

Instantaneous rotation axes during active head movements

Steven T. Moore^{a,*}, Eishi Hirasaki^{a,b}, Theodore Raphan^c and Bernard Cohen^a

^a*Department of Neurology, Mount Sinai School of Medicine, New York, NY, USA*

^b*Laboratory of Biological Anthropology, Osaka University, Osaka, Japan*

^c*Department of Computer and Information Science, Brooklyn College, Brooklyn, NY, USA*

Received 21 June 2004

Accepted 9 November 2004

Abstract. Rotation axes were calculated during active head movements using a motion analysis system. The mean rotation axis for 1 Hz head pitch when seated was posterior (6 mm) and inferior (21 mm) to the interaural axis, shifting 16 mm downwards when standing. During seated 2 Hz head pitch the rotation axis was close to the interaural axis, shifting downwards 15 mm when standing. This downward shift suggests that cervical vertebrae were recruited during head pitch with the trunk unsupported. The proximity of the pitch axis to the otoliths implies minimal otolith activation during small-amplitude, high-frequency pitch rotations, such as those encountered during locomotion. The mean rotation axis for 1 Hz yaw rotation was located slightly posterior (10 mm) to the interaural axis at the midpoint between the vestibular labyrinths when both seated and standing. In addition, the orientation of the plane of yaw rotation relative to the stereotaxic horizontal plane (pitched 5° nose-down) was essentially fixed in head coordinates, regardless of the pitch orientation of the head, suggesting that yaw movements occur about an axis restricted by the mechanical structure of the atlanto-axial joint. The results demonstrate that the instantaneous rotation axes technique overcomes the inherent instability of the helical-axis representation for small head movements.

Keywords: Rotation axis, head rotation, locomotion, VOR, otoliths

1. Introduction

During natural activities, such as active gaze shifts and walking, there are small rotations of the head on the trunk [3,4,6]. These head rotations involve up to seven cervical vertebrae, and the location of the axis of head rotation is not obvious. This information is necessary, however, for a full understanding of the activation of the vestibular labyrinths during natural head movements. The location of the head rotation axis relative to the eyes is a factor in determining the required gain of the angular vestibulo-ocular reflex (VOR), particularly for near visual targets. In addition, during high-frequency

head rotation, the otoliths are subject to both a tangential and centripetal linear acceleration proportional to the radial distance from the otoliths to the axis of head rotation.

Axes of head rotation have been estimated using a helical axis representation of the head/neck complex [8–12], most recently by Medendorp et al. [5]. The latter study calculated head rotation axes utilizing a helical axis representation of head position in space, which modeled head movement as a rotation about and a translation along a unique space-fixed axis. The axis of head rotation for a given head movement was determined as the axis where the translational component was minimized. Rotation axes were determined for low frequency (estimated to be 0.2 Hz), large amplitude (up to 40°) head movements with the trunk fixed. For yaw head movements these axes were clustered around the midpoint between the two vestibular labyrinths, and for

*Corresponding author: Steven Moore Ph.D., Mount Sinai School of Medicine, Department of Neurology, Box 1135, 1 E 100th St., New York NY 10029, USA. Tel.: +1 212 241 9306; Fax: +1 212 831 1610; E-mail: steven.moore@mssm.edu.

pitch head movements the axes were located below the interaural axis on a circle within the sagittal plane of approximately 20–40 mm diameter [5].

The helical axis technique [5,8–12] is unstable when the angle of head movement is small, and in practice is only reliable for head rotation greater than 6° [5]. Furthermore, rotation axes calculated from head movements with the trunk fixed may not be representative of natural head-on-body movements. The purpose of this study was to develop a technique for calculation of instantaneous rotation axes during trunk-free, small amplitude, high-frequency head movements, such as those encountered during locomotion [3,4,6]. In this paper we provide data on the location of the rotation axes of the head during active high-frequency pitch (1–2 Hz) and yaw (1 Hz) head rotations when sitting and standing. In addition, an analysis of the relative orientation of the stereotaxic horizontal plane and the plane of yaw rotation during head yaw with the neck statically flexed or extended is presented.

2. Methods

Five subjects (three males and two females) with normal vestibular and head/neck function participated in this experiment. The study was performed in accordance with the ethical standards of the 1964 Declaration of Helsinki and informed consent was obtained from all subjects. Subject age ranged from 26 to 32 years (mean 29.2), and height from 1.55 to 1.8 m (mean 1.69). Subjects were asked to perform active head pitch and yaw rotations in time with a digital metronome at a frequency of 1 Hz. Four subjects (two male, two female) also performed head pitch at 2 Hz (one subject was unable to perform this task). Subjects were positioned 2 m from a blank wall and adopted a natural posture. Subjects were instructed to perform ‘small’ and ‘large’ head rotations for 10 s, with 3 trials being performed for each condition. The actual amplitudes of these movements were self-determined, but were consistent across the five subjects (see Results). Head movements were performed when seated (with the trunk supported) and while standing. In addition, two subjects were asked to perform yaw head rotations at 1 Hz with the head held in three different pitch orientations: 1) upright (normal standing posture), 2) head pitched downward (nose-down) and 3) pitched upwards (nose-up).

2.1. Measurement apparatus

Head and trunk movements were recorded using a video motion analysis system (Optotrak 3020, Northern Digital, Ontario Canada) at a sampling rate of 150 Hz. The sensor tracked the three-dimensional (3D) position of 10 active infra-red (IR) markers attached to a lightweight (120 g) headband, and 5 IR markers attached to a small plate (30 g) taped securely to the skin of the subject’s back between the scapulae at the level of the 3rd thoracic vertebra (T3). The raw position data of these markers were used to form rigid body models of the head and trunk. A marker was also placed on the back of the neck at the level of the seventh cervical vertebra (C7). The 3D coordinates of the left and right orbitale,¹ and the left and right tragon,² relative to the head-rigid-body were determined using a digitizing probe (Northern Digital, Ontario Canada). For a complete description of the motion analysis techniques used in this study see [3,4,6].

2.2. Measurement coordinate system

A right-handed space-fixed coordinate frame $\{X_S, Y_S, Z_S\}$ was defined with the positive X_S (‘Earth horizontal’) axis parallel to the forward-facing direction of the subject and normal to gravitational vertical. The Y_S -axis was positive to the subject’s left and the positive Z_S -axis upward vertical. A head-fixed coordinate frame $\{X_H, Y_H, Z_H\}$ was defined using the four head landmarks (left and right orbitale and tragon), which lay in the stereotaxic horizontal ($X_H - Y_H$) plane, with the interaural (Y_H) axis passing through the left and right tragon (positive to the subject’s left). The naso-occipital (X_H) axis was positive forward, and the Z_H axis was normal to the $X_H - Y_H$ plane (positive upwards). The origin of the head-fixed frame was located on the interaural axis at a point midway between the left and right tragon. A trunk-fixed coordinate frame $\{X_T, Y_T, Z_T\}$ was defined as X_T parallel to the dorsoventral axis (positive forward), Y_T parallel to the transverse axis (positive to the subject’s left), and Z_T normal to the $X_T - Y_T$ plane (positive upwards). The center IR marker of the trunk-rigid-body was defined as the origin of the trunk-fixed frame. Calibration data was acquired with the subject seated and assuming a natural posture while looking straight ahead, which was

¹The inferior point of the lower margin of the orbit.

²A point in the depth of the notch just above the tragus of the ear.

defined as the reference position. Similarly, calibration was performed when standing in a natural posture and looking straight ahead. Rotation of the head-rigid-body in space was represented as Euler angles relative to the orientation of the head-fixed coordinate frame when in the reference position, using a Fick sequence (see [6] – yaw left and pitch down positive). Translation of the origin of the head-rigid-body in space was also measured relative to the reference position of the head. Trunk rotation and translation in space were measured relative to the trunk reference position in an analogous manner. Head movement was also calculated in the trunk-fixed coordinate frame from the head and trunk movement in space.

2.3. Data processing

Translation and rotation of the head-rigid-body were calculated in both 3D space- and trunk-fixed coordinates, and filtered with a 3-point median filter followed by a 5-point moving average filter with a bandwidth of 10 Hz [3,6]. The head rotation data were converted to axis-angle form ($\Phi\hat{n}$) in trunk coordinates, where Φ is the angle of rotation about an axis aligned with the unit vector $\hat{n} = (n_1, n_2, n_3)$, and n_1, n_2, n_3 are the direction cosines along the X_T, Y_T, Z_T axes, respectively. In this study the assumption was made that head rotation was confined to a plane [5], with the axis of rotation normal to the plane of rotation. Head movements were largely confined to the sagittal ($X_T - Z_T$) trunk plane during active head pitch (Fig. 1 A,B), and the axis of rotation was n_2 . For head yaw, the plane of rotation was typically pitched up or down relative to the trunk horizontal ($X_T - Y_T$) plane by up to 10° . The normal to this plane, $\hat{n} = [\alpha n_1 + \beta n_3]$, was calculated from a planar least mean squares error fit to the 3D coordinates of the left and right tragon in trunk coordinates from a 10 s data trial. The pitch (γ) of the plane of yaw rotation relative to trunk horizontal was given by $\arctan(\alpha/\beta)$. Although \hat{n} represents the orientation of the head rotation axis, the unique spatial location of \hat{n} at a given point in time, which we term the *instantaneous rotation axis*, is not known and must be calculated from the head position data in trunk coordinates as follows.

Head position was represented as a homogeneous transformation [7] in the form of a displacement matrix \mathbf{D} . \mathbf{D} contains information on both the rotation (Φ) about, and translation of, the origin of the head-rigid-body in the plane of rotation. For pitch rotation, \mathbf{D} is given as,

$$\mathbf{D} = \begin{bmatrix} \cos \Phi & \sin \Phi & x \\ -\sin \Phi & \cos \Phi & z \\ 0 & 0 & 1 \end{bmatrix} \quad (1)$$

where $\hat{n} = n_2$, and (x, z) is the location of the origin of the head-rigid-body in the sagittal trunk ($X_T - Z_T$) plane. (For yaw rotation, the translation components are replaced by (x', y') , which are the coordinates of the origin of the head-rigid-body in the plane defined by $\hat{n} = [\alpha n_1 + \beta n_3]$). The incremental movement of the head ($\mathbf{D}_{\Delta t}$) from time t to $t + \Delta t$ (where Δt is 1/150 s) is related to the displacement of the head at time t (\mathbf{D}_t) and $t + \Delta t$ ($\mathbf{D}_{t+\Delta t}$) by

$$\mathbf{D}_{t+\Delta t} = \mathbf{D}_t \cdot \mathbf{D}_{\Delta t}, \quad (2)$$

and can be calculated from the head position at time t and $t + \Delta t$ as follows.

$$\mathbf{D}_{\Delta t} = \mathbf{D}_t^{-1} \cdot \mathbf{D}_{t+\Delta t} \quad (3)$$

If Δt is small, the movement of the head is close to a pure rotation about an instantaneous rotation axis parallel to \hat{n} , which passes through a fixed point in space. The intersection of this axis with the plane of rotation in trunk coordinates, denoted (x_r, z_r) for head pitch ((x'_r, y'_r) for yaw rotation), is determined from the eigenvector of $\mathbf{D}_{\Delta t}$.

$$\begin{bmatrix} d_{11} & d_{12} & d_{13} \\ d_{21} & d_{22} & d_{23} \\ 0 & 0 & 1 \end{bmatrix} \cdot \begin{bmatrix} x_r \\ z_r \\ 1 \end{bmatrix} = \lambda \begin{bmatrix} x_r \\ z_r \\ 1 \end{bmatrix} \quad (4)$$

where d_{ij} is the element of $\mathbf{D}_{\Delta t}$ in the i th row and j th column. Note that the eigenvector is an augmented vector, with the third component defined to be 1 [7]. The component d_{33} represents a scaling factor that we have set to 1, and therefore the eigenvalue λ must equal 1. It is now possible to derive an analytical solution to the intersection of the instantaneous rotation axis (x_r, z_r) with the trunk sagittal ($X_T - Z_T$) plane.

$$\begin{bmatrix} x_r \\ z_r \end{bmatrix} = \begin{bmatrix} \frac{-d_{23} - z_r(d_{22}-1)}{d_{21}} \\ \frac{d_{21}d_{13} - d_{23}(d_{11}-1)}{d_{11}(d_{22}-1) - d_{22} - d_{21}d_{12} + 1} \end{bmatrix} \quad (5)$$

It is not possible to calculate instantaneous rotation axes when the angular velocity of the head is zero. Thus, axes were not calculated 33 ms either side of a peak or valley in the head angular position (Fig. 1C). The mean rotation axis was defined as the mean and standard deviation (SD) of the instantaneous rotation axis components for a 10 s trial. The SD provided a measure of the spatial spread of the axes. For yaw rotations the computed values of (x'_r, y'_r) were projected onto the trunk horizontal plane ($X_T - Y_T$) by dividing

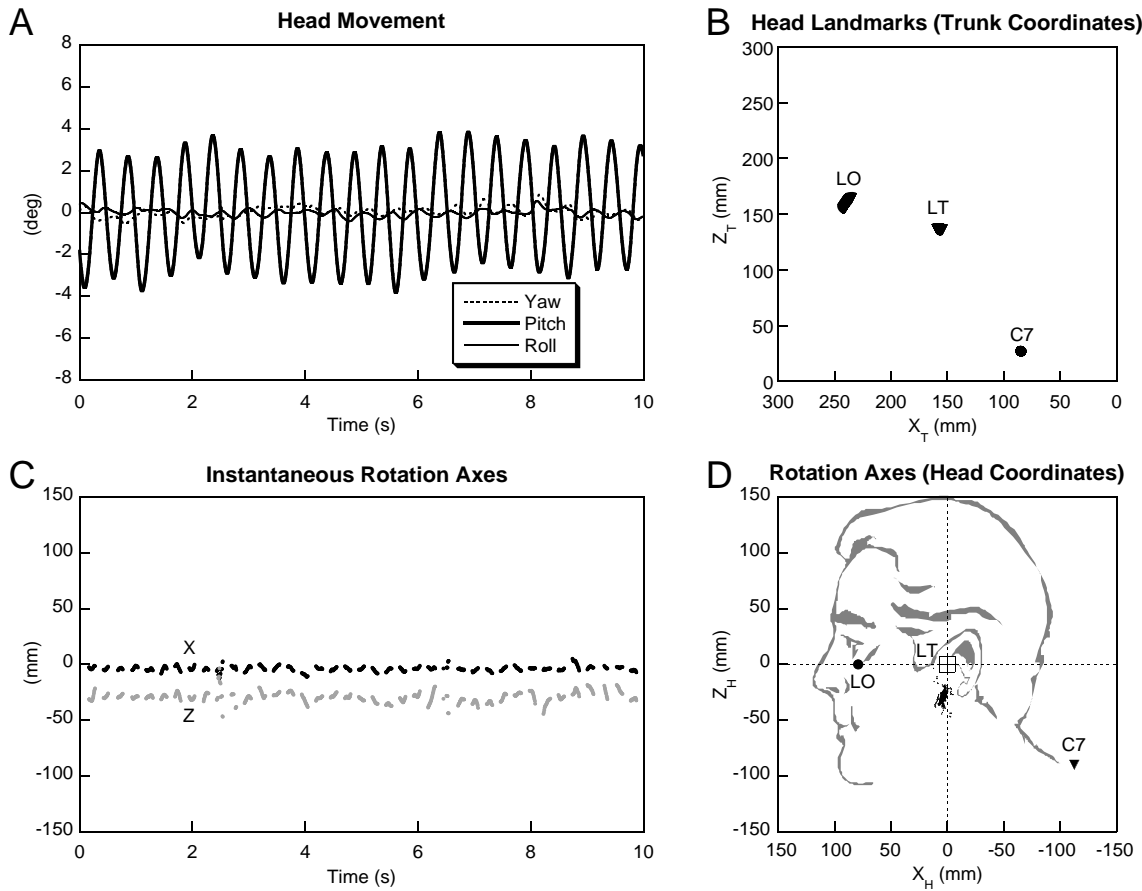


Fig. 1. Typical subject data for a small (3.1° peak) pitch head rotation at 2 Hz while standing. (A) Fick angles representing rotation of the head-rigid-body in trunk coordinates. (B) Translation of the head landmarks in trunk coordinates (LO – Left Orbitale; LT – Left Tragian; C7 – 7th cervical vertebra). (C) Coordinates of the intersection of the instantaneous rotation axes with the sagittal head ($X_H - Z_H$) plane plotted as a function of time, and (D) relative to the head-fixed coordinate frame.

x'_r by the cosine of the pitch of the plane of yaw rotation relative to trunk horizontal ($\cos(\gamma)$). Finally, the rotation axes for both pitch and yaw rotations were represented in the head coordinate frame with the head in the reference position (Fig. 1D). The location of the mean rotation axis was compared using repeated measures ANOVA for the six sitting and six standing trials during 1 and 2 Hz pitch, and 1 Hz yaw, head rotation. Shifts were considered significant for $P < 0.01$.

3. Results

Data from a standing subject during active pitch head rotation at 2 Hz (Fig. 1) illustrates the process for determination of the instantaneous rotation axes. The unfiltered head-on-trunk rotation data was close to a pure pitch rotation (mean peak amplitude 3.1°), with peak

yaw and roll components less than 5% of the head pitch (Fig. 1A). The movement of the head landmarks in the trunk sagittal plane (Fig. 1B) demonstrated that the axis of rotation was above C7, which exhibited virtually no movement. The instantaneous rotation axes, calculated from the head movement data using Eq. (5) and represented in head coordinates (Fig. 1C), were tightly clustered about a point slightly posterior and approximately 30 mm inferior to the interaural axis (Fig. 1D: $x_r = -3.8 \pm 2.2$ mm; $z_r = -29.1 \pm 4.6$ mm)

For pitch head movements at 1 Hz the trials were divided into two bins: small amplitude rotations (less than 6° peak) and large amplitude (greater than 6° peak). The mean peak pitch amplitude for all subjects was $4.4 \pm 0.8^\circ$ for small and $10.3 \pm 4.0^\circ$ for large rotations while seated, and $4.4 \pm 1.2^\circ$ and $10.1 \pm 4.1^\circ$ for small and large rotations while standing. There was no significant difference ($P > 0.01$) in the location of the

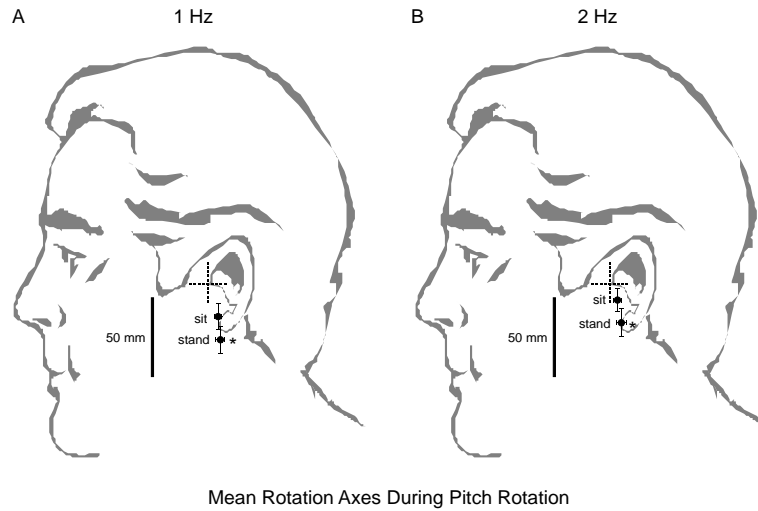
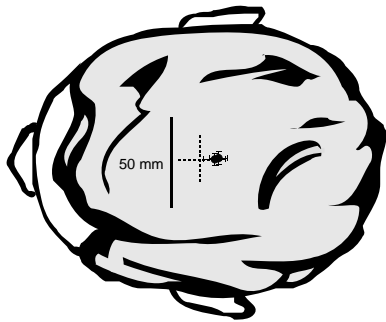


Fig. 2. Mean rotation axes during active pitch head movements were located slightly posterior and inferior to the interaural axis (mean and SD of all subject data). (A) 1 Hz pitch while sitting and standing. (B) 2 Hz pitch while sitting and standing. The asterisk (*) indicates the significant downward shift in the mean rotation axis when standing.



Mean Rotation Axes During 1 Hz Yaw Rotation

Fig. 3. Mean rotation axes during 1 Hz yaw rotation while both sitting and standing were situated slightly posterior to the interaural axis at the midpoint between the two labyrinths (mean and SD of all subject data).

mean rotation axis between small and large amplitude pitch movements. Consequently, the mean rotation axis was determined from the instantaneous rotation axis data from all small and large amplitude trials. When sitting (Fig. 2A), the mean rotation axis during sinusoidal head pitch rotation at 1 Hz was located slightly posterior and approximately 20 mm inferior to the interaural axis ($x_r = -5.6 \pm 2.5$ mm; $z_r = -21.3 \pm 8.5$ mm). There was a significant downward shift in the mean rotation axis of approximately 16 mm ($P < 0.01$) when the subject was standing (Fig. 2A: $x_r = -7.1 \pm 2.9$ mm; $z_r = -36.4 \pm 8.9$ mm).

When performing active head pitch at 2 Hz only small amplitude head movements were possible, with peak amplitude of $2.1 \pm 0.3^\circ$ when both sitting and

standing (mean and SD of all trials). The mean rotation axis during 2 Hz head pitch was located close to the interaural axis when sitting (Fig. 2B: $x_r = -4 \pm 2.6$ mm; $z_r = -10.5 \pm 7.6$ mm), and shifted downwards ($P < 0.01$) approximately 15 mm when standing (Fig. 2B: $x_r = -6.5 \pm 3.3$ mm; $z_r = -25.3 \pm 9.1$ mm), in a similar manner as for 1 Hz head pitch.

Yaw head rotations were performed at 1 Hz, and were of larger amplitude than for pitch head movements. Trials were divided into small (less than 12° peak) and large (greater than 12° peak) amplitude bins, with a mean amplitude of $8.4 \pm 1.9^\circ$ and $18.0 \pm 5.6^\circ$ for small and large yaw movements while sitting, and $9.7 \pm 1.9^\circ$ and $19.1 \pm 5.3^\circ$ when standing. Neither the amplitude of yaw rotation nor whether the subject was sitting or standing influenced the location of the mean rotation axis ($P > 0.01$), which was situated slightly posterior to the interaural axis at the midpoint between the two vestibular labyrinths (Fig. 3), when both seated ($x_r = -8.0 \pm 6.3$ mm; $y_r = 0.5 \pm 3.5$ mm) and standing ($x_r = -10.1 \pm 5.0$ mm; $y_r = 1.2 \pm 3.9$ mm).

For each yaw rotation trial the mean position of the head landmarks (the trignon and orbitale) were calculated in spatial coordinates from the average of their 3D position data over a 10 s trial. The orientation of the stereotaxic horizontal ($X_H - Y_H$) plane in space was obtained from a planar least squares fit to these averaged landmark positions (Fig. 4A). The orientation of the plane of yaw rotation in space was obtained from a planar least squares fit of the entire 3D position data of the left and right trignon during each 10 s trial

(Fig. 4A). Data from a typical 1 Hz yaw rotation trial while standing is shown in Fig. 4A. The stereotaxic horizontal plane was pitched up slightly from the spatial horizontal (X_S) by 0.5° , and the plane of yaw rotation was pitched down relative to X_S by 8° . This was consistent across all five subjects, with the stereotaxic horizontal plane slightly pitched up from the spatial horizontal during yaw rotation when both seated ($-2.3 \pm 1.7^\circ$) and standing ($-0.4 \pm 1.6^\circ$). The plane of yaw rotation was pitched downwards relative to Earth horizontal in both the seated ($3.1 \pm 1.3^\circ$) and standing ($4.7 \pm 0.9^\circ$) conditions. It is interesting to note that the relative pitch angle between the stereotaxic horizontal plane and the plane of yaw rotation was maintained when both sitting and standing. The yaw rotation plane was pitched an average of 5.4° (2.3° plus 3.1°) down from the stereotaxic horizontal when sitting, and 5.1° (0.4° plus 4.7°) when standing.

To determine whether the orientation of the plane of yaw rotation relative to the stereotaxic horizontal plane was fixed in head coordinates, yaw head movements were executed with the neck statically flexed or extended. Two standing subjects performed 1 Hz yaw head rotation after placing the head in a maintained nose-down position (3 trials of 10 s), and with the head held in a maintained nose-up position (3 trials of 10 s). Data from a typical subject trial is shown in Fig. 4. With the head upright the yaw rotation plane was pitched $8.2 \pm 0.2^\circ$ (mean of 3 trials) down from the stereotaxic horizontal plane (Fig. 4A). When the head was pitched 34° nose-down the plane of yaw rotation was pitched down $10.6 \pm 1.2^\circ$ relative to the stereotaxic horizontal (Fig. 4B). During yaw rotation with the head pitched 29° nose-up (Fig. 4C) the yaw rotation plane was pitched down $7.0 \pm 2.1^\circ$ relative to the stereotaxic horizontal. Similar results were obtained for the second subject. The yaw rotation plane was pitched down $4.8 \pm 0.5^\circ$, $5.4 \pm 0.7^\circ$ and $7.9 \pm 1.1^\circ$ relative to the stereotaxic horizontal during 1 Hz yaw rotation with the head upright, pitched 34° nose-down and 53° nose-up, respectively. Thus, the orientation of the plane of yaw rotation relative to the stereotaxic horizontal plane was maintained to within a few degrees over a large range of neck flexion and extension.

4. Discussion

The results of this study demonstrate that the mean rotation axis for high frequency (1–2 Hz) pitch head movements is located slightly posterior and inferior to

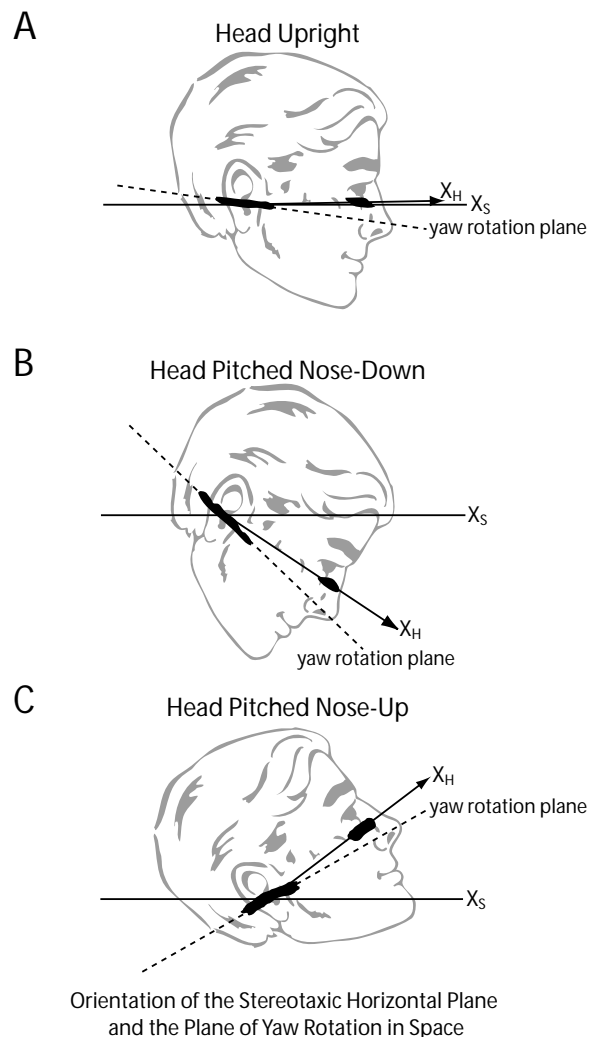


Fig. 4. Orientation of the stereotaxic horizontal ($X_H - Y_H$) plane and of the plane of yaw rotation in space during 1 Hz yaw rotation (while standing) with the head held in different pitch positions (data from a typical subject trial). Black dots represent the position of the right trigion and right orbitale in space during a 10s trial. (A) With the head upright, the yaw rotation plane was pitched 8.5° down from the stereotaxic horizontal plane. (B) With the head statically pitched 34° nose-down, the yaw rotation plane was pitched 10.2° down from the stereotaxic horizontal. (C) During 29° nose-up head pitch, the plane of yaw rotation was pitched 8° down from stereotaxic horizontal. The orientation of the plane of yaw rotation relative to the stereotaxic horizontal was essentially fixed in head coordinates.

the interaural axis. There was considerable spread in the vertical component of the instantaneous rotation axes over a 10 s trial, however, which suggests that pitch rotations do not occur about a single fixed axis. Head pitch rotation is performed as sequence of incremental rotations about axes that tend to oscillate vertically in space with the flexion and extension of the neck over

a range of approximately ± 10 mm. Head pitch axes were unaffected by the amplitude of the head movement, but were closer to the interaural axis for higher frequency (2 Hz) rotations, which were of similar amplitude and frequency to those generated during locomotion [3,4,6]. The data suggest that there is little activation of the linear VOR by tangential and centripetal linear accelerations during small, high frequency, active head pitch rotations due to the small radial distance from the mean rotation axis to the otoliths [1,6].

These findings are consistent with previous results for low frequency, large amplitude head pitch [5], with one exception. The Medendorp study [5] demonstrated a posterior shift of approximately 30 mm in the helical axis during 40° nose-up head tilt relative to 40° nose-down. This was likely due to the fact that such large head movements recruited most of the cervical vertebrae, resulting in a significant bending of the cervical column and a subsequent posterior shift in the rotation axis during neck extension, and an anterior shift when flexing the neck. In contrast, these large anterior-posterior shifts in the rotation axis were not observed in the current study, where head pitch movements were sinusoidal oscillations at high frequencies (1 or 2 Hz) with relatively small amplitudes. When sitting, the proximity of the rotation axis to the interaural axis suggests that the condyles of the occipital bone of the skull were essential rocking back and forth on the superior facets of the first cervical vertebra (the atlas) [2]. When standing with the trunk unsupported, the downward shift (16 mm) in the pitch axis suggests recruitment of the atlas, and possibly of the second cervical vertebrae (the axis). In either case, there was likely to have been minimal flexing of the cervical column during small pitch oscillations, and consequently no anterior-posterior shift in the rotation axis.

The mean rotation axis for yaw rotation is located slightly posterior to the interaural axis at the midpoint between the vestibular labyrinths. Rotation axes during horizontal rotations were more tightly clustered, and were unaffected by the amplitude of the head movement, whether the subject was seated or standing, or the pitch orientation of the head. These results are consistent with the hypothesis that yaw head movements occur about an axis restricted by the mechanical structure of the compound atlanto-axial joint. That is, the atlas, which supports the skull, is essentially limited to yaw rotation about the odontoid process 'pivot' (*dens*) of the axis [2].

An interesting result was that the orientation of the plane of yaw rotation relative to the stereotaxic horizon-

tal plane (pitched down 5° on average) was essentially fixed in head coordinates. This suggests that the semi-circular canals would receive the same stimulus during yaw head rotation, regardless of the pitch orientation of the head. The plane of the lateral canals is pitched up approximately 20° with respect to the stereotaxic horizontal [1]. Thus, during active head yaw the pitch orientation of the lateral canals would be approximately 25° out of the plane of rotation. This would ensure that all three semi-circular canal pairs are substantially stimulated during natural yaw head movements. This is consistent with previous results indicating maximal gain of the horizontal angular VOR in monkeys occurs for rotations in the stereotaxic horizontal plane [13]. Placing the lateral semi-circular canals in the plane of rotation during vestibular testing may not be a representative stimulus for natural yaw head movements.

Acknowledgements

Supported by NASA grants NCC 9-128 and NNJ04HF51G (Steven Moore), DC05204 (Bernard Cohen), DC05222 (Theodore Raphan) and EY01867.

References

- [1] I.S. Curthoys, R.H.I. Blanks and C.H. Markham, Semicircular canal functional anatomy in cat, guinea pig and man, *Acta Otolaryngol* **83** (1977), 258–265.
- [2] H. Gray and C.D. Clemente, *Anatomy of the human body*, Lea and Febiger, Philadelphia, 1985.
- [3] E. Hirasaki, S.T. Moore, T. Raphan and B. Cohen, Effects of walking velocity on vertical head and body movements during locomotion, *Exp Brain Res* **127** (1999), 117–130.
- [4] T. Imai, S.T. Moore, T. Raphan and B. Cohen, Interaction of the body, head and eyes during walking and turning, *Exp Brain Res* **136** (2001), 1–18.
- [5] W.P. Medendorp, B.J.M. Melis, C.C.A.M. Gielen and J.A.M. van Gisbergen, Off-centric rotation axes in natural head movements: implications for vestibular reafference and kinematic redundancy, *J Neurophysiol* **79** (1998), 2025–2039.
- [6] S.T. Moore, E. Hirasaki, B. Cohen and T. Raphan, Effect of viewing distance on the generation of vertical eye movements during locomotion, *Exp Brain Res* **129** (1999), 347–361.
- [7] R.M. Murray, Z. Li and S.S. Sastry, *A mathematical introduction to robotic manipulation*, CRC Press, Inc, Boca Raton, 1994.
- [8] M.M. Panjabi, M.H. Krag and V.K. Goel, A technique for measurement and description of three-dimensional six degree-of-freedom motion of a body joint with an application to the human spine, *J Biomech* **14** (1981), 447–460.
- [9] C.W. Spoor, Rigid body motion calculated from spatial coordinates of markers, *J Biomech* **13** (1980), 391–393.

- [10] J.M. Winters, J.D. Peles, P.J. Osterbauer, K. Derickson, K.F. Deboer and A.W. Fuhr, Three-dimensional head axis of rotation during tracking movements. A tool for assessing neck neuromechanical function, *Spine* **18** (1993), 1178–1185.
- [11] H.J. Woltring, R. Huiskes, A. De Lange and F.E. Veldpauw, Finite centroid and helical axis estimation from noisy landmark measurements in the study of human joint kinematics, *J Biomech* **18** (1985), 379–389.
- [12] H.J. Woltring, K. Long, P.J. Osterbauer and A.W. Fuhr, Instantaneous helical axis estimation from 3-D video data in neck kinematics for whiplash diagnostics, *J Biomech* **27** (1994), 1415–1432.
- [13] S.B. Yakushin, M. Dai, J.-I. Suzuki, T. Raphan and B. Cohen, Semicircular canal contributions to the three-dimensional vestibuloocular reflex: A model-based approach, *J Neurophysiol* **74** (1995), 2722–2738.

Copyright of Journal of Vestibular Research: Equilibrium & Orientation is the property of IOS Press and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.