on, and thus tilt, as a function of head position. Note that this analysis could be done only with these stimulation-induced movements that produce large torsional head rotations. Normal head movements, which are largely horizontal in direction, would likely produce similar results in both head and space coordinates because the vertical axis (for horizontal head movements) remains space fixed in both cases. It is the torsional axis that changes its behavior across the two coordinate frames.

To quantify this observation across all animals and all INC sites, we computed the average and SDs of the mean velocity vectors—in the torsional, vertical, and horizontal dimensions—and then conducted pairwise t-tests on the SDs between head coordinates and space coordinates. We expected a significant difference in the SDs of the horizontal and vertical components between these two conditions, with head coordinates consistently showing lower SDs than space coordinates.

The t-test results for the four monkeys were as follows (P values <0.05 indicate that variability was significantly lower in head coordinates): M1: vertical P = 0.282, horizontal P = 0.001; M2: vertical P = 0.009, horizontal P = 0.001; M3: vertical P = 0.003, horizontal P = 0.012; M4: vertical P = 0.000, horizontal P = 0.000. Thus there was a consistent trend for SD to be lower in head coordinates than in space coordinates. This trend was significant in seven of eight comparisons and most highly significant in the monkey with the greatest number of INC sites tested (M4 with 41 sites compared with M1, 6 sites; M2, 11 sites; and M3, 7 sites).

Figure 7 goes on to plot corresponding head positions in above (E and F) and behind (G and H) views. The complex position trajectories illustrated here (and in Fig. 1) are simply the result of rotating the head about head-fixed torsional axes. For example, with right INC stimulation (G), when the head looks left a head-fixed CW rotation should produce downward rotation components in space and looking right should produce upward components. Looking up should produce leftward movements and looking down should produce rightward movements. This should give rise to a circling pattern in plots of horizontal (ordinate) versus vertical (abscissa) position (G and H), where head-fixed CW rotations produce a CCW circling pattern and head-fixed CCW rotations produce a CW circling pattern of position trajectories (dashed arrows). The actual data plotted on these panels show this predicted pattern. Thus this circling pattern (i.e., these position-dependent horizontal and vertical components in space coordinates) is consistent with and predicted by a head-fixed torsional axis in Fick coordinates that rotates with gaze.

**DISCUSSION**

The INC forms part of the neural integrator for eye orientation (Crawford et al. 1991; Fukushima 1991; Helmchen 1998; King et al. 1981). Specifically, the INC appears to integrate signals for holding the torsional and vertical components of eye position. We recently proposed that the INC performs a similar function for head orientation (Klier et al. 2002). This was based on the finding that immediately after muscimol inactivation of the INC, the head shows exponential, position-dependent patterns of torsional and vertical drift similar to that seen in the eye, and that during INC stimulation the head shows ramplike torsional rotations that tend to hold their final orientation, at least until corrected by an active gaze shift.

Here, we have confirmed that the INC encodes head movements in vestibular-like or canal-like coordinates: stimulation of the right INC produces CW-up and CW-down positions, whereas the left INC produces CCW-up and CCW-down orientations. Importantly, we showed that these coordinates obey a Fick strategy in which the torsional and vertical axes of head rotation are dependent on, and rotate with, the position of the head, as in a Fick gimbal. In this way, when CW and CCW signals from the two sides of the INC are balanced, torsion of the head would be constrained to a 2D twisted surface that obeys Donders’ law.
Neural coordinate systems

It has long been established that stimulation of the midbrain reticular formation produces roll movements of the head (Hassler 1972; Hassler and Hess 1954), although these earlier researchers simply did not have the technology for quantitative measurements of 3D eye and head kinematics available today. However, our main observations support these earlier observations. Moreover, at first glance, the head-movement patterns that we observed during microstimulation of the interstitium of Cajal in the head-free monkey are consistent with the pattern of eye movements elicited during head-fixed INC stimulation (Crawford et al. 1991). Stimulating the right INC produces large CW head movements, whereas left INC stimulation produces similar head movements, but in the CCW direction. During unilateral pharmacological inactivation of the INC (and to some extent the adjacent riMLF and cMRF), the eye and head shift torsionally in the opposite directions (Crawford and Vilis 1992, 1993; Crawford et al. 1991; Fukushima and Fukushina 1992; Fukushina et al. 1985; Helmchen et al. 1998; Klier et al. 2002; Suzuki et al. 1995; Waitzman et al. 2000a,b). These observations support the idea that the control of torsional movement components (CW and CCW movements for both the eye and the head) is segregated across the midline of the midbrain (Crawford and Vilis 1992, 1993; Crawford et al. 1991).

Even the systematic (i.e., nonposition-dependent) components of vertical head (and eye) rotation produced by INC stimulation are much smaller and more variable than the torsional components. Interpreted in light of the vestibular inputs to the INC and the tuning directions of INC and riMLF units during vestibular stimulation (Fukushina et al. 1980; Henn et al. 1991), and the tonic eye position dependency of INC units during fixation (King et al. 1981), this appears to be because up- and down-tuned units are intermingled on each side of the INC. Taken together with the torsional tuning directions of these neurons (Fukushina et al. 1980; Henn et al. 1991) and the stimulation/inactivation data discussed above, this suggests that the INC (and riMLF) oculomotor neurons are organized into an eye muscle–like or vestibular canal–like coordinate system, with up-CW and down-CW populations on the right side and up-CCW and down-CCW populations on the left.

Our current head data are consistent with this idea, but interpreted in this light, suggest that up and down head movement units are not perfectly intermingled on each side (these would cancel out to produce zero systematic vertical rotation). Rather, different stimulation sites on each side appear to run the gamut between sites encoding up-torsion to pure torsion to down-torsion (Fig. 4, top). This suggests that there may be some anatomic segregation of up/down head movement signals in the INC, but at the level of anatomic resolution of advancing different electrodes and, at the number of different penetrations that we were able to obtain in each animal, we were not able to find a consistent anatomic pattern to this segregation. Because neck muscles are not presumably organized along the simple lines of eye muscles (Corneil et al. 2001; Richmond et al. 2001), this general organization may result in part from vestibular input. Likewise, another unexplored possibility is that the different axes of rotation that we obtained from different INC sites correspond to activation of distinct muscle synergies.

As in the oculomotor system, head movements showed the least systematic components in the horizontal direction during INC stimulation and these appear to be even smaller or nonexistent (for most sites) when the vertical axis for horizontal rotation is defined as aligning with the axis of rotation for the Fick constraint observed in normal gaze-shifting head movements (Fig. 4, bottom). This is similar to the observation that stimulation of midbrain oculomotor centers produces axes of rotation that align orthogonally to Listing’s plane of the eye, except that Listing’s plane is essentially fixed in the head (Crawford 1994), whereas the Fick surface is essentially fixed in the body (Misslisch et al. 1994).

Moreover, during INC stimulation, the head showed significant position-dependent movement components in both the vertical and horizontal components. As shown in Figs. 5–7, these arise because the stimulation-evoked axes were fixed in the head, generating a particular circling pattern of horizontal and vertical head-position dependencies in space (Fig. 7).

All of these observations are consistent with the idea that both torsional and vertical head control by the INC are organized in a Fick-like coordinate system. Specifically, the torsional axis is fixed in the head such that it produces the position-dependent patterns observed above in space coordinates (Fig. 7). This also explains similar position-dependent patterns that we observed during torsional eye and head drift after unilateral INC inactivation in the head-free monkey (Farshadmanesh et al. 2005). However, this is only part of a Fick-like coordinate system. To confirm this, one would have to measure 3D axes of rotation during stimulation of the horizontal head control system, which in contrast should produce horizontal rotations about a body-fixed vertical axis that does not rotate with the head. The functional significance of these observations will be considered in the next section.

Implementation of Donders’ law

There is an intimate relationship between neural coordinate systems and neural solutions to the degrees-of-freedom problem (e.g., Donders’ law for the eye and head). In the case of the oculomotor system, the brain stem appears to use a canal- or muscle-like coordinate system (Fukushina et al. 1980; Henn et al. 1991) that aligns with the head-fixed Listing’s plane (Crawford 1994; Crawford and Vilis 1992; Suzuki et al. 1995) such that CW torsion relative to Listing’s plane is represented in the right midbrain and CCW is represented on the left. This unique arrangement gives rise to a simple principle: to obtain zero torsion movement and position vectors in Listing’s plane, the brain must activate the riMLF and INC symmetrically across the midline. It now appears that the position-dependent saccade axis tilts required for Listing’s law (i.e., the half-angle rule) are implemented by the eye muscles themselves (Demer 2002, 2006; Ghasia and Angelaki 2005; Klier et al. 2006).

The current investigation suggests that an analogous mechanism is used to control the head. However, the head does not follow Listing’s law but rather the Fick strategy, so this mechanism requires that the neural coordinate systems for head control are arranged in Fick coordinates. If the neural coordinates for head control are organized like that of the eye (i.e., with up-CW and down-CW populations in the right midbrain and up-CCW and down-CCW populations on the left), but organized in Fick coordinates, then symmetric bilateral activa-

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tion of the up or down populations across the midline will produce position vectors with zero torsion in Fick coordinates (i.e., the Fick strategy observed in behavior; Glenn and Vilis 1992; Radau et al. 1994). Our data confirm this to be the case for the INC. The other requirement for this neural coding scheme, again not yet tested, is that the vertical axis for horizontal head rotation is fixed in the body and aligns with the vertical Fick axis observed in behavior. With any other scheme, a simple activation of the horizontal population would produce violations of Donder’s law. Finally, it remains to be tested whether the position dependencies required to implement this scheme are provided by neurons, the neck musculo-skeletal system, or some combination of the two.

The other aspect of the neural mechanism for Donder’s law is that it must be able to violate (or produce different forms of) Donders’ law when required and correct those violations when necessary. Obviously, humans can voluntarily violate Donders’ law of the head at will (i.e., by rolling the head from side to side), and we automatically modify it to suit different tasks (Ceylan et al. 2000), so the Fick constraint is not fundamentally mechanical. The system must choose to balance torsion at zero (as described above) or selectively activate one side of the INC to produce head torsion, as we observed in our INC stimulation data. Further, we demonstrated the capacity of this system to correct torsional violations of Donder’s law head after INC stimulation—presumably by endogenously activating torsional units on the opposite side of the midbrain. Thus as with the oculomotor system, the head muscles may implement some of the position dependencies of Donders’ law. Evidence for this has come from anatomical studies showing that the atlas and axis of the spinal column are fit together in such a way as to facilitate a default Fick strategy (Richmond and Vidal 1998). Ultimately, however, it is up to the CNS to choose to produce torsional components or to constrain torsion to zero in some coordinate system.

Gaze, eye, and head control

Because the INC uses different strategies for eye and head movements, does this imply that it encodes separate eye and head commands (i.e., in contrast to a common gaze command)? Such a duality would not be hard to believe, especially because the neural integrator is just one step removed from the motoneurons of the eyes and head. However, this need not be the case at the level of individual neurons. Again, the coordinate system of a given neural structure is determined, not only by the computations made in the given area, but—more important—by the connections the area has with downstream structures (Pellionisz and Llinarés 1980; Smith and Crawford 2005). Thus the INC may project to eye motoneurons in one way (which causes the eye axes to align with Listing’s plane) and in a completely different way to the motoneurons of the neck muscles (allowing the head’s axes to adopt a Fick strategy). In this manner, it is theoretically possible for the INC, as well as other nuclei, to control different body parts in modality-specific coordinates. However, although this may or may not be true for some individual neurons, our view is that the INC must have enough separate eye/head projections from different units to be able to act as a dual, separate eye/head controller, even if these are then nested within an overall circuit for gaze control.

This does raise the question of how the gaze control system deals with different effectors and different internal coordinate systems. If the assumption of a common gaze command in the INC is true, then the fact that the coordinate axes for the eyes and head do not align may lead to problems in eye–head coordination. For example, a movement command along any of the three coordinate axes would cause the eye and head to move in different directions because these axes themselves are not aligned. Note, however, that this potential dilemma is not so great, given that Listing-like and Fick-like coordinates are chosen by the brain. The Listing strategy ensures that the three coordinate axes for eye movements are all fixed in the head. Similarly, the Fick strategy ensures that both the torsional and horizontal axes for head rotation are fixed in the head as well. Therefore misalignment of these two strategies would occur only with the vertical axis. For example, during an upward head movement the space-fixed vertical axis for head rotations would remain upright (relative to space), whereas the head-fixed vertical axis for eye movements would tilt back with the head. This becomes a lesser problem when one considers that the head’s contribution to gaze is mainly horizontal, with only very small vertical components. Nevertheless, we predict that there are control signals that account for these differences.

Behavior-related coordinate systems and plasticity

If the coordinate axes of the head had been found to align with anatomical structures such as the canals, eye muscles, or some stereotaxic landmark, then head movements would likely be fixed and unchangeable. However, because the head’s axes, much like the eyes’, are aligned with a behavior-related strategy, then it is likely that different head movement strategies can be learned. Proof of such plasticity has already been found using a goggle paradigm (Ceylan et al. 2000; Crawford et al. 1999). In that situation, humans and monkeys wore opaque goggles that occluded all vision except for a tiny aperture in one eye. To look around, the monkey had to use its head to cover a much larger area than before the occlusion (akin to viewing a visual scene while using binoculars). When 3D head movements were measured, it was found that the head quickly abandoned its normal Fick strategy for a Listing strategy (seemingly appropriate because the head was now moving like an eye). What are the implications of this for an internal coordinate system that aligns with these behavioral coordinates? How can it switch so fast?

Again, neural coordinates need not be hard wired because they depend on upstream (and in this case) downstream neural connections, which clearly change with different behavioral sets (Constantin et al. 2004). Because Listing’s law and the Fick strategy require two very different forms of position-dependent axes (half-angle rule for all axes in Listing’s, full angle for Fick’s horizontal axis, and zero angle for Fick’s vertical axis), this plasticity might seem to argue against a mechanical implementation of these position dependencies for the head. However, any set of mechanics can be used, undone, or reinforced neurally—any of which would influence the motor coordinates of the upstream neural structures—and it is extremely difficult to know the source of the change in behavior without doing specific neurophysiological experiments. Ultimately, the organization of the coordinate system used by the INC probably arises from a combination of sensory inputs,
plant mechanics, and the kinematic necessities of eye–head coordination.

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