Off-Centric Rotation Axes in Natural Head Movements: Implications for Vestibular Reaference and Kinematic Redundancy

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Medendorp, W. P., 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: 2025–2039, 1998. Until now, most studies concerning active head movements in three dimensions have used the classical rotation vector description. Although this description yields both the orientation of the head rotation axis and the amount of rotation, it is incomplete because it cannot specify the location of this rotation axis in space. The latter is of importance for a proper picture of the vestibular consequences of active head movements and has relevance for the problem of how the brain deals with the inherent kinematic redundancy of the multijoint head-neck system. With this in mind, we have extended the rotation vector description by applying the helical axes approach, which yields both the classical rotation vector as well as the location of the rotation axis in space. Subjects (n = 7), whose head movements were recorded optically, were instructed to shift gaze naturally to targets in 12 different directions at an eccentricity of 40°. The results demonstrate that the axes for these head movements occupy consistently different spatial locations. For purely horizontal movements, the rotation axis is located near a point midway between the two ear canals. For gaze shifts in other directions, the rotation axes are located below the ear canals along two circles, one for movements with an upward component (up circle), the other (typically larger in size) for movements with a downward component (down circle). Purely vertical movement (up and down) axes were located on the lower pole of the up and down circles, respectively. It was found that both circles, the upper poles of which coincided, became larger in size as movement amplitude increased, which means that the axis location shifts to lower and more eccentric locations with respect to the skull for larger flexion and extension movements. Although this pattern could be recognized in most subjects, there were consistent intersubject differences in the absolute size of the circles, their increase with movement amplitude, and in the relative sizes of the up and down circles. Because multiple vertebrae are involved in head movements, there are theoretically many possibilities to execute a certain head movement. The differences in circle patterns among subjects indicate different strategies in resolving this kinematic redundancy problem, a fact that was not apparent from the classical rotation vector part of our description, which yielded a rather uniform picture. A simple model suggests that the downward shift of the location of the rotation axis requires a modulation in vestibulo-ocular reflex gain of ≈10% to maintain fixation of a near target during vertical head movement. The involvement of the otolith system in this process remains to be determined.

INTRODUCTION

This paper concentrates on the problem of how the complex movements of the head can be recorded and described in a manner that does justice to both the motor aspects and their vestibular consequences. To illustrate that this is not a trivial problem, let us first consider the now commonly used method to describe eye positions relative to the head by means of rotation vectors (Haustein 1989). With this tool, any instantaneous three-dimensional (3-D) eye position is described as the result of a virtual rotation from a fixed reference position to the current position. The orientation of the rotation vector specifies the direction of the eye rotation axis, whereas its length denotes the amount of rotation about that axis. Because the eye is enclosed in the orbit, it is reasonable to assume that these rotation vectors describe eye rotations through the center of the globe. Thus because the center of rotation of the eye is almost fixed in the head, eye positions can be described in good approximation as the result of pure rotations about axes whose orientations may vary, but the locations of which are fixed.

For head movements, which are less constrained, the situation is clearly different because there is no immediately obvious location of the head rotation axis. These movements are described relative to the trunk (or relative to some other coordinate system in space), and it is quite obvious that the center of the head generally not only rotates but also translates relative to this coordinate system.

To describe rigid body motion, many different parsings are possible. For example, the center-of-mass method, which would be quite suitable for describing vestibular consequences of head movement, describes head motion as a rotation about the head’s center of mass and a translation of this center of mass. Another description, which we present in this paper, can be found in the biomechanical literature in which it is fairly usual to describe complex movements in 3-D in terms of helical axes (Panjabi et al. 1981; Spoor and Veldpaus 1980; Woltring et al. 1985). This helical axis method seems ideally suited to describe the motor aspects of the head-neck system while still allowing the inclusion of the vestibular consequences.

Using the concept of helical axes, any head position can be uniquely described with respect to a certain reference position by a rotation about and a translation along a single unique axis at a specific spatial location. The strength of this description is that it parses the head motion by locating a rotation axis such that the translational component is as small as possible. This is suitable for our purpose because head motion ultimately is produced by rotating, not translating, joints; i.e., the translational component of skeletal motion is very small. For this reason, the helical axis description may give the best clue as to which joints are moving.
To illustrate what can be gained by using this approach, Fig. 1 shows an example of two different head movements. In each case, the current position can be reached from the reference position by a virtual rotation about an axis, located somewhere in the neck region. Although the orientation of the head is the same in Fig. 1, A and B, the position of the head relative to the trunk differs by a translation due to the different locations of the rotation axes. The rotation vector description, which only gives the orientation of the head, is inadequate to characterize these differences in head position. The helical axis approach, however, extends the classical rotation vector description by yielding both the direction of the rotation axis, which is identical to the direction of the rotation vector (see METHODS) and the uniquely defined spatial location of this rotation axis.

Although the helical axis description has been used in many biomechanical studies, to the best of our knowledge it has never been applied in studies focusing on neural strategies concerning problems related to the kinematic redundancy of the head-neck system. In the present study we introduce the helical axes approach in this field of research in an attempt to get a more complete description of head posture. In the next section, we will first make clear why it is of interest to know the location of the rotation axis in addition to the orientation and the amplitude of the head rotation.

**Biological relevance of the location of the head rotation axis**

The vestibulo-ocular reflex (VOR) contributes to stabilization of images on the retina during movements of the head. Recent work has shown that the VOR is influenced by the viewing distance, the target eccentricity, and the axis about which the head is rotated (Crane et al. 1997; Snyder and King 1992; Viirre and Demer 1996). The VOR has to take into account both the translation and the rotation of the head to stabilize a near target on the retina. Buizza et al. (1981) proposed that the VOR is mediated by a combination of semicircular canal input and otolith input. In their model, the canals compensate for head rotation by rotating the eyes opposite to the head at the same angular velocity. The compensation for the translational component of head movement, driving the eyes with a signal that is opposite to this translation and that is scaled by viewing distance, originates from the otoliths. Whereas Buizza et al. used the approximation that the eyes are at the center of the head, in their study of VOR properties in near vision, Viirre et al. (1986) took account of the fact that the eyes and vestibular organs are at different locations. They found the magnitude of the VOR gain in monkeys to be >1.0 in near vision; this was explained by the fact that a rotation of the head generally will lead to a translation of the eyes such that good stabilization of retinal image requires a compensation for both the rotation and the translation. Snyder and King (1992) made further study of the compensatory behavior of the VOR for combined angular and linear motion. They rotated monkeys about earth-vertical axes in the midsagittal plane at several distances behind and in front of the eyes. The initial VOR response due to these passive body rotations had an inappropriate default gain. Within 100 ms, however, the VOR response became nearly perfect by adjusting eye velocity in three separate stages: initially only showing a compensation for viewing distance, sequentially also for otolith translation and finally by including the translation of the eye relative to the target. Recently, Viirre and Demer (1996) investigated the VOR gain in humans during eccentric passive rotation in pitch and found the VOR gain to increase for proximate as compared with distant targets. Based on these and other findings, Crane et al. (1997) proposed a model in which linear acceleration, as sensed by the otoliths, is scaled by target distance and is added to angular acceleration, as detected by the semicircular canals, to control the compensatory eye movement.

**Approach**

These findings suggest that it would be of interest to have knowledge about both the orientation of the head and the location of the rotation axis in space during natural head movements. The magnetic dual search coil technique, originally designed to record 3-D eye movements (Forman et al. 1987), is excellent as a tool to detect the orientation of an object in three dimensions, but its insensitivity to coil translations makes it unsuitable to determine the location of the rotation axis. To circumvent this problem in getting an on-line representation of the exact movement of the head in 3-D space, we have used an infrared tracking system. The subject wears a helmet with several infrared emitting diodes (ireds); this provides the opportunity to calculate the helical axis parameters (see following text). This full description of head movement in 3-D was used to investigate to what extent the location of the rotation axis of the head will vary in head-free, but chest-fixed, subjects. The helical axis method used in this study describes the head-neck movement by specifying the location of a single rotation axis that minimizes the residual translation term. This approach seems particularly suited for this system, the joints of which generate rotations rather than translations and where the location of a single rotation axis is not self-evident.

**METHODS**

This section outlines the experimental protocol and the mathematical basis underlying our description of head position.
Subjects and stimuli

Seven human subjects, aged between 22 and 53 y, participated in the experiments. Six of them were naive as to the purpose of the experiment. To minimize the movements of the chest, a harness was used to strap the subjects tightly to a chair, which supported the back up to the shoulder blades. The targets, at 40° eccentricity, consisted of reflecting mirrors (size 10 × 10 cm) directed toward the subject that were mounted on a vertical fronto-parallel screen placed at a distance of 55 cm before the subject. Subjects were instructed to orient their heads toward the target until they could see their faces in the mirror. The circular stimulus array contained a total of 12 numbered targets, arranged like the hours on a clock, at equal angular spacings (φ) of 30° along the circumference. The 12:00 target was defined to be at φ = 0°. The center of the circle, which was marked as a black spot, was straight ahead at eye level. Before the experiment, the subject was familiarized with the positions of the targets on the screen. At the start of each trial, he was asked to fixate at the center of the screen. Thereafter, the subject was instructed, on a verbally commanded random target number, to shift gaze with natural speed from the center to the particular target, to fixate carefully and then to move back to the center again. Trials in which the subject initially shifted his gaze in the wrong direction were excluded from the measurement. Every experiment consisted of five sequences of all 12 targets in random order. Each sequence lasted for ~1 min. About 1 min of rest was provided between the sequences. During each sequence, data were collected continuously using a sample frequency of 100 Hz.

Measurement and calibration of head position

We used an OPTOTRAK 3020 digitizing and motion analysis system (Northern Digital) to record head position in 3D. It operates by tracking active irides attached to a moving object through a precalibrated space by means of three lens systems mounted in a fixed frame. To determine the position of the head, we constructed a helmet, carrying a flat disk on top of which eight irides were mounted equidistantly in a circular array (radius 5.6 cm). The total weight of the helmet, which was firmly fixed to the head, was <0.25 kg. The OPTOTRAK frame was mounted on the ceiling above and behind the sitting subject at a distance of ~3 m. The OPTOTRAK system was tilted 30° downward relative to the ceiling such that the irides were visible in a large range of movement. In this configuration, the system provided on-line information about the 3-D position of the irides with an accuracy better than 0.2 mm. To determine the position of four well-defined head landmarks relative to the irides on the helmet, a calibration was performed before the actual experiment began. During this calibration, the subject faced the OPTOTRAK frame while wearing the helmet together with four additional irides, one on each ear near the auditory canal and one on each closed eyelid. The 3-D positions of all 12 irides, which uniquely defined the position of the head with respect to the helmet, were recorded for 1 s. From then on, great care was taken to ensure that the helmet remained stable on the head during the entire experiment.

We used this calibration to transform the spatial locations of the irides on the helmet to a new body-fixed coordinate system, the origin of which coincided with the center of the interaural axis when the subject was looking straight ahead to the center of the circle at the beginning of the experiment. With the head in this reference position, the anteriorly-pointing x axis of the right-handed coordinate system was in alignment with the axis perpendicular to the screen, the leftward-pointing y axis was aligned with the interaural axis, and the z axis pointed upward. Knowledge about the absolute spatial locations of the irides on the helmet in this coordinate system provided sufficient information to determine the helical axis parameters of instantaneous head posture.

Description of head positions

In general, the head not only changes its orientation, but also shifts its center of gravity with respect to the trunk during a free gaze movement. Accordingly, six independent parameters are required to describe the head position in space, i.e., three for the orientation of the head and three for the translation of its mass center. Many earlier 3-D studies (Gleni and Villis 1992; Radau et al. 1994; Theeuwen et al. 1993) have focused on the orientation of the head, which could be described by 3-D rotation vectors. In none of these studies was the translation of the head taken into account. In the present study, we will describe complete head postures with a description in which the orientation and translation of the head are considered by using the helical axes description. In the concept of helical axes, a transition of a body segment from a certain reference position to a new position can be described as a rotation about a certain unique axis and a translation along that axis. Hence, the translation orthogonal to this axis is minimized, which makes sense because, as was pointed out in the INTRODUCTION, head motion is produced by rotating not translating joints. Further this description remains very close to the classical rotation vector description because the direction of the rotation axis is identical to the direction of the rotation vector and the rotation angle is simply related to the amplitude of the rotation vector, see Eq. 3.

Figure 2 depicts, in vectorial terms, the transition of the head from one position to another position to illustrate how the helical axis parameters can be derived. Figure 2 shows that the initial position ($\hat{x}_I$) and final position ($\hat{x}_F$) of a landmark on an object are related by

$$\hat{x}_F - \hat{x}_I = R(\theta) \cdot (\hat{x}_I - \hat{x}_I) + t \cdot \hat{n}_L$$ (1)
where \( R(\theta) \) is the rotation matrix with \( \theta \) the angle of rotation about the helical axis. The direction of the helical axis is defined by unit vector \( \hat{n}_s \), the translation along the helical axis is given by scalar \( t \). The sense of rotation and the direction of \( \hat{n}_s \), conform to the right-hand rule. The vector \( \delta \) is the vector from the origin of the coordinate system, as defined above, perpendicular to the helical axis. Define \( \delta \) by \( \delta = t \cdot \hat{n}_s + (I - R) \cdot \delta \) then
\[
\delta = R(\theta) \cdot \delta + \delta
\]
The rotation matrix \( R(\theta) \) and the translation vector \( \delta \) (which is the translation of the mean marker distribution) can be determined by a least-squares algorithm as described by Veldpaus et al. (1988).

When \( R(\theta) \) and \( \delta \) are known, the helical axis parameters \( \hat{n}_s \), \( \delta \), \( \theta \), and \( t \) can be calculated (see for example, Panjabi et al. 1981; Spoor and Veldpaus 1980; Woltring et al. 1985).

The orientation of the helical axis is directly related to the classical rotation vector \( \hat{r} \) (Haustein 1989) by
\[
\hat{r} = \tan(\theta/2) \cdot \hat{n}_s
\]
The helical axis parameters \( \hat{n}_s \) and \( \theta \) in Eq. 1 are identical to those in Eq. 3. The direction of the rotation vector denotes the orientation of the helical axis, and its length (tan \( \theta/2 \)) can be taken as a measure for the amount of rotation along that axis. The rotation vector \( \hat{r} \) corresponding to the rotation matrix \( R(\theta) \) can be determined from the elements of the rotation matrix (Haslwanter 1995) by
\[
\hat{r} = \frac{1}{1 + (R_{11} + R_{22} + R_{33})} \begin{pmatrix} R_{32} - R_{23} \\ R_{13} - R_{31} \\ R_{21} - R_{12} \end{pmatrix}
\]
By projecting the translation vector \( \delta \) onto an axis parallel to the helical axis
\[
t = \hat{n}_s \cdot \delta
\]
we obtain the displacement \( t \) along this axis, where it has to be noted that a positive sign of \( t \) implies that the translation is in the direction of the unit vector \( \hat{n}_s \). Winters et al. (1993) have reported that the translation along the helical axis for biomechanical systems like the head is rather small (within 0.5 cm). However, because it may have some vestibular consequences, it was calculated in the present study.

To document the location of the rotation axis, we computed the smallest vector \( \delta \) from the origin to the helical axis, i.e., the vector from the origin perpendicular to the helical axis, which follows from \( \hat{n}_s \cdot \delta = 0 \) (Spoor and Veldpaus 1980)
\[
\delta = -\frac{1}{2} \hat{n}_s \times (\hat{n}_s \times \delta) + \frac{\sin \theta}{2(1 - \cos \theta)} \hat{n}_s \times \delta
\]
Note that \( \delta \) is dependent on both the orientation of the helical axis and the translation of the head, as given by the mean marker distribution \( \delta \). Furthermore, in case \( \theta = 0 \), there is no rotation at all. In this case of a pure translation, the helical axis is not defined, which means that \( \hat{n}_s \), \( \delta \), and \( t \) are not unique. This explains that \( \hat{n}_s \) is extremely sensitive to disturbances if \( \theta \) is small. In such cases, the helical axis parameters cannot be determined accurately. In practice, the helical axis could be determined reliably only for head movements >6°. From the above analysis, it may seem that eight parameters are necessary to describe the helical axis. However, only six of them are independent, namely: two angles to specify the orientation unit vector \( \hat{n}_s \), rotation \( \theta \) about the axis, translation \( t \) along the axis, and two coordinates of an intersecting point on the axis defined by \( \delta \) (axis location, for short). So, in summary, all head positions in our study will be described with respect to a certain reference position by the helical axis parameters. The orientation of the rotation axis can be described by the classical rotation vector \( \hat{r} \), which implies \( \hat{n}_s \) and \( \theta \). The location of the rotation axis in space is represented by \( \delta \), the translation along this axis is given by \( t \).

In RESULTS we will describe separately the orientation of the rotation axis, then its location, and finally the translation along this axis. The changes in head position with respect to the reference position during a natural movement can be depicted by a sequence of rotation axes and their spatial locations.

Data analysis and representation

Using the calibration and methods described above, head positions were calculated from raw recorded position data and were characterized in terms of helical axis parameters. The beginning and the end of each head movement were determined from the on- and offset of the rotational component change. Because the location of the rotation axis could not be determined accurately for positions close to the reference position, only head deviations exceeding 6° were analyzed.

As reported before (Glenn and Vilis 1992; Radou et al. 1994; Theeuwen et al. 1993), the rotation vectors describing the orientation of the head tend to fit in a second-order twisted surface. To check this, we fitted several surfaces to the rotational components \( (r_x, r_y, r_z) \) of the data
\[
r_r = a_1 + a_{21} r_x + a_{31} r_y + a_{41} r_z + a_{51} r_x r_y + a_{61} r_y r_z + a_{71} r_z r_x + a_{81} r_y^2 + a_{91} r_z^2 + \epsilon
\]
by minimizing the residual error \( \epsilon \). If the parameters \( a_{1} - a_{9} \) are zero, the surface is planar, as would be the case if Listing’s law holds perfectly. Adding \( a_{5} - a_{7} \) (twist score) as an extra parameter allows the surface to twist, whereas \( a_{4} \) and \( a_{9} \) yield a parabolic curvature in the \( r_y \) and \( r_z \), direction, respectively. To check whether the addition of extra parameters \( a_{4} - a_{7} \) is warranted, we applied a statistical analysis based on the bootstrap method (Efron and Tibshirani 1991). This procedure implies that several times (in our case, 200 times) a subset of rotation vectors \( (N \) data samples generated by drawing them randomly, with replacement, from the original dataset of \( N \) points) is fitted by Eq. 7. In this way, each

![FIG. 3. Head orientation in terms of classical rotation vectors. Frontal, side, and top view of the classical rotation vectors describing 1 to-and-fro movement in each of the 12 separate directions (numbered like the hours on the face of a clock). In the frontal view, the parts of the movement away from and back to the center follow slightly curved trajectories. Note that movements toward opposite targets have opposite directions. Axes are calibrated in rotation vector units (which implies that 0.25 on each scale corresponds to ~30°) (see Haustein 1989). Subject: JG.](image-url)
realization of a new data set yields different parameter estimates, because the data set is different each time. Thereafter, the mean value and standard deviation of each parameter can be computed. We state that a parameter significantly contributes to the fit when its mean value is different from zero by \( \pm 2 \times \) SD (95% acceptance level or confidence level).

The thickness of the fitted surface (in degrees) is given by the standard deviation of the distances of all samples in the \( r_z \) direction to the fitted surface.

**RESULTS**

We now shall describe the head positions adopted in the course of gaze shifts in different directions by using the helical axis approach as described in METHODS. The helical axis describes how a given head position can be obtained uniquely from a certain reference position by a single rotation and translation along an axis in body coordinates. To recapitulate briefly, the orientation of the helical axis can be related to the classical rotation vector by Eq. 3; while the location of this axis will be described by a 3-D vector according to Eq. 6. The translation along the helical axis is defined by Eq. 5. We will describe the three parts of the helical axis separately, starting with the orientation, which is most familiar. Subsequently, the spatial locations of these axes will be presented and their relation with target direction \( \phi \) and the axis orientation will be clarified. Finally, we will characterize the translation term along the helical axis and its dependence on the orientation of this axis. For the sake of clarity, the figures throughout this section consistently present the results of subject JG. However, intersubject differences will be illustrated and discussed in detail. The data of all subjects are summarized in Tables 1–3.

**Orientation of the rotation axis**

Characteristic head movements toward each of the 12 eccentric targets and back to center are depicted by rotation vectors in Fig. 3. For each movement, the sequence of rotation vector endpoints for intermediate positions is given in body-fixed coordinates. The frontal view in Fig. 3A, showing the horizontal \( (r_x) \) and vertical \( (r_y) \) components, demonstrates that centrifugal and centripetal movements had slightly different curved trajectories. Furthermore, the trajectories of rotation vectors for movements toward opposite targets are in opposite directions. The side and top views (Fig. 3, B and C) show that the torsional components of these head movements are limited. In comparison with earlier studies, Fig. 3 shows nothing uncommon nor any new features and just serves to illustrate that, in this respect, our description yields results similar to those of the magnetic dual search coil technique.

To test the validity of Listing’s law for the head, we first fitted

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**TABLE 1. Second-order twisted surface fitted to the rotation vector data by Eq. 7**

<table>
<thead>
<tr>
<th>Subject</th>
<th>( a_1 )</th>
<th>( a_2 )</th>
<th>( a_3 )</th>
<th>( a_4 )</th>
<th>( a_5 )</th>
<th>( a_6 )</th>
<th>Thickness, deg</th>
</tr>
</thead>
<tbody>
<tr>
<td>JG</td>
<td>0.0035 (0.0002)</td>
<td>(-0.010 (0.001))</td>
<td>(-0.011 (0.001))</td>
<td>0.007 (0.006)</td>
<td>(-0.639 (0.009))</td>
<td>(-0.007 (0.006))</td>
<td>1.10</td>
</tr>
<tr>
<td>WM</td>
<td>0.0016 (0.0002)</td>
<td>0.026 (0.001)</td>
<td>(-0.002 (0.001))</td>
<td>0.051 (0.007)</td>
<td>(-0.797 (0.009))</td>
<td>(-0.117 (0.003))</td>
<td>0.91</td>
</tr>
<tr>
<td>SA</td>
<td>(-0.0031 (0.0002))</td>
<td>(-0.026 (0.002))</td>
<td>0.033 (0.002)</td>
<td>0.167 (0.011)</td>
<td>(-0.900 (0.022))</td>
<td>(-0.059 (0.008))</td>
<td>1.10</td>
</tr>
<tr>
<td>BB</td>
<td>0.0011 (0.0002)</td>
<td>0.032 (0.002)</td>
<td>0.044 (0.001)</td>
<td>0.115 (0.009)</td>
<td>(-1.133 (0.013))</td>
<td>(-0.029 (0.004))</td>
<td>1.16</td>
</tr>
<tr>
<td>AB</td>
<td>(-0.0000 (0.0001))</td>
<td>(-0.028 (0.002))</td>
<td>0.075 (0.002)</td>
<td>(-0.042 (0.008))</td>
<td>(-0.597 (0.013))</td>
<td>0.005 (0.005)</td>
<td>1.10</td>
</tr>
<tr>
<td>TD</td>
<td>0.0044 (0.0002)</td>
<td>(-0.019 (0.002))</td>
<td>(-0.105 (0.002))</td>
<td>0.094 (0.008)</td>
<td>(-0.783 (0.016))</td>
<td>0.087 (0.006)</td>
<td>1.63</td>
</tr>
<tr>
<td>GM</td>
<td>0.0018 (0.0002)</td>
<td>(-0.006 (0.001))</td>
<td>(-0.072 (0.001))</td>
<td>0.109 (0.006)</td>
<td>(-0.276 (0.008))</td>
<td>(-0.059 (0.003))</td>
<td>0.74</td>
</tr>
</tbody>
</table>

The parameters are expressed in body-fixed coordinates. Behind each value its confidence interval (2 \( \times \) SD) is given in parentheses. The orientation of the plane is determined by the coefficients \( a_2 \) and \( a_3 \) (see text). The fact that these coefficients are small indicates that the surfaces are nearly aligned with the \( r_z \) plane of our coordinate system.
a planar surface to all rotation vector data from each subject. The thicknesses of these planes varied between 0.91 and 2.25°. However, according to Radau et al. (1994), a first-order fit is not necessarily the best representation of the data. By adding only the twist score $a_5$ as an extra parameter, the thicknesses decreased strongly in all subjects. A statistical analysis (see METHODS) showed that the data can be best described by a second-order curved surface. The additional improvement in the goodness of fit, resulting from also adding $a_4$ and $a_6$ (thickness 0.74–1.63°), was significant for all subjects. On average, the thickness was found to be $1.1 \pm 0.27°$ (SD), indicating rather small deviations from Donders’ law. The optimal parameters of this second-order twisted surface fit and the corresponding thicknesses of the best-fit surfaces are listed in Table 1.

We also considered the orientation of this second-order twisted surface in body coordinates. Because the coefficients of the quadratic terms $r_x^2$ and $r_z^2$ in Eq. 7 are small, fitting a flat plane to the rotation vectors yields about the same values for the coefficients $a_2$ and $a_3$ for the flat plane and for the curved surface. The vector orthogonal to this flat plane is called the primary direction. For all subjects, we found the primary direction to be close to the straight-ahead position, which corresponds to the positive $x$-axis direction. Deviations remained within 2° from the midsagittal plane and ranged $\geq 6°$ from the horizontal plane.

The direction of the head rotation axes can be obtained by normalizing the rotation vectors, as mentioned in Eq. 3. Each rotation vector is split into a normalized three-compo-

FIG. 5. Horizontal and vertical head movements expressed by a rotation axis and its location in space. Left: movement from the center toward the 3:00 target. A: rotation axes during this movement were directed along the vertical axis, indicating a horizontal movement. Rotation axis remains almost the same throughout the movement. B: rotation axis points in the negative vertical direction. Normalized rotation vector components remain almost constant throughout the movement, indicating a parallel-axes rotation. C: 3 components of the location of the rotation axis remain almost constant and close to the origin, the center of the interaural axis. D: middle column shows results in the same format for a movement toward the 6:00 target. E: rotation axes are directed along the positive horizontal axis and remain almost parallel. F: location of the axis is not fixed but shifts along the $z$ axis during this movement, indicating that the axis of rotation slowly moves downward with respect to the body. G: right column shows the results for a purely vertical movement toward the 12:00 target. H: compared with the 6:00 movement, the directions of the rotation axes are in opposite direction. I: rotation axes for 12:00 are much more posteriorly located with respect to the 6:00 movement. ant., anterior; post., posterior; H, horizontal ($r_y$ axis); V, vertical ($r_z$ axis); T, torsional ($r_x$ axis). Subject: JG.
nent vector, indicating the rotation axis direction $\mathbf{n}$, and a
calar $\theta$, denoting the amount of rotation about that axis.
The relation between rotation vector components and axis
direction is illustrated in Fig. 4, which shows the same move-
ment toward the 4 o’clock target as in Fig. 3. Figure 4A
depicts the three rotation vector components of the to-and-fro
movement. At movement onset, the length of the vector
(Fig. 4B) is almost zero. After initiation of the movement,
the rotation vector components grow steadily, indicating an
increase in movement amplitude. When the head is stable
in the new eccentric position, the components remain con-
stant and during the backward movement they decrease
again. Finally, Fig. 4C depicts the normalized direction of
the rotation axis. As explained in METHODS, the latter is only
well defined for movement amplitudes of $>6^\circ$ (· · ·). Note
that only if the three components of the normalized axis
direction remain constant in the course of the movement,
the associated rotation vectors will remain parallel.

Location of the rotation axes

As a measure for the spatial location of the rotation axes,
we have used vector $\mathbf{s}$, computed with Eq. 6, which denotes
the point on the rotation axis closest to the origin ($S$ point
for short). In our study, we only analyzed the $S$ points of
rotation axes belonging to outward (centrifugal) movements.
The parts of the movements back to center were not consi-
tered. Taking, for example, a rightward movement toward
the 3:00 target, one would predict the orientation of the
rotation axis to be mainly vertical along the negative vertical
axis of our right-handed coordinate system, whereas its loca-
tion would be expected to be closer to the origin.

Figure 5A shows that the orientation of the rotation axis is
indeed vertical. The direction of the rotation axis during
the movement is depicted in Fig. 5B, which clearly shows
that the direction of this axis is in the negative vertical direc-
tion and remains almost constant throughout the movement.
In Fig. 5C, the three components of axis location $S$ are given
as a function of the movement amplitude. As expected, the
$S$ point lies near the origin. The fact that its position remains
more or less constant indicates that the rotation axis remains
almost fixed in space as the movement progresses. Plotting
the axis of rotation and its spatial location in body coordi-
nates, as shown in Fig. 5A, provides a more direct demon-
stration of the stability of the rotation axis during this type
of natural movements.

The results for the movement toward a 6:00 target (Fig.
5D) show a different pattern. As one would predict, the
rotation axes for this downward movement are mainly hori-
Zontal and point in the positive horizontal direction (see Fig.
5E). A new feature of this movement is that the location
of $S$ is not constant. The location of the axis moves gradually
downward along the $z$ axis as the movement progresses (see Fig. 5F), whereas the direction of the rotation axis remains
more or less constant in a large part of the movement.

Figure 5G depicts the movement toward a 12:00 target.
The rotation axes for this upward movement are pointing
in the negative horizontal direction (see Fig. 5H). Not
too surprisingly, comparison of Fig. 5, E and H, shows
that the rotation axes for movements toward 6:00 and

\[ \text{FIG. 6. Reproducibility of the direction and location of the rotation axis. Left and right: best-fit lines to three 6:00 movements measured on 2 different days (subject BB). Error bars (given in just 1 direction) denote the SDs of the data points to the fitted line in that particular part of the movement. Generally, the error bars are quite small indicating stereotyped behavior within one experiment. Between the 2 experimental sessions there is a large similarity. A small difference can be seen for the $x$ component in the 2 experimental sessions. On day 2, the infrared emitting diodes (ireds) were not visible by the OPTO-TRAK camera for amplitudes $>25^\circ$.} \]
12:00 targets are parallel but in opposite direction. This was a general phenomenon: in all subjects, we found the axes for movements toward opposite targets to be almost parallel and pointing in opposite directions. This finding is in line with the data shown in Fig. 3. Furthermore, Fig. 5I shows that the axes for the 12:00 movement are not fixed in space either but move downward along the $z$ axis, as was observed for 6:00 movements. Finally, it should be noted that the axes for the 12:00 movements are located more posteriorly than those for the 6:00 movement (compare the $x$ component in Fig. 5, $F$ and $I$).

To check day-to-day reproducibility, we repeated the entire experiment in four subjects (JG, BB, WM, and SA). As a representative example, Fig. 6 depicts the direction and location of the rotation axes for three movements toward the 6:00 target for subject BB on two different days. The lines are the results of linear regression. The error bars denote the standard deviations of the data points of the trials to the fitted line in three stages of the movement. The error bars are larger for small movement amplitudes, denoting more scatter of data points around the fitted line in that range. In general, however, the errors are modest indicating a quite reproducible behavior of the subject within one experiment. With respect to the reproducibility among experiments, Fig. 6 shows that the direction of the rotation axes, pointing in the positive horizontal direction, is almost the same on the two days. Some minor differences can be observed between the vertical and torsional component of the axis direction. Concerning the location of the rotation axes, on both days they move steadily downward along the $z$ axis, from $-40$ to $70$ mm below the origin, as the movement progresses. A small difference is seen in the trajectory of the $x$ component; on day 1 the axis of rotation initially is located more anteriorly, whereas on day 2, the $x$ component of the $S$ point remains quite stable throughout the movement. Also in the other three subjects, the results of the experiment on day 2 were similar and showed the same tendencies as in the first experiment.

**Intersubject differences in the solution of the kinematic redundancy problem**

The kinematic redundancy of the head-neck system has its basis in the number of neck joints as well as in the large number of muscles acting across these joints. An interesting problem is how the movement control system deals with this redundancy problem. Our results show that the emerging picture depends strongly on which aspect of head movement is considered. When the analysis considers only the orientation of the head to characterize head posture (see earlier text), the data confirm that Donders’ law holds in good approximation (Table 1). This result reflects a reduction in the number of rotational degrees of freedom: the rotation

**TABLE 2. Dependence of $z$ component of rotation axis location on movement amplitude for flexion and extension**

<table>
<thead>
<tr>
<th>Subject</th>
<th>Flexion</th>
<th>Extension</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Slope, mm/deg</td>
<td>$r$</td>
</tr>
<tr>
<td>JG</td>
<td>$-1.7 (0.2)$</td>
<td>$-0.92$</td>
</tr>
<tr>
<td>WM</td>
<td>$-2.3 (0.4)$</td>
<td>$-0.77$</td>
</tr>
<tr>
<td>SA</td>
<td>$-0.4 (0.6)$</td>
<td>$-0.13$</td>
</tr>
<tr>
<td>BB</td>
<td>$-1.6 (0.2)$</td>
<td>$-0.94$</td>
</tr>
<tr>
<td>AB</td>
<td>$0.5 (0.2)$</td>
<td>$0.43$</td>
</tr>
<tr>
<td>TD</td>
<td>$-1.6 (0.2)$</td>
<td>$-0.92$</td>
</tr>
<tr>
<td>GM</td>
<td>$-0.8 (0.2)$</td>
<td>$-0.54$</td>
</tr>
</tbody>
</table>

Flexion and extension movements presented from Fig. 7. Behind each value its confidence interval ($2 \times SD$) is given in parentheses. The correlation coefficient $r$ is a measure of how well the $z$ component of axis location and movement amplitude correlate.
vectors that describe the orientation of the head relative to the reference position are contained within a two-dimensional surface. Furthermore we showed that the orientation of this surface is more or less the same among subjects.

It should be realized, however, that this characterization of head postures is severely limited because it says nothing about the location of the head rotation axis. Because the neck consists of multiple joints, there are many possible locations of the head rotation axis that all can yield in the same head orientation but will produce a different translation of its mass center and therefore a different head posture (see Fig. 1). As shown in Fig. 7, when this is taken into account, there is a strong suggestion of different strategies in resolving the kinematic redundancy among subjects. The figure illustrates the trajectories of the z component of the S point for purely vertical movements toward the 6:00 and 12:00 target from four subjects in three sequences. There is a general trend for the rotation axes in flexion to be located at a lower level than the rotation axes in extension movements. Although these differences are minor in subjects JG and BB, they are very clear in subjects TD and GM. Note that there are also intersubject differences in the location of the rotation axis belonging to the same movements. For example, the rotation axis for flexion in subject GM is at a much lower location than that of subject JG.

Figure 7 further shows a general trend for the rotation axis to move downward as flexion or extension increases (except for extension in subject BB). To check whether the dependence of the z component with movement amplitude was significant, we fitted a straight line to this type of data in all subjects. The slopes of these lines are presented in Table 2. For the flexion movement, we found negative slopes (range −2.3 to −0.8 mm/deg) in five subjects; this appeared to be significantly different from zero in a two-tailed t-test (P < 0.05), confirming that there is a downward trend in the location of the rotation axis with movement amplitude. By contrast, we found a rather small, but statistically significant, positive slope (+0.5 mm/deg) in subject AB; the slope in subject SA (−0.4 mm/deg) was not significant. For the extension movement, we obtained similar results: five subjects had significant negative slopes ranging from −1.9 to −0.3 mm/deg. The two remaining subjects (WM and BB) are also intersubject differences in the location of the rotation axis belonging to the same movements.

### Table 3. S circle fit

<table>
<thead>
<tr>
<th>Subject</th>
<th>Movement</th>
<th>Component</th>
<th>b₁</th>
<th>b₂</th>
<th>R²</th>
<th>b₁</th>
<th>b₂</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>JG</td>
<td>Flexion</td>
<td>Sx</td>
<td>14.1 (1.9)</td>
<td>−2.0 (1.3)</td>
<td>0.66</td>
<td>−13.7 (1.6)</td>
<td>−13.7 (1.2)</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sy</td>
<td>0.5 (1.3)</td>
<td>0.74</td>
<td></td>
<td>−16.2 (2.0)</td>
<td>−18.1 (1.4)</td>
<td>0.70</td>
</tr>
<tr>
<td>WM</td>
<td>Flexion</td>
<td>Sx</td>
<td>30.5 (3.8)</td>
<td>−0.9 (2.6)</td>
<td>0.69</td>
<td>−29.5 (3.2)</td>
<td>−26.4 (2.4)</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sy</td>
<td>−3.5 (3.4)</td>
<td>−0.4 (2.4)</td>
<td>0.04</td>
<td>−4.1 (2.5)</td>
<td>−1.4 (1.8)</td>
<td>0.09</td>
</tr>
<tr>
<td>SA</td>
<td>Flexion</td>
<td>Sx</td>
<td>33.4 (4.9)</td>
<td>−0.6 (3.8)</td>
<td>0.67</td>
<td>−34.8 (2.4)</td>
<td>−25.9 (1.8)</td>
<td>0.90</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sy</td>
<td>−9.4 (3.3)</td>
<td>1.5 (2.2)</td>
<td>0.21</td>
<td>3.7 (2.0)</td>
<td>7.5 (1.3)</td>
<td>0.10</td>
</tr>
<tr>
<td>BB</td>
<td>Flexion</td>
<td>Sx</td>
<td>27.9 (2.2)</td>
<td>−2.2 (1.8)</td>
<td>0.88</td>
<td>−34.4 (2.3)</td>
<td>−30.3 (1.6)</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sy</td>
<td>21.3 (2.4)</td>
<td>−2.6 (1.6)</td>
<td>0.75</td>
<td>−27.1 (1.8)</td>
<td>−22.7 (1.3)</td>
<td>0.90</td>
</tr>
<tr>
<td>AB</td>
<td>Flexion</td>
<td>Sx</td>
<td>56.9 (3.6)</td>
<td>−1.7 (2.4)</td>
<td>0.88</td>
<td>−43.9 (2.5)</td>
<td>−42.6 (1.9)</td>
<td>0.91</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sy</td>
<td>−6.3 (4.0)</td>
<td>−1.6 (2.7)</td>
<td>0.07</td>
<td>−6.5 (1.6)</td>
<td>−3.4 (1.2)</td>
<td>0.34</td>
</tr>
<tr>
<td>TD</td>
<td>Flexion</td>
<td>Sx</td>
<td>28.1 (2.3)</td>
<td>−2.1 (1.5)</td>
<td>0.85</td>
<td>−26.4 (1.6)</td>
<td>−28.3 (1.2)</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sy</td>
<td>8.6 (2.3)</td>
<td>2.1 (1.6)</td>
<td>0.35</td>
<td>−12.7 (1.7)</td>
<td>−12.4 (1.3)</td>
<td>0.68</td>
</tr>
<tr>
<td>GM</td>
<td>Flexion</td>
<td>Sx</td>
<td>33.9 (2.3)</td>
<td>1.2 (1.6)</td>
<td>0.88</td>
<td>−29.1 (1.8)</td>
<td>−27.7 (1.4)</td>
<td>0.89</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sy</td>
<td>3.8 (2.3)</td>
<td>2.1 (1.6)</td>
<td>0.16</td>
<td>−11.0 (1.0)</td>
<td>−9.0 (0.8)</td>
<td>0.78</td>
</tr>
</tbody>
</table>

Parameters b₁ and b₂ in mm; b₂ was found to be very close to zero and is therefore not listed in the table. SD in parentheses.
had statistically significant positive slopes (0.6 and 0.2 mm/deg, respectively).

In summary, the data on flexion and extension of the head presented so far have shown that, dependent on the amplitude of the movement, the axis locations ranged between +20 and −100 mm from the interaural line. The data also demonstrate clear intersubject differences. In the next section, we discuss the location of the rotation axes for other movement directions in more detail.

Relation between axis location and movement direction

Figure 8 shows the locations of point S in body space for subject JG, by plotting all location vectors for positions at 25° eccentricity in the outward movement in three different views. Five movements were made to each target, and the coordinates of the S point for each target direction are indicated by the number of the target. Trials in which the subject initially chose the wrong target direction were excluded from the analysis, so that some target numbers appear less than five times in the figure. As the panels show, each S point component shows a systematic dependence on target direction. Close inspection of the S-component behavior suggested that its coordinates periodically were related to target direction. Specifically, the frontal view panel suggests that both for movements to the targets at the upper part of the clock (upper targets) and for movements to targets at the lower part of the clock (lower targets), the S points occupy a roughly circular path in the fronto-parallel body plane. Furthermore, for the upper targets requiring extension movements, the S points lie more posteriory, whereas for the lower targets, requiring flexion movements, the S points are situated more anteriorly (Fig. 8, side view and top view panels). Not every subject showed such a systematic behav-

![Figure 8](image_url)

**FIG. 8.** S-point locations taken from 5 centrifugal movements to each of the 12 targets at 25° eccentricity in the frontal plane in 4 subjects. ——, best-fit results obtained with Eqs. 8 and 9 (see RESULTS). One S circle is the result of movements toward the upper targets, the other of movements toward the lower targets. Numbers denote target positions on the clock-face stimulus array. For some targets, <5 S points are presented in the figure either because the irises were not visible in that part of the movement or because a trial was excluded from the analysis.
ior in the $S_y$ component as clearly as subject JG. In all subjects, we found that the possible axis locations in $x$ direction remained within 2 cm from the origin.

For all subjects, we found a strong relation between target direction on the one hand and $S_x$ and $S_z$ components on the other hand. To further explore the possibility that the $S$ points scattered around circular trajectories, we separately fitted these $S$ components for the upper targets as well as for the lower targets at $25^\circ$ eccentricity to periodic functions of the following general form

$$S_x = b_1 \sin (2 \pi \varphi / b_2) + b_3$$

$$S_z = b_1 \cos (2 \pi \varphi / b_2) + b_3$$

where $\varphi$ is the direction of the target (see METHODS) and $b_1$, $b_2$, and $b_3$ are constants. Because the optimal $b_1$ value could be different in the two fits, we allowed for the possibility that $S$-point trajectories could be elliptical rather than circular.

The fit results in Table 3 confirm that both the $y$ and $z$ components of axis location have a strong relation with target direction in all subjects. As shown in Table 3, we found large intersubject differences in the values of the fitted constants $b_1$ and $b_3$. The absolute values for $b_1$, representing the size of the circle, are generally smaller for extension movements (range 3.5–27.1 mm) than for flexion movements (range 13.7–56.9 mm). The values for $b_2$ were found to be close to zero and therefore were not presented in Table 3. The results listed in Table 3 and shown in Fig. 8 may be summarized as follows: as the head completes all centrifugal movements to all clock-face targets ($\varphi$: 0–360$^\circ$), the $S$-trajectory traces two circular paths in the frontoparallel plane. One $S$ circle (up circle) is the result of movements toward the upper targets, and the second $S$ circle (down circle) corresponds to the lower target movements.

Figure 9, showing the $y$ and $z$ components of the $S$ point for four subjects, illustrates that the two fits indeed yield two circles in the frontal $yz$ plane but also highlights, as mentioned earlier, that there are intersubject differences. In subjects JG and BB, the up and down $S$ circles have more or less equal diameters, indicating rather symmetrical patterns for flexion and extension movements. For other subjects (GM and TD), we found circles with clearly different diameters, indicating more asymmetrical patterns. In such cases, we invariably found larger circles for flexion movements. As long as the $S$ circles had reasonably large diameters with respect to the scatter in the data, we found large goodness-of-fit values, i.e., $R^2 > 0.7$ (see Table 3). However, for $S$ circles with a small diameter, which always belong to extension movements, the goodness-of-fit was much less, even though, as shown in Fig. 9, the tendency of a circular pattern still could be observed in such cases.

We also checked whether there was a significant correlation between axis location and movement amplitude for all target directions. For movements with flexion or extension components, the data presented earlier in Figs. 5–7 suggest that the locations of the axes are not fixed but tend to move downward with increasing movement amplitude. In Fig. 10, we present the trajectories of the $S$ point for subject GM for movements requiring flexion at 10, 15, 20, 25, and 30$^\circ$ movement amplitude. The spatial location of the rotation

![Image](http://jn.physiology.org/)

**FIG. 10.** Frontal view of $S$-point locations taken from movements with a flexion component for various movement amplitudes (10, 15, 20, 25, and 30$^\circ$). For the 6:00 target, 1 $S$ point is missing (for 30$^\circ$ amplitude). For purely horizontal movements (3:00 and 9:00), the location of the $S$ point remains more or less constant. For movements with a vertical component, however, there is a shift of the $S$ point in a direction away from the origin for larger movement amplitudes. Subject: GM.
axis for 3:00 and 9:00 movements (pure horizontal movements) remains almost constant. For the other targets, which require flexion components, there is a clear trend for the distance of the S point to the origin to increase with movement amplitude. We found similar results in the other subjects presented in Fig. 9.

Translation along the helical axis

If the head movements recorded in this study result mainly from rotations about joints (see Introduction), one would expect the translation component, found with the helical axis description, to be quite limited. The maximum values of the translation along the rotation axis found in our subjects were indeed rather small and ranged from 1.5 to 5 mm (average 3.1 mm). For purely vertical movements (6:00 and 12:00), the translation term was found to be near zero, whereas the largest values of the translation term were found for purely horizontal movements (3:00 and 9:00).

DISCUSSION

Accounting for translation in the description of head posture

In general, head movements in free gaze shifts not only involve changes in the orientation but also translations of the center of gravity of the head with respect to the trunk. This combination of rotation and translation is the result of changing the alignments of the cervical vertebrae that link the skull to the trunk. Graf et al. (1992) have studied the biomechanics of the head-neck system and the range of motion of each segment of the neck in a number of vertebrates. They concluded that the main component of horizontal head movements, which occur mainly by rotation in the atlantoaxial joint, is supplemented by small rotations of the other cervical vertebrae relative to each other. They also found that vertical movements are concentrated around the atlanto-occipital articulation and the cervico-thoracic junction. Because of these motions in the cervical spine, a change in head posture typically involves a change in head orientation in combination with a translation of the center of mass. Up until now, most studies concerning head movements made use of the coil technique and hence could determine only the orientation of the head. In our study, we have extended the rotation vector description by applying the helical axes approach. Using this concept, any head position can be described with respect to a certain reference position as if it were due to a rotation and a translation along a single unique axis. The advantage of this approach is that it yields the classical rotation vector as well as the location in space of the rotation axis.

The reader should be aware of the fact that we have used this tool to describe head positions adopted in the course of movement, not with the aim of studying head velocity. All the positions adopted by the head during head movements are expressed with respect to a common reference position. Therefore the data in Figs. 5–10 describe the location of the rotation axes used to rotate and translate the head from the reference position to the sequence of head positions that make up the movement trajectory of the head. The trajectory of the head during the movement in Cartesian space can be reconstructed easily when rotation and translation along the helical axes are known. We shall first concentrate on the rotation vector part of our study. In this respect, our descriptive approach resembles that of earlier studies on head movements based on the coil technique and, therefore, would be expected to yield similar results.

Rotation vector part

If head orientations in space obeyed Listing’s law, as do eye orientations in the head, these rotation vectors should all be confined to a flat plane (see Methods). The fact that a second-order curved surface gives a significantly better fit of our data than a flat plane indicates that the head does not follow Listing’s law exactly. The torsional variations about the best-fit second-order surfaces (thickness) ranged between 0.74 and 1.63°, indicating that in a strict sense the head does even not obey Donders’ law, which requires that head orientation for a given direction is always the same. However, judged from rotation vector data, the deviations from Donders’ law are rather small because the thickness of the fitted surface was on average only 1.1 ± 0.27°.

The twist scores of the second-order curved surface varied between −0.28 and −1.13, on average −0.73 ± 0.27. As has been noted before (Glenn and Vilis 1992; Radau et al. 1994; Theeuwen et al. 1993), the fact that they are all negative indicates that the orientations of the head behave qualitatively like those of a Fick gimbal, which has a horizontal axis nested within a space-fixed vertical axis. Glenn and Vilis (1992) found an average twist score of −0.68 ± 0.21 and a thickness of 2.56 ± 0.53° in body-fixed subjects, whereas Theeuwen et al. (1993) reported a twist score of −0.68 ± 0.13 and a thickness of 2.7 ± 0.4°. Radau et al. (1994) studied the behavior of the head relative to the chest when the body was free to move and found an average twist score of about −0.95 and a thickness of 2.28 ± 0.89°.

We conclude that, as far as the rotational components of head movement are concerned, the results obtained with our recording technique and description format are in line with the data reported in the literature.

Location of the head rotation axes

Despite the important features revealed by the earlier descriptions of head movement in terms of classical rotation vectors (e.g., Radau et al. 1994; Tweed et al. 1995; Viirre et al. 1986), the rotation vector approach cannot yield a complete picture because it passes over the fact that the head also translates relative to the body. The helical axes description presented in this paper can include the translational components of head movement by its ability to determine the best-fitting spatial location of the rotation axis and yet is connected closely to the powerful tool of the classical rotation vectors.

The fact that the classical rotation vectors follow curved trajectories during gaze shifts of the head, see Fig. 3, indicates that the axes of rotation do not remain perfectly parallel throughout the movement. However, taking into account that we are dealing with a complex head-neck anatomy, which contains >30 muscles, the deviations are quite small. Based on this type of evidence, then, one might argue in line with
suggesting that the same cervical joints are used to achieve is too small to have much influence on the VOR in fixating movements with an extension component. In some subjects, see anterior-posterior difference in the location of the rotation axes for movements with extension components. This pattern the head, which, owing to linear accelerations of the head, has a flexion or extension head position of the same eccentricity. However, in most subjects, we found a smaller circle corresponding to the steadily increasing recruitment found for vertical movements and the maximum translation of gravity. Our description provides a general estimate of the center of gravity of the head, see METHODS was reasonably by a single axis rotation. for head movements in various directions occupy different spatial locations scattered around a circle and that the axes are increasingly shifted as movement amplitude increases. The fact that we found circles of different size among subjects illustrates that different subjects use different strategies in resolving the kinematic redundancy problem. It should be noted that the classical rotation vector results in our study, like previous studies, yield a much more homogeneous picture with little, if any, indication of individual movement strategies. Clearly, our data strongly argue against regarding the validity of Donders’ law, on the basis of such data, as the expression of a generally valid solution for the kinematic redundancy problem.

**Modulation of the VOR by eccentric head rotation**

In all subjects, we found that the translation along the rotation axis (which must not be confused with the translation of the center of gravity of the head, see METHODS) was small, never exceeding 5 mm. Hardly any translation was found for vertical movements and the maximum translation of ~5 mm occurred during horizontal movements. Winters et al. (1993) mentioned translation terms of the same size, also occurring during horizontal movements, and explained this as being generated between the vertebrae in the C1–C2 complex. The fact that the translations were rather small further justifies the use of the helical axes description as an appropriate tool for describing movements about joints that produce rotations rather than translations.

Several studies (Buizza et al. 1981; Crane et al. 1997; Snyder and King 1992; Viirre and Demer 1996; Viirre et al. 1986) with passive rotation have shown that the gain of the VOR can be modulated by the location of the head rotation axis. In this context, we will now discuss the possible functional consequences of the location of the rotation axis and its shift with movement amplitude in natural head movements on the modulation of the VOR. The movements of the head are detected by the vestibular organs. The semicircular canals detect angular rotations of the head, whereas the oto-liths mainly measure linear acceleration, including the direction of gravity. Our description provides a general estimate of the location of the rotation axis of the head, which may be used by the VOR to improve its performance. Figures 8–10 show that the range of possible axis locations is clearly delineated. Most S locations fit in a “box” of 4 × 10 × 10 cm in the x, y, and z directions, respectively. The extra anterior-posterior difference in the location of the rotation axis during vertical flexion or vertical extension movements is too small to have much influence on the VOR in fixating a near target. However, the situation is different for the up-down left-right plane where we found considerably more freedom of axis location in both the lateral and up-down direction. The shift of the rotation axis for movements with a vertical component results in an additional translation of the head, which, owing to linear accelerations of the head, will excite the oto-liths.

To estimate how the downward shift of the rotation axis during vertical head movements affects the desired compensatory eye movement in fixating a near target, we did some
simulations (see Fig. 11). In the example to be discussed, the eye is located 8 cm in front (x axis) and 3 cm above (z axis) the origin, which is the center of the interaural axis. The angular velocity vector of head rotation is directed along the y axis and has a bell-shaped amplitude profile. The center of rotation moves linearly with the rotation angle downward along the negative z axis with a slope of $-1.5$ mm/deg (see Table 2) starting at 2 cm below the origin. The derivative of eye position is the cross product of angular velocity and the vectorial difference between eye position and center of rotation. In Fig. 11, the results of this study are shown.

**FLEXION**

**EXTENSION**

**FIG. 11.** Simulation of vestibulo-ocular reflex (VOR) modulation required by eccentric head rotation assuming the eye was located 8 cm in front (x axis) and 3 cm (z axis) above the origin (the center of the interaural axis). Angular velocity vector is directed along the y axis and has a bell-shaped amplitude profile. Rotation angle is the integral of the angular velocity vector. In case of a fixed-axis rotation, the center of rotation remains fixed in space. For a moving-axis rotation, the center of rotation $c^*$ moves linearly with rotation angle along the z axis with a slope of $-1.5$ mm/deg. Derivative of eye position is the cross product of angular velocity and the vectorial difference between eye position and center of rotation. **Top:** trajectories of the eye due to both a fixed-axis rotation and a rotation with shifting rotation center for an extension as well as a flexion movement. **Middle:** required VOR gain is given as a function of target distance for both a fixed axis and a moving axis rotation. **Bottom:** contribution of the translation of the rotation axis to the required VOR gain. e, initial eye position; $e'$, end position eye for moving axis; $e^*$, end position eye for fixed axis rotation; $T$, target; $c^*$, fixed center of rotation; $c^*$, moving center of rotation.
The figure shows that only for near targets (within 50 cm) the downward shift of the rotation axis has some effect on the required VOR gain. In this case of a flexion movement, the required VOR gain has to be larger than for the case of a fixed axis rotation. In the bottom left panel, the part of the VOR gain due to the translation of the rotation axis is given as function of the total required VOR gain. From this simulation it follows that a maximum of 10% of the ideal VOR gain is due to the downward translation of the rotation axis. In Fig. 11, right, the required VOR gain is given for an extension movement of the head. The downward translation of the rotation axis has a decreasing effect on the required VOR gain in comparison with a fixed axis rotation (see Fig. 11, middle). The bottom right panel shows that a maximum of 15% of the VOR-gain is due to the translation of the rotation axis in this particular example. In summary, the contribution of translation of the rotation axis on the required VOR gain in fixing a nearby target is limited, but not negligible.

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