Rotation Axes of the Head During Positioning, Head Shaking, and Locomotion

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1Institute for Neural and Intelligent Systems, Department of Computer and Information Science, City University of New York (Brooklyn College), Brooklyn, New York; 2Department of Neurology, Mount Sinai School of Medicine, New York, New York; and 3Department of Otorhinolaryngology, Osaka University School of Medicine, Osaka, Japan

Submitted 6 June 2007; accepted in final form 19 September 2007

Kunin M, Osaki Y, Cohen B, Raphan T. Rotation axes of the head during positioning, head shaking and locomotion. J Neurophysiol 98: 3095–3108, 2007. First published September 26, 2007; doi:10.1152/jn.00764.2007. Static head orientations obey Donders’ law and are postulated to be rotations constrained by a Fick gimbal. Head oscillations can be voluntary or generated during natural locomotion. Whether the rotation axes of the voluntary oscillations or during locomotion are constrained by the same gimbal is unknown and is the subject of this study. Head orientation was monitored with an Optotrak (Northern Digital). Human subjects viewed visual targets wearing pin-hole goggles to achieve static head positions with the eyes centered in the orbit. Incremental rotation axes were determined for pitch and yaw by computing the velocity vectors during head oscillation and during locomotion at 1.5 m/s on a treadmill. Static head orientation could be described by a generalization of the Fick gimbal by having the axis of the second rotation rotate by a fraction, \(k\), of the angle of the first rotation without a third rotation. We have designated this as a \(k\)-gimbal system. Incremental rotation axes for both pitch and yaw oscillations were functions of the pitch but not the yaw head positions. The pivot point for head oscillations was close to the midpoint of the interaural line. During locomotion, however, the pivot point was considerably lower. These findings are well explained by an implementation of the \(k\)-gimbal model, which has a rotation axis superimposed on a Fick-gimbal system. This could be realized physiologically by the head interface with the dens and occipital condyles during head oscillation with a contribution of the lower spine to pitch during locomotion.

INTRODUCTION

Changes in head position are critical to direct gaze during natural motion. A better understanding of the coordinate frames and axes that govern head rotation both globally and incrementally would give insight into how fixation is accomplished. Understanding of head rotation axes under static and dynamic situations, however, is limited. One reason for this is that the head-neck system is a complex biomechanical linkage with multiple degrees of freedom (Ishii et al. 2004a, b), coupled with a complex musculature for moving the head on the trunk (Peterson et al. 2001). Despite this complexity, some simplifications have proven useful in examining the coordinate frames and axes that govern head movement.

One such simplification is to model the head as a rigid sphere rotating about its center of mass (Ceylan et al. 2000; Glenn and Vilis 1992; Stark et al. 1980, 1988), but constraints reduce the degrees of freedom of head movement (Ceylan et al. 2000; Crawford et al. 1999; Radau et al. 1994). A similar reduction in degrees of freedom govern eye positioning mechanisms. Although the eyes are capable of moving about roll, pitch, and yaw axes of the head in response to vestibular stimulation, the rotation axes during visual fixation lie in a plane, obeying Listing’s law (Helmholz 1867; Tweed and Vilis 1987). Head orientations in three dimensions do not obey Listing’s law (Glenn and Vilis 1992), but the axes are constrained to a curved surface by the less restrictive Donders law (Glenn and Vilis 1992; Haslwanter et al. 1991; Straumann et al. 1991).

Each surface shape, be it planar or twisted, has its own particular sensory and motor consequences (Crawford 1997; Crawford and Guitton 1997; DeSouza et al. 1997). By examining the relationship between the roll of the head in space as a function of pitch and yaw, it was inferred that the curved surface generated by this relationship corresponded to a Fick gimbal, where the roll was zero. That is, the yaw axis of rotation is fixed relative to the trunk, the pitch axis moves with the head, and there is no roll (Radau et al. 1994). Studies in the monkey indicate that the functional relationship between head roll and the corresponding pitch and yaw components give rise to a more planar surface, thereby obeying Listing’s law (Crawford et al. 1999). In humans using pinhole goggles, however, the difference between the surfaces with and without using pinhole goggles was shown to be small (Ceylan et al. 2000). There has been considerable speculation as to why the head positioning mechanism might follow a Fick-like system. These range from optimizing perception of lines in the horizon (Glenn and Vilis 1992; Hore et al. 1992), to improving binocular alignment of the eyes with the horizon (Crawford and Vilis 1995), to reducing the workload on the neck muscles (Glenn and Vilis 1992; Radau et al. 1994). A satisfactory model has not been developed to explain the underlying organization of the system, however.

The physiological constraints that maintain Fick-like gimbal behavior depend on anatomical constraints. The \(C_1\)-inferior articular facets, which support the head on the spinal column, are circular, flattened and slightly convex and are directed downward and medialward, articulating with \(C_2\) (Gray 1918). The head pitches through movement of the occipital condyles on the superior facets of \(C_1\), while it rotates about the vertical bony component of the dens, the portion of \(C_2\), which pro-

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trudes through the odontoid process of C1 (Ishii et al. 2004a,b). We have recently hypothesized that the dens and condyles are critical for determining the incremental axes about which the head rotates (Kunin 2004). However, the cervical spine flexes, rotates, and extends the head relative to the trunk, which would move the yaw and pitch axes away from the occipital condyles and the dens (Dutia 1991; Graf et al. 1992; Ishii et al. 2004a; Vidal et al. 1988). This complex structure has suggested that the axes of gaze shifts to targets at different locations occupy different spatial locations (Medendorp et al. 1998). However, no model-based understanding of mathematical relationship between the rotation axes for the wide range of head movements in three dimensions has been determined.

The purpose of this study was to determine how the axes of rotation vary during voluntary and natural movements, and how these axes might be related to the anatomical structures. As noted in the preceding text, the axes of eye rotation are constrained for static positions of fixation and saccades so that they lie in Listing’s plane, but they are unconstrained during head movements that activate the vestibuloocular reflex (VOR). We questioned whether there was a similar lack of constraint for oscillatory head movements that would activate the vestibular system. Our hypothesis was that the rotations of the head about roll, pitch, and yaw do not intersect at a common pivot point and that the axes would lie along lines in space that are unique to the direction about which the head rotates. We also hypothesized that these lines would vary as a function of head orientation on the body. To study this, we developed a new methodology to determine incremental rotation axes and their localizations in three dimensions using displacement matrices. The axes associated with incremental rotations were then compared with the axes of head orientation during natural locomotion with and without pinhole goggles to fixate points in the visual field binocularly. A model was then developed that shows how the constraints of the spinal column on which the head rotates explain the behavior of the axes during head positioning and locomotion.

METHODS

Subjects

Three general conditions were studied in this report: head orientation, head oscillation in different orientations and head oscillation during locomotion. Six subjects were studied during both head orientation and head shaking (3 female and 3 male). Three of these subjects (3 males) as well as one additional subject (female) were studied during locomotion. Their ages ranged between 32 and 57. Subjects viewed visual targets with pinhole goggles to assume static head positions. They then made small voluntary head oscillations at each of these head orientations. Finally, their head movements were recorded during locomotion on a linear treadmill. The experiments were approved by the Institutional Review Boards of the Mount Sinai School of Medicine and the City University of New York and were performed in accordance with the ethical standards established in the 1964 Declaration of Helsinki. Subjects gave their informed consent prior to the inclusion in the study. Privacy and anonymity of the data associated with the subjects were maintained.

Data acquisition

Head and trunk movements were recorded using the OPTOTRAK 3020 video motion analysis system (Northern Digital, Ontario, Canada). Briefly, the OPTOTRAK system sends a pulse to each of the markers (light-emitting diodes, LEDs) and uses a bank of three cameras (the sensor) to triangulate the location of the LED in three dimensions. Each marker is pulsed in sequence. The Optotrak system then tracks the three-dimensional position of each LED and stores this information in a computer file. Twenty-one markers on the head, trunk, and legs were utilized in this study. This allowed measurement of the head and trunk in space in three dimensions at a sampling rate of 100 Hz both when stationary and while walking on a treadmill. The OPTOTRAK system was positioned 4 m from the subject; in this configuration, the accuracy of translational measurement was 0.3 mm (manufacturer’s specification) with accuracy in pitch and yaw of 0.1° (See Hirasaki et al. 1999 for a complete description of the OPTOTRAK characteristics.)

Marker placement and determination of head coordinate frame

Coordinate frames and rigid bodies were formed by combining groups of markers. The spatial coordinate frame to which movements of the head were referenced was obtained from a set of four markers that were embedded 24 cm apart in a square plastic plate (Fig. 1A). During head positioning and voluntary head oscillation, the plate was attached to the screen that held the visual targets. The sides of the plate were aligned with the spatial horizontal and vertical axes.

The spatial coordinate frame was obtained by choosing one of the LED locations as the origin (Fig. 1A, LED 1). A line connecting LEDs 1 and 2, aligned with the spatial vertical and directed upward, was the \( z_\text{S} \) axis (Fig. 1A). A line connecting LEDs 1 and 4, aligned with the spatial horizontal in the direction of walking and orthogonal to the \( z_\text{S} \) axis, was the \( y_\text{S} \) direction (Fig. 1A). A line normal to the LED plate (dashed arrow) that formed a right-handed coordinate frame was the \( x_\text{S} \) axis (Fig. 1A).

The rigid body for determining translation and rotation of the head consisted of 12 LEDs (markers) that were embedded in a lightweight headband (Fig. 1B). The head coordinate frame was determined using a head calibration device that was composed of a plastic frame that had three LEDs worn by the subject only at calibration time (Fig. 1D). The right and left LEDs were placed at the right and left external auditory meati (EAM), and the central LED lay over the bridge of the nose. The plane formed by the LEDs was adjusted so that it intersected the inferior rim of the orbits. Thus this plane contained the Reid’s baselines on either side of the head (Fig. 1B, e, f, d). The \( y \) axis \((y_\text{H})\) was defined as the interaural axis with its positive direction from the right to the left ear (Fig. 1B, right). The origin of the head coordinate frame was chosen at the point where the LED over the nose projected onto the interaural axis. This was approximately at the midpoint of the line segment joining the points e and f (Fig. 1B, right). The positive \( x \) axis \((x_\text{H})\) was along the line from the origin to the landmark on the nose. The positive \( z \) axis \((z_\text{H})\) was chosen to complete the right-handed coordinate triple and is designated by the symbol \( \bullet \).

Coordinate and rotation conventions in three dimensions

Various conventions and coordinate frames have been adapted to represent three-dimensional rotations (Goldstein 1980). In this study, head orientations in space are described by the Euler angles \( \psi \), \( \theta \), and \( \phi \) in accordance with the Fick convention. This convention assigns the first angle \( \phi \) to rotation about the spatial vertical axis, which coincides with the axis out of the top of the head. We refer to this rotation as yaw. The second angle \( \theta \), describes rotation about an interaural axis after the head has rotated in yaw. This rotation is pitch. The final rotation is roll by angle \( \psi \) about the naso-occipital axis (Fig. 1C). Thus \( \phi \), \( \theta \), and \( \psi \), the Euler-based yaw, pitch, and roll angles, form a Fick gimbal system.

Head orientation could also be described by roll, pitch, and yaw about the spatial coordinates, \( x_\text{S} \), \( y_\text{S} \), and \( z_\text{S} \), respectively. This is the
axis-angle or rotation-vector-based roll, pitch, and yaw components and has been referred to as Listing’s convention. Each of these conventions leads to a unique description of head orientation in three dimensions. Whereas there is some ambiguity in the usage of roll, pitch, and yaw for these various conventions, they all follow the convention that roll is a rotation about some $x$ axis, pitch about some $y$ axis, and yaw about some $z$ axis. The context will clarify the convention for the usage. The question that we address here is whether voluntary head rotations and oscillations as well as head oscillations during locomotion follow some consistent convention and whether it can be theoretically related to the structure of the spinal column and its interface to the head.

### Calibration

Calibration was done by asking the subjects to stand erect on a platform while being slowly rotated for 30 s over 360°. Subjects held onto a bar connected to the rotor to maintain their stability. The coordinates of the LEDs on the head rigid body (Fig. 1B) and those associated with the landmarks were determined dynamically using a rigid-body building program (6DARCHITECT, Northern Digital). From this, the coordinates of the headband LEDs were determined with respect to a coordinate frame defined by the landmark LEDs as described in the preceding text. Following the calibration procedure and the determination of the head coordinate frame, the Reid’s plane calibrator was removed, but all movements of the head could be determined relative to space or this coordinate frame.

### Experimental protocol

Subjects were first asked to orient their heads by looking at an array of 49 targets placed 60 cm from the subject. The targets were arranged in accordance with a Fick gimbal projected onto a plane (Fig. 1C). The targets were 10° apart and ranged from $-30°$ to $+30°$ in pitch and yaw. This arrangement was based on the assumption that the head orientation system is close to a Fick gimbal. In later experiments, 25 targets were spaced 15° apart to reduce the experimental time. Subjects viewed the targets through binocular pinhole goggles. The pinholes were aligned so that the head was in the zero position when looking at the central target. This forced the subjects to align their naso-occipital axes ($x$ axis) along their line of sight so that the head was pointed at a given target (Ceylan et al. 2000).

Three paradigms were executed for each of the head orientations. Subjects first fixed their heads by looking at one of the 25 targets for 3 s. These head orientations were represented by a rotation matrix or rotation vector relative to a primary orientation and were referred to as global head positions. Subjects then oscillated their heads for 3 s in yaw in each of these orientations and, on the same or a different occasion, in pitch. These head oscillations were represented by incremental rotations about the given head orientation. Head-oscillation axes were also determined during treadmill locomotion at walking velocities of 0.9, 1.2, 1.5, 1.8, 2.1, and 2.4 m/s while fixating a target at 25 cm. These involuntary head oscillations were also represented by incremental rotations during locomotion. The incremental rotations were the angular velocity vectors at those particular positions. The close viewing distance during locomotion was chosen so that the angular head velocity was maximal, which made computation of rotation axes more robust. In initial experiments, neither the goggles nor the targets were used, and subjects were directed to look into different directions. At each head orientation, they were given verbal feedback on the pitch and yaw coordinates of the head until the head orientation was correct. The data from the initial and subsequent experiments were not different and were combined in the analysis. The equivalence between the initial and subsequent experiments using the pinhole goggles verified that the goggles had produced the appropriate head positions and shortened the experimental time.
Data processing

ANALYSIS OF DATA FOR AXIS OF HEAD ROTATION. Orientations of the head were represented by rotation vectors (Haustein 1989) composed of 300 samples obtained from 3 s of data collection at each position. Using this convention, the relationship between the x (roll) and y-z (pitch-yaw) product was utilized to develop a methodology for determining the gimbal structure associated with the head (see Conceptual and mathematical basis).

RESULTS

General properties of head orientation and oscillations

Figure 2 shows the yaw, pitch, and roll of the head as Euler angles and the character of the voluntary oscillations that were superimposed during the experimental protocol. The process by which the head orientations were achieved is considered in Head orientation in three dimensions. Oscillations of the head in yaw (Fig. 2A, top), were approximately sinusoidal and of constant amplitude in association with changes in head position in yaw (top) and pitch (middle). Roll oscillations increased when the head was positioned in extreme positions in pitch (bottom). Although the roll was on an expanded scale (note ordinate), the finding that the axis of yaw oscillations of the head developed a roll component as the head was pitched, indicates that the yaw axis of the oscillations did not move exactly with the head yaw axis although the deviation was small.

Pitch oscillations, on the other hand, were sinusoidal and of constant amplitude (Fig. 2B, middle) regardless of the yaw or pitch head position (top and bottom), and there was little or no oscillation in yaw when the head was sinusoidally pitched. Thus the axes of rotation in pitch were close to the interaural axis of the head. To determine these axes more precisely, an algorithm was developed that computed the instantaneous axis of the head oscillation in three-dimensional space (see Incremental Head Rotation: Mathematical Basis).

Head orientation in three dimensions

CONCEPTUAL AND MATHEMATICAL BASIS. In general, three parameters are required to describe orientation of a rigid body (Goldstein 1980). Based on the idea that head orientation follows Donders’ law, two parameters are sufficient to describe the surface of head orientation (Ceylan et al. 2000). In a Fick-gimbal system the roll angle of which is zero, the parameterization of the head rotation in space can be given by a

\[
\begin{align*}
\phi &= 15^\circ, \theta = 15^\circ \\
\phi &= 30^\circ, \theta = 15^\circ
\end{align*}
\]

FIG. 3. A: head orientations according to a truncated Fick-gimbal model, i.e., where roll is equal to zero. B and C: for Helmholtz and Listing’s models—simulations of roll (r_x) vs. pitch-yaw product (r_yr_z) components of the rotation vector over a range of simulated head orientations. Plots of roll (r_x) vs. pitch-yaw product (r_yr_z) components of the rotation vector were also generated for a mechanical model of a Fick gimbal. The plots were generated for extension (B) and flexion (C) separately.
rotation about the spatial vertical, followed by a rotation about the rotated pitch axis. The roll component of the axis-angle representation of the head is determined by its pitch and yaw components, forming a two-dimensional surface. Ceylan et al. (2000) utilized a gimbal score to reflect this constraint using a ratio of the quaternion components

\[ s = \frac{q_3}{q_1} \]  

(1)

where \( s \) is the gimbal score and \( q_0, q_1, q_2, q_3 \) are the components of the quaternion representing the rotation (Tweed and Vilis 1987). The gimbal score can be equivalently represented in terms of the components of a rotation vector describing the rotation (Haustein 1989) as

\[ s = \frac{r_z}{r_xr_y} \]  

(2)

where the rotation vector, \( \mathbf{r} \), is directed along the axis of the rotation and has the magnitude of the tangent of half the angle of the rotation (Haustein 1989). This representation allows the value of the gimbal score to be estimated given several orientations of a rigid body by using linear regression on the plots of \( r_z \) versus the product \( r_xr_y \). We demonstrated this model with a mechanical Fick-gimbal system where the roll was zero, i.e., a truncated Fick gimbal, on which an artificial head was mounted (Fig. 3A). The artificial head was positioned in the same orientations as during experiments and the relationship between \( r_z \) versus the product \( r_xr_y \) was plotted (Fig. 3, B and C). For both extension (B) and flexion (C), the regression line had a slope equal to -1 and little variance (Fig. 3, B and C, circles). A similar plot for a Helmoltz gimbal, which is governed by a pitch about a spatial horizontal axis, followed by a rotation about the rotated yaw axis, would give a slope of +1 (Fig. 3, B and C, diamonds). A Listing’s law mechanism, which is a rotation from primary position about axes that lie in a plane would give a slope of 0 (Fig. 3, B and C, squares) because roll is zero.

**K-GIMBAL MODEL.** Although the gimbal score is a measure of how close the system is to a 2 df rotating gimbal system, there is no clear relationship of how the gimbal score reflects the actual rotatory kinematic system. To explore how close the head movement control is to a 2 df system, we generalized the notion of gimbal score and utilized a metric based on a coefficient, \( k \) (k-gimbal model), which reflects the fraction of the angle by which the second axis rotates with respect to the angle of rotation about the first axis. We then determined how close the data were to a k-gimbal model prediction.

For the \( k \)-gimbal model, there are two choices for the first rotation axis, either yaw or pitch as described in the preceding text. Based on the anatomy of the joints between \( C_1 \) and \( C_2 \), and \( C_1 \) and the occipit, we chose the representation, in which the first angle of rotation is about the pitch axis given by \( \theta \). The yaw axis, about which the second rotation takes place, is oriented by a fraction, \( k \), of the pitch angle of rotation. Analytically, the first rotation about the spatial y axis can be given as

\[ R_y(\theta) = \begin{pmatrix} \cos \theta & 0 & \sin \theta \\ 0 & 1 & 0 \\ -\sin \theta & 0 & \cos \theta \end{pmatrix} \]  

(3)

The magnitude of the second rotation is \( \varphi \), and it occurs about an axis that has been rotated by a fraction \( k \) of the first rotation angle, \( \theta \). The unit vector along this axis, \( \hat{\mathbf{a}}_z \), is given by

\[ \hat{\mathbf{a}}_z = R_y(\theta)\hat{\mathbf{a}} \]  

(4)

where \( \hat{\mathbf{a}} \) is a unit vector along the z axis and \( R_y(\theta) \) is given by

\[ R_y(\theta) = \begin{pmatrix} \cos \theta & 0 & \sin \theta \\ 0 & 1 & 0 \\ -\sin \theta & 0 & \cos \theta \end{pmatrix} \]  

(5)

The second rotation about this axis, \( R_z \), can therefore be described by a similarity transformation

\[ R_z = R_y(\theta)R_z(\varphi)R_y(\theta) \]  

(6)

where \( R_z(\varphi) \) is the rotation about the spatial z axis by an angle \( \varphi \). Composing the transformation in (Eqs. 5 and 6), the total transformation, \( R(\theta, \varphi) \) can be given as

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**FIG. 4.** Comparison of amount of roll observed in the data (\( \psi_{\text{data}} \)) with what would be obtained if the head followed the Fick gimbal (\( \psi_{\text{Fick}} \)) or Listing’s Law (\( \psi_{\text{List}} \)) when the head points up-left (A), up-right (B), center (C), down-left (D), and down-right (E). The angles \( \phi \) and \( \theta \) at each of the head orientations are the Fick yaw and pitch angles and their SDs over all trials and subjects. Note that the data (\( \psi_{\text{data}} \)) do not fit either the Fick or the Listing’s law models for all head positions.
It should be noted that if $k = 0$, then $R(\theta, \varphi)$ represents an orientation according to the first two rotations of a Fick gimbal. If $k = 1$, then $R(\theta, \varphi)$ represents a Helmholtz gimbal where the pitch about a spatial horizontal axis is the first rotation. For $k = 0.5$, $R(\theta, \varphi)$ represents a gimbal that satisfies Listing’s law. Thus the $k$-gimbal model is capable of representing a wide range of models.

Equation 7 also gives the following relationship between the roll component of the rotation vector, $r_x$, and the pitch and yaw components of the rotation vector for each head orientation as

$$r_x = r_z \tan \left( \frac{k \theta - \theta}{2} \right)$$

$$r_y = \tan \left( \frac{\theta}{2} \right)$$

Incorporating a possible offset in roll ($r_{x0}$) and combining (Eqs. 8 and 9), the relationship between the rotation axis component, $r_x$ as a function of $r_z$ and $r_y$ is

$$r_x = r_z \tan \left( 2k \tan^{-1} r_y - \tan^{-1} r_z \right)$$

Equation 10 can then be used to fit data on head orientation to determine the $k$ value and the organization of the $k$-gimbal system.

**EXPERIMENTAL RESULTS**

Fick angles, $\theta$, $\phi$, $\psi$ for data obtained from all subjects for head orientations at up-left (Fig. 4A, $\phi = 27.5 \pm 4.0^\circ$; $\theta = -31.8 \pm 5.7^\circ$; $\psi_{\text{data}} = -3.9 \pm 5.7^\circ$), up-right (Fig. 4B, $\phi = -29.5 \pm 3.8^\circ$; $\theta = -32.3 \pm 4.5^\circ$; $\psi_{\text{data}} = 3.1 \pm 5.1^\circ$), center (Fig. 4C, $\phi = -1.1 \pm 2.9^\circ$; $\theta = -4.0 \pm 4.9^\circ$; $\psi_{\text{data}} = -1.5 \pm 2.2^\circ$), down-left (Fig. 4D, $\phi = 28.2 \pm 3.8^\circ$; $\theta = 25.9 \pm 4.5^\circ$; $\psi_{\text{data}} = 1.1 \pm 5.0^\circ$), and down-right (Fig. 4E, $\phi = -31.3 \pm 3.0^\circ$; $\theta = 26.8 \pm 4.2^\circ$; $\psi_{\text{data}} = -3.6 \pm 4.6^\circ$) had substantial roll components at the tertiary positions. This did not match the predictions of the truncated Fick-gimbal model at any head orientation (Fig. 4, A–E, $\psi_{\text{Fick}} = 0$). The head orientations also

![Graphs showing linear regressions of roll ($r_x$) vs. pitch-yaw product ($r_y r_z$) for subjects CC (A and D), MK (B and E), and YO (C and F) computed in extension (A–C) and flexion (D–F). Due to coordinate misalignment in pitch, the regression lines were obtained separately for each yaw orientation.](http://jn.physiology.org/)

**FIG. 5.** Linear regressions of roll ($r_x$) vs. pitch-yaw product ($r_y r_z$) for subjects CC (A and D), MK (B and E), and YO (C and F) computed in extension (A–C) and flexion (D–F). Due to coordinate misalignment in pitch, the regression lines were obtained separately for each yaw orientation.
did not obey Listing’s law (Fig. 4, A–E, \( \psi_{\text{List}} = -8.0^\circ; \psi_{\text{List}} = 8.7^\circ; \psi_{\text{List}} = 0.0^\circ; \psi_{\text{List}} = 6.6^\circ; \psi_{\text{List}} = -7.6^\circ \)).

We next considered whether Eq. 10, i.e., the \( k \)-gimbal model, was capable of fitting these experimental data. We found \( k \) by obtaining the best fit to the data from the orientations of the head for each subject using the simplex method for nonlinear optimization (Matlab 7.0, Mathworks). Orientations corresponding to flexion and extension were fitted separately, and different \( k \) values were obtained. As a basis of comparison, we also estimated the gimbal score, \( s \), by fitting a line through the \( x \) component of the rotation vector versus the product of \( y \) and \( z \) components as described above. Using Eqs. 8 and 9, the relationship between gimbal score and parameter \( k \) was approximately linear, given by

\[
k = \frac{s + 1}{2}
\]  

(11)

We also estimated the value of \( k \) by first finding the gimbal score and then using Eq. 11. This approach gave the same results but had significantly better computational efficiency.

When data for different yaw (\( \phi \)) components of the head rotation were considered, the amount of roll was different for complementary head orientations during flexion and extension and so the two were analyzed separately. Figure 5 shows a plot of \( r_x \) versus the product of \( r_y * r_z \), which can be compared with the idealized plots of Fig. 3. The different colors correspond to data taken in different yaw orientations of the head. The circles represent the actual data and the lines are the linear regressions associated with the data for each yaw head position. For head extension (Fig. 5, A–C), the averaged data over three trials for three typical subjects had a declining roll component, \( r_x \), as a function of the pitch-yaw product, \( r_y * r_z \), for head yaw ranging from –30 to 30°. The linear regression lines representing the gimbal scores for each yaw head position had similar negative slopes for extension (Fig. 5, A–C) and flexion (Fig. 5, D–F).

The coefficient \( k \) for three of the subjects with five or more repeated trials were (mk-flexion: 0.26 \( \pm \) 0.09; mk-extension: 0.17 \( \pm \) 0.08; tr-flexion: 0.16 \( \pm \) 0.08; tr-extension: 0.21 \( \pm \) 0.06; yo-flexion: 0.27 \( \pm \) 0.04; yo-extension: 0.17 \( \pm \) 0.08). The coefficient \( k \) for extension over all subjects was 0.17 \( \pm \) 0.08.

Similar behavior was observed during flexion, with an
average $k$ over all subjects having a value of $0.22 \pm 0.10$. The $k$ values for flexion and extension were significantly different (matched $t$-test, $P > 0.05$), although the difference was small.

Thus the $k$-gimbal model suggests that voluntary head orientations are achieved not by Fick, Listing, or Helmholtz gimbal systems (Ceylan et al. 2000) but rather by a gimbal system that is tied to fractional changes in axis orientation as the head is moved into different orientations. The value of $k = 0.2$, shows that the head rotates as a gimbal where the first rotation axis is about pitch, and the second axis is 20% of the angle of pitch rotation. This behavior is probably not only related to the articulation of the head on the spinal column but to varying involvement of lower portions of the cervical spinal column during pitch and yaw movements in different head orientations (see Implementation of k-gimbal model).

**Incremental head rotations in three dimensions**

**Mathematical basis.** To determine the incremental axes of head rotation during oscillation, we developed a methodology for filtering movements of the head displacements using twists and exponential coordinates (Murray et al. 1994). Let $D_{-n}, D_{-n+1}, \ldots, D_{\phi}, \ldots, D_{n-1}, D_n$ be a sequence of displacements given in a spatial coordinate frame, sampled from a small portion of the rigid body trajectory. We will assume that the sampled trajectory is “smooth” so that incremental displacements between, $D_k$ and $D_{k+1}$, could be approximated by a single incremental displacement matrix $e^\Xi$, obtained from the twist $\Xi$ for $k$ ranging from $-n$ to $n-1$. This allowed us to define a matrix $B$ over the window $-n, \ldots, 0, \ldots, n$, relative to the spatial frame of reference, such that each $D_k$ could be obtained as this incremental displacement from $B$

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**Fig. 7.** A: pictorial representation of the angle between the incremental axis of rotation ($\omega$) and the yaw axis of the head ($z$). When the head is pitched forward by an angle $\alpha_1$ relative to the upright (Red $z$ re $z_s$), the angle is $\phi_1$. When the head is pitched back by an angle $\alpha_2$ relative to the upright (Black $z$ re $z_s$), the angle is $\phi_2$. B–E: for each of 3 subjects and all subjects combined, there was a linear decline in angle between the incremental axis of rotation and the head yaw. In all instances, the incremental axis of rotation was close to the head yaw axis.
The incremental displacement, \( \Delta_k = D_k D_{k-1}^{-1} \), could then be approximated as

\[
\Delta_k \approx e^{\Xi B} (e^{\Xi B})^{-1} = e^{\Xi B} B (e^{\Xi B})^{-1} = e^{\Xi B}
\]

and

\[
\Delta_k \approx e^{2\Xi B}
\]

independent of \( B \). To find the matrix, \( \Xi \), that gives the “best” approximation over the range of displacement matrices, \( D_{-n}, D_{-n+1}, \ldots, D_0, \ldots, D_{n-1}, D_n \), we utilized a procedure that is similar to minimizing the mean squared error for one-dimensional data. The value of the displacement matrix at some sample, \( D_k \), can be multiplied by the inverse of the predicted displacement, \( (e^{\Xi B})^{-1} \). If the data were predicted perfectly by the approximation, then the matrix multiplication should be the identity transformation, \( I \). Therefore an appropriate error at each sample displacement is the norm of the difference between the matrix product \( D_k (e^{\Xi B})^{-1} \) and the identity matrix \( I \).

Thus the total error, \( E \), can be defined as

\[
E = \sum_{i=1}^{n} \left\| D_i (e^{\Xi B})^{-1} - I \right\|^2
\]

where we choose \( \| \cdot \| \), as the quadratic norm for matrices (Blum 1972; Press et al. 1992). The matrices \( \Xi \) and \( B \) that minimize \( E \) can then be determined.

A straightforward minimization procedure for finding \( B \) and \( \Xi \) would involve utilization of nonlinear optimization techniques (Press et al. 1992). The minimization procedure was simplified, however, by minimizing the residual norm (Blum 1972) for the incremental displacement, \( \Delta_k \), which has the effect of eliminating the matrix \( B \) from the minimization procedure and is given as follows

\[
E = \sum_{i=1}^{n} \left\| \Delta_i (e^{2\Xi B})^{-1} - I \right\|^2 \rightarrow \min
\]

Because each \( \Delta_k \) is a displacement in its own right, it is generated by some twist, which is a function of \( \Delta_k \), denoted by \( \Xi(\Delta_k) \). Thus instead of minimizing Eq. 16, we can minimize the function \( T \), given by

\[
T = \sum_{i=1}^{n} \left\| \Xi(\Delta_i) - 2k \Xi \right\|^2
\]

FIG. 8. A: roll, pitch and yaw components of angular head velocity during voluntary head oscillation in pitch. B–E: distribution of instantaneous rotation axes in the pitch (x-z) plane while looking at the center (B), up-right (C), up-left (D), and down-right (E). Data were obtained from a representative subject (MK).
The optimal estimate of $\Xi$ in the least squares sense can be given as follows (Kunin 2004)

$$\Xi = \frac{3}{n(n + 1)(2n + 1)} \sum_{i=1}^{n} \Xi(\Delta_i)$$  \hspace{1cm} (18)

The original sum of the differences over the window given by

$$E = \sum_{i=1}^{n} \left[ \Delta(e^{2\Xi})^{-1} - I \right]$$  \hspace{1cm} (19)

can serve as a measure of the goodness of fit. The smaller the value of $E$, the better the fit. Obtained in this way, the optimal twist estimate, $\Xi$, yields both the angular velocity estimate $\omega$, and pivot point estimate, $q_0$, which can be given as

$$q_0 = \omega \times v$$  \hspace{1cm} (20)

where $v$ is the differential translation part of the twist. This point in three-dimensional space $q_0$, is a point on the rotational axis corresponding to the incremental displacement, $e^\Xi$.

**VOLUNTARY HEAD OSCILLATION.** For yaw head movements, the angular velocity, $\omega$, in head coordinates, oscillated approximately sinusoidally and was maintained close to the yaw axis, with a small roll and still smaller pitch components (Fig. 6A). The point of intersection of the axes with the yaw ($x$-$y$) plane was close to the origin of the head coordinate frame when the head was directed at the center target (Fig. 6B). The zoomed inset shows the compactness of the data values. There were small variations of the point of intersection of the axes as the head was moved from center (Fig. 6B, $x = -5.4$ mm, $y = -0.1$ mm) to up-right (Fig. 6C, $x = -8.1$ mm, $y = 4.1$ mm), up-left (Fig. 6D, $x = -11.7$ mm, $y = -0.6$ mm), and down-right (Fig. 6E, $x = -18.5$ mm, $y = 0.7$ mm). The concentration of points close to a single axis is shown by the dense color in each of these four positions. A principal component analysis of the distribution of the intersection points indicated that the ellipse of the variance had a maximum singular value of 21.62 mm (Fig. 6C, up-right) and an eccentricity of 2 (variance of data points along $x$ being twice that along $y$) with the major axis close to the naso-occipital axis. Over all subjects and trials, however, the location of the intersection point was not correlated with head orientation in any direction in 12 of the 15 experiments. This indicates, there was no consistent correlation between intersection point and head orientation, and that the pivot point of the rotation was within 40 mm of the interaural axis in the mid-sagittal plane.

The average vector along the axis of head oscillation over all head orientations and all subjects was $(0.27, 0.0, 0.96)$ in head coordinates, which was within $16^\circ$ of the $z$ axis of the head 

$$(z = 0.96) \text{ (Fig. 7A). There was a substantial } x \text{ component (} x = 0.27\text{), indicating that the } z \text{-axis oscillation was tilted forward relative to the stereotaxic vertical. When the head was upright, the yaw axis of the head was along } z \text{, and the velocity axis was along } \omega \text{ (Fig. 7A). When the head was pitched forward, the yaw axis of the head was along } z \text{, and the velocity axis was along } \omega \text{. The general finding was that the angle between the velocity vector along the head oscillation axis, } \omega, \text{ and the } z \text{ axis of the head decreased with head pitch forward and increased with head pitch back (Fig. 7, B–D). When the angle at } 0^\circ \text{ of head tilt was equalized across all subjects, there was a linear relationship between head pitch and change in oscillation axis with small SD (} \sigma = 3.7^2; \text{ Fig. 7E). Of note, when the head was tilted forward or back, the axis of yaw oscillation was tilted less than the pitch angle of the head. This difference was small, and did not conform to predications of the } k \text{-gimbals model, which governed static head orientations. Thus there must be transient effects during dynamic head oscillations that tend to bring the axis of rotation closer to the head yaw axis than would be predicted from the } k \text{-gimbals model.}

Pitch oscillation of the head had almost no roll or yaw components (Fig. 8A). The points of intersection of the pitch axes with the pitch plane had an eccentric distribution that was more elongated than the distribution of the intersection of the yaw oscillation axis in the yaw plane (Fig. 6, B–E). The average intersection points during pitch oscillation also deviated to a greater extent from the origin of the head coordinate frame (Fig. 8B, $x = -21.6$, $z = -15.8$) to up-right (Fig. 8C, $x = -10.5$, $z = 1.0$), bottom-right (Fig. 8D, $x = -32.6$, $z = -27.1$), and up-left (Fig. 8E, $x = -36.4$, $z = -30.6$) than during yaw oscillation. The average point of intersection of the instantaneous pitch axis with the pitch plane of the head was
~22 mm behind the interaural axis and 16 mm below the origin of the head coordinate frame. The average $x$ coordinates of the point of intersection of the pitch oscillation axis with the pitch plane was negatively correlated with the angle of pitch of the head in individual subjects (Fig. 9, A–C). The data for all subjects was normalized by setting pivot $x$ (Fig. 9, A–C) for each subject’s regression line to zero. When this was done, the $x$ coordinate of the pivot point declined linearly with small SD ($\sigma = 7.6$ mm; Fig. 9D). That is, as the head pitched down, the intersection was further back in head coordinates along the naso-occipital axis (Fig. 9). The average vector along the axis of head oscillation over all head orientations and all subjects was (0, 1.0, 0) in head coordinates, supporting the conclusion that the pitch axis in head coordinates was unaffected by any head position or dynamics.

HEAD OSCILLATION DURING LOCOMOTION. Treadmill walking at 1.5 m/s, while wearing the pinhole goggles and fixating a target at 25 cm, generated roll and yaw oscillations of the head at the stride frequency and pitch oscillations related to the step frequency (Hirasaki et al. 1999; Moore et al. 1999; Raphan et al. 2001). The head also translated vertically and horizontally (Hirasaki et al. 1999). There was greater variation in the oscillation amplitude and frequency, probably due to the presence of the pinhole goggles. The latter were used, however, to equalize the locomotor conditions to those during head oscillation. Walking without the goggles was also done to provide further comparison with natural locomotion.

The intersection point of the pitch axes while walking with the goggles and fixating at 25 cm (Fig. 10B, $x = -20$ mm, $z = -147$ mm) was considerably lower than during voluntary head oscillation with goggles (Fig. 9). The point of intersection was altered somewhat when walking slower at 0.9 m/s (Fig. 10C, $x = -42$ mm, $z = -123$ mm), but was still much lower along the $z$ axis than during voluntary head oscillation. When walking at 1.5 m/s and viewing a target at 25 cm without goggles, the intersection point was consistent with walking with goggles and at slower walking velocities (Fig. 10D, $x = -36$ mm, $z = -130$ mm). Fixating a target without goggles at 1 m while walking generated an intersection point that was similar to the other conditions (Fig. 10E, $x = -28$ mm, $z = -123$ mm). The average intersection point over all subjects was ($x = -30$ mm, $z = -149$ mm). The average vector along the axis of head...
oscillation for all subjects was (0.116, 0.990, −0.073) in head coordinates, showing that the dominant direction of the axis about which the head rotates was aligned with the pitch axis of the head. There was no correlation among the walking velocity, viewing conditions, direction of the average axis of head rotation, and the location of the point about which the head rotated. Thus during locomotion the pitch axis of the head was aligned with the interaural axis and was lower on the spinal column than when pitching the head voluntarily.

**Implementation of the k-gimbal model for head rotation**

One realization for the k-gimbal model that is responsible for rotating the head would be to have a pitch rotation axis superimposed on a Fick-gimbal system as shown in Fig. 11A. This is consistent with how the head interfaces with the dens, occipital condyles, and the lower spinal column. Let \( \theta_1 \) be the angle of pitch rotation of the lower joint (Fig. 11B), \( \theta_2 \) the pitch angle of the head rotation about the upper joint, and \( \phi \) the yaw angle of the head rotation. The equations governing the rotations can be given as follows

\[
\begin{align*}
\theta_1 + \theta_2 &= \theta \\
\theta_1 &= k \theta \\
R(\theta_1, \phi, \theta_2) &= R_y(\theta)(R_y(\phi)R_z((1-k)\theta)) = R_y(\theta_1)R_y(\phi)R_z(\theta_2)
\end{align*}
\]

(21)

(22)

where Eq. 22 is equivalent to Eq. 7.

**FIG. 11.** A: model of the k-gimbal implementation. The upper pitch and yaw rotation implements a Fick gimbal. The addition of the pitch rotation below the Fick gimbal implements the k-gimbal system. B: angular orientations, \( \theta_2 \), \( \phi \), and \( \theta_1 \) associated with the k-gimbal orientation. See text for full description.

**DISCUSSION**

This study demonstrates that the rotation axes for positioning the head from a primary position follow a simple “k-gimbal model.” The k-gimbal can be implemented by a sequence of two pitch joints with an interposed yaw joint (Fig. 11). The upper axes for this structure implement a two-dimensional Fick gimbal the movements of which are in pitch and yaw. The k-gimbal realization arises due to the linkage of the upper pitch and yaw joints to the chain of cervical vertebrae that implement the lower pitch axis. We also developed a mathematical methodology to determine incremental head rotation axes in three dimensions using displacement matrices (Kunin 2004; Kunin et al. 2006a,b). Using this methodology, which filters the translations and rotation in three dimensions, it was possible to obtain instantaneous axes of rotation as a function of time. From this, we were able to show that voluntary head oscillations about static head positions in pitch and yaw, and oscillations during locomotion had velocities that were not aligned with the axes of the k-gimbal. Rather, consistent with findings of others (Medendorp et al. 1998), the pitch and yaw incremental rotation axes were more closely aligned with the pitch and yaw axes of the head, regardless of head orientation. Moreover, the pivot points about which the head rotated were different for the different head rotations. Thus the model of head rotation axes developed from this study links the skeletal geometry to the constraints of Donders’ law during voluntary head positioning and also explains the consequences of head perturbations that occur during natural movement.

The finding that the points of intersection of the incremental pitch rotation axes during voluntary head oscillations were close to the origin of the head coordinate frame is consistent with previous suggestions that head movements are essentially aligned with the axes determined by vertebra and joints from \( C_2 \) and above (Dutia 1991; Richmond and Vidal 1988; Vidal et al. 1988). The finding that incremental rotations of the head during locomotion were significantly lower than \( C_2 \) supports the idea that the lower vertebrae play a more significant role in moving the head during locomotion than during voluntary head rotations and may be a result of the fore-aft movement of the body during locomotion. Engaging many levels of vertebral motion during locomotion would increase the radius of curvature of head rotation in space and could give the head movement controller more flexibility in maintaining heading (forward gaze) and aligning the head yaw axis with the spatial vertical. Maintenance of invariant yaw and roll in space would provide a stable platform for the visual system to process information during locomotion.

The different coordinate schema for global and voluntary incremental rotation axes may be related to the functions of the different types of head-positioning maneuvers. During global positioning, the head must be oriented relative to space so that the eyes can be positioned for generating gaze without requiring ocular compensatory mechanisms. Incremental rotations, on the other hand, are more apt to occur during perturbations of the head, which activate the vestibular apparatus to induce compensatory eye movements. The gain of the aVOR is maximal for yaw and pitch, being close to 1.0, and is only −0.6 for roll (Henn 1988; Tweed et al. 1994). By maintaining the axes of voluntary incremental head rotations close to the pitch and yaw axes of the head, optimal ocular compensation...
could be maintained during incremental head movement, regardless of where one pointed the head during the movement without necessitating active roll compensation. This implies that incremental rotations that occur during voluntary head oscillations and during locomotion are governed by other factors, such as dynamic muscle action, that alter the axes of head rotation in relation to the k-gimbal axes, which are more spatially oriented.

Although it has been widely postulated that rotations of the head are in accordance with the skeletal geometry of the vertebra (Dutia 1989, 1991; Richmond and Vidal 1988; Vidal et al. 1986, 1988), more recent investigations have suggested a neuro-muscular basis for head-positioning geometry (Ceylan et al. 2000; Radau et al. 1994). Based on differences of orientation observed when subjects were asked to direct the head toward targets with and without monocular pin-hole goggles, it was suggested that there is a transformation from Fick-like to Listing-like behavior (Ceylan et al. 2000). Our data showed no difference in the distribution of head pointing with and without goggles, however (Fig. 5), and the k-gimbal value of $k \approx 0.22$ that we obtained was equivalent to the gimbal score of $s = 0.6$ found by Ceylan et al. (2000) for comparable sized head movements. Thus the differences between wearing and not wearing goggles in the Ceylan et al. (2000) study may be attributed to the different-sized head movements for the two conditions as well as to an increase in the torsional thickness of the Donders’ surface associated with larger head movements (Ceylan et al. 2000).

An appealing aspect of the generalized k-gimbal is that it can be directly related to anatomical structures of the head and neck. In the model, global head positioning is essentially governed by a Fick gimbal, implemented anatomically by the joints of head positioning control at and above the level of C2 (Fig. 11). These include the occipital condyles that link C1 to the skull, producing pitch. Yaw rotation of the head is produced by rotation of C1 about the dens, the protruberent pivot points and axes of rotation, head position would be naturally governed by a Donders’ surface not by a Listing’s plane. The natural spinal structures may also explain why Donders’ law for head movement is obeyed even when muscle stiffness caused by spasmotic torticollis compromises head orientation (Medendorp et al. 1999) and eye-head coordination (Maurer et al. 2001).

There is a considerable literature on the physiology governing head movements (Freedman and Sparks 1997; Freedman et al. 1996; Harris 1980; Isa and Sasaki 2002; Roucoux and Guittion 1980; Wilson and Melvill-Jones 1979). However, the neural control mechanisms that govern head movements, especially in three dimensions, are not well known, and only recently have been studied in the primate (Crawford et al. 2003; Isa and Sasaki 2002; Klier et al. 2001, 2002a,b). The midbrain interstitial nucleus of Cajal (INC) functions as a neural integrator for holding head orientation (Klier et al. 2001), just as the neural velocity-position integrator encodes eye orientation during eye movements (Robinson 1971; 1968). Driving these integrators, the superior colliculus encodes gaze commands in retinal coordinates (Klier et al. 2001). If the superior colliculus encodes gaze shifts as a two-dimensional rotational command, then the vectorial command must be separated downstream in the brain stem to hold the head and eyes in a particular orientation. The knowledge that the head movements are coded according to the k-gimbal model, as determined in this study, would therefore be important for defining the neural signals that determine head trajectory and for understanding how the head velocity-position integrator activates the neck muscles in maintaining the final head orientation.

ACKNOWLEDGMENTS

We thank L. Tundis of the Brooklyn College Machine Shop for fabricating the calibration device, pinhole goggles, and the target array that were utilized in this study.

GRANTS

This work was supported by National Institute of Deafness and Other Communications Disorders Grants DC-05222 and DC-05204.

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