



Three-dimensional eye position during static roll and pitch in humans

Christopher J. Bockisch^{a,*}, Thomas Haslwanter^{a,b}

^a Department of Neurology, University Hospital Zürich, Frauenklinikstr. 26, 8091 Zürich, Switzerland

^b Institute of Theoretical Physics, ETH Zürich, Switzerland

Received 12 July 2000; received in revised form 27 February 2001

Abstract

We investigated how three-dimensional (3D) eye position is influenced by static head position relative to gravity, a reflex probably mediated by the otolith organs. In monkeys, the torsional component of eye position is modulated by gravity, but little data is available in humans. Subjects were held in different head/body tilts in roll and pitch for 35 s while we measured 3D eye position with scleral coils, and we used methods that reduced torsion artifacts produced by the eyelids pressing on the contact lens and exit wire. 3D eye positions were described by planar fits to the data (Listing's plane), and changes in these planes showed how torsion varied with head position. Similar to findings in monkeys, the eyes counterrolled during roll tilts independent of horizontal and vertical eye position, reaching a maximum torsion of 4.9°. Counterroll was not proportional to the shear force on the macula of the utricles: gain (torsion/sine of the head roll angle) decreased by 50% from near upright to ear down. During pitch forward, torsion increased when subjects looked right, and decreased when they looked left. However, the maximum change of torsion was only -0.06° per degree of horizontal eye position, which is less than reported in monkey. Also in contrast to monkey, we found little change in torsion when subjects were pitched backwards. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Listing's law; Otolith; Scleral search coils; Three-dimensional eye movements; Vestibulo-ocular reflex

1. Introduction

Fuelled by the availability of accurate three-dimensional (3D) eye position recordings, interest in ocular torsion has increased among visual psychophysicists, oculomotor physiologists, and mathematicians. Recent research in humans has concentrated on behaviors where torsion varies with vergence for obtaining clues about the functional importance of ocular torsion, but has ignored other sources of variation of torsional eye position. In monkeys, ocular torsion also varies with head orientation with respect to gravity (Haslwanter, Straumann, Hess, & Henn, 1992), presumably through input from the otolith organs. Hess and Angelaki (1997a,b) have speculated that these torsional eye movement patterns during pitch tilts, which are larger in dynamic conditions, reflect an orienting mechanism that seeks to stabilize eye orientation relative to gravity.

In humans, however, the dependence of eye position on gravity during dynamic reorientations is considerably smaller (Haslwanter, Hess, & Aw, 1999a), suggesting that the vestibular-ocular systems in man and monkey use different control strategies. Whether the dependence of torsion on horizontal and vertical eye position in humans is suppressed under dynamic conditions, or if it is already absent in static conditions, is not known because the effect of static orientation on 3D eye position has not been measured.

In monkeys, the effect of gravity on 3D eye position has been determined by Haslwanter et al. (1992), who found that the torsional component of eye position was modulated by static head roll and pitch position. Torsion during head roll was not unexpected: when the monkey was put into an ear down position, the eyes rotated in the opposite direction by up to 6° ('ocular counterroll'). The magnitude of counterroll was independent of gaze direction. Surprisingly, torsional eye position changes were also found with head pitch: when monkeys were supine, leftward eye positions were asso-

* Corresponding author. Tel.: +41-1-2554507.

E-mail address: chris.bockisch@nos.usz.ch (C.J. Bockisch).

ciated with clockwise torsion, whereas rightward eye positions were associated with counterclockwise torsion. In prone positions the opposite behavior was observed.

In humans, most previous studies of eye position during head roll have been restricted to recording ocular torsion when looking straight ahead. Slow continuous rotation ($\sim 3^\circ/\text{s}$) about the naso-occipital axis ('head roll') has been used to study otolith-ocular responses because it avoids stimulating the semicircular canals (Diamond, Markham, Simpson, & Curthoys, 1979). While fixating a target, the eyes counterroll (Diamond et al., 1979; Collewijn, Van der Steen, Ferman, & Jansen, 1985), partially compensating for the head roll. The amount of ocular counterroll during slow head roll is small, however, reaching a maximum of about 6° when the head is rolled $60\text{--}90^\circ$ (Diamond & Markham, 1983). One study in humans measured torsion not only for looking straight ahead, but also for different gaze directions (Klier & Crawford, 1998). That study, in which the body stayed upright and the head was rolled by 45° , reported torsional shifts of about 7.4° and 9.5° for monocular and binocular viewing, respectively. No pitch data have been reported in humans.

There are several reasons to believe that otolith control of static eye position may differ in human and non-human primates. Recent studies of the dynamic contribution of the otolith organs to the vestibulo-ocular reflex (VOR) show interspecies differences. For example, during yaw-rotations about an earth horizontal axis ('barbecue spit' rotation) in rhesus monkeys, ocular torsion in eccentric eye positions is strongly modulated by head orientation with respect to gravity (Hess & Angelaki, 1997b); humans show no such modulation (Haslwanter et al., 1999a). Further, dynamic otolith signals increase the gain of the torsional VOR in humans (Schmid-Priscoveanu, Straumann, & Kori, 2000) but not monkeys (Hess & Angelaki, 1997b). Humans also have reduced otolith-canal interaction compared to monkeys during pitching-while-rotating (Raphan, Cohen, Suzuki, & Henn, 1983; Hess & Angelaki, 1993; Haslwanter, Jaeger, & Fetter, 1999b). Finally, since adaptive mechanisms continuously fine-tune oculomotor performance, we expect that otolith influence on eye movements depends upon the demands placed on vision during typical movements, which could vary by species.

In the experiments presented below we measured 3D eye position with human subjects in different static roll and pitch positions to determine the contribution of the otoliths to the control of 3D eye position. We found torsional changes during head roll similar to that for monkeys, but our human data for pitch rotations were different. A brief report of these results has been presented previously (Bockisch, Jaeger, Duersteler, & Haslwanter, 2000).

2. Methods

2.1. Subjects

Our six volunteers ranged in age from 32 to 38 years (34.8 ± 2.5 , mean \pm S.D.), were free of any known vestibular or ocular pathologies, and had previously worn eye coils in oculomotor experiments.

2.2. Apparatus

The 3D human turntable at the Department of Neurology, Zürich, is driven by three servo-controlled motorized axes (Acutronic, Switzerland), and controlled with LabVIEW™ software. All axes needed for this paradigm can be accelerated up to $200^\circ/\text{s}^2$ or more. Subjects were comfortably seated in a chair, and secured with safety belts and evacuation pillows molded to the upper body and legs. The interaural line and the midline were positioned at the intersection of the three axes of the turntable. Head movements were restrained by an individually adjusted mask (Sinmed BV, The Netherlands), made of a thermoplastic material (Posicast™) that was molded to the contour of the head after warming. The mask was attached to the back of the chair and very effectively restricted head movement without causing discomfort, and holes cut in the mask allowed unrestricted vision.

Subjects viewed with both eyes, and the 3D position of one eye was measured with the dual search coil technique, with search coils manufactured by Skalar (Delft, The Netherlands). The head was surrounded by a chair-fixed coil frame (side length 0.5 m) that produced three orthogonal magnetic fields with frequencies of 42.6, 55.5 and 83.3 kHz (Remmel type system, modified by A. Lasker, Baltimore) (Remmel, 1984). Details of our calibration procedure have been given elsewhere (Straumann, Zee, Solomon, Lasker, & Roberts, 1995). Briefly, we zeroed voltage offsets while placing the search coils in a metal tube to shield them from the magnetic fields. Then we measured the relative gains of the three magnetic fields with the search coils on a gimbal system placed in the magnetic field at the same location as the measured eye. The orientation of the coil on the eye was determined during the experiment by recording the signals obtained when the subject fixated a central reference target. Eye- and chair-position signals were digitized with a 16 bit analog-to-digital converter, sampled at 500 Hz, and analyzed offline with MatLab software (The MathWorks, Boston MA).

Visual fixation targets (0.5° diameter dots) were placed on a chair-fixed screen 60 cm in front of the subject (vergence angle $\approx 6^\circ$). In addition to a central fixation point, targets were placed along two concentric rings with radii of 10° and 20° . Each ring had eight

equally spaced dots, placed on the primary axes and main diagonals. (The stimulus can be appreciated from the fixation positions in Fig. 1.)

Since torsion depends on the vergence angle (Mok, Ro, Cadera, Crawford, & Vilis, 1992), we performed pilot studies in one subject (TH) over the full range of roll orientations, with targets at 60 cm and 1.5 m, and both target distances produced the same results. Since we used the same targets at all head orientations, we did not confound the effect of gravity on eye position with target distance.

2.3. Procedure

Subjects began each trial by fixating the central target for 5 s while upright. With a metronome set to 70 beats/min, subjects fixated each of the targets. To control hysteresis effects of 3D eye position such as those that occur when looking in a circular pattern (Ferman,

Collewijn, & van den Berg, 1987; DeSouza, Nicolle, & Vilis, 1997), subjects were instructed to first fix the central position, and then look to each target along one radial direction before looking back to the central target. The subject then chose a different radial direction, and continued until all targets were fixated at least once. This procedure was performed with subjects in the upright position, as well as in the different tilted orientations. For tilted orientations, the chair was rotated to a new roll or pitch position and held there for at least 45 s. The subject was then returned to the upright position for at least 15 s, fixated the central reference position, and was subsequently moved into a new roll or pitch position. Returning to upright after each position helped to keep the subject comfortable and facilitated data analysis (see Section 2.4). The total duration of each experiment was about 35–40 min. Eye movements were measured in each chair position once for every subject.

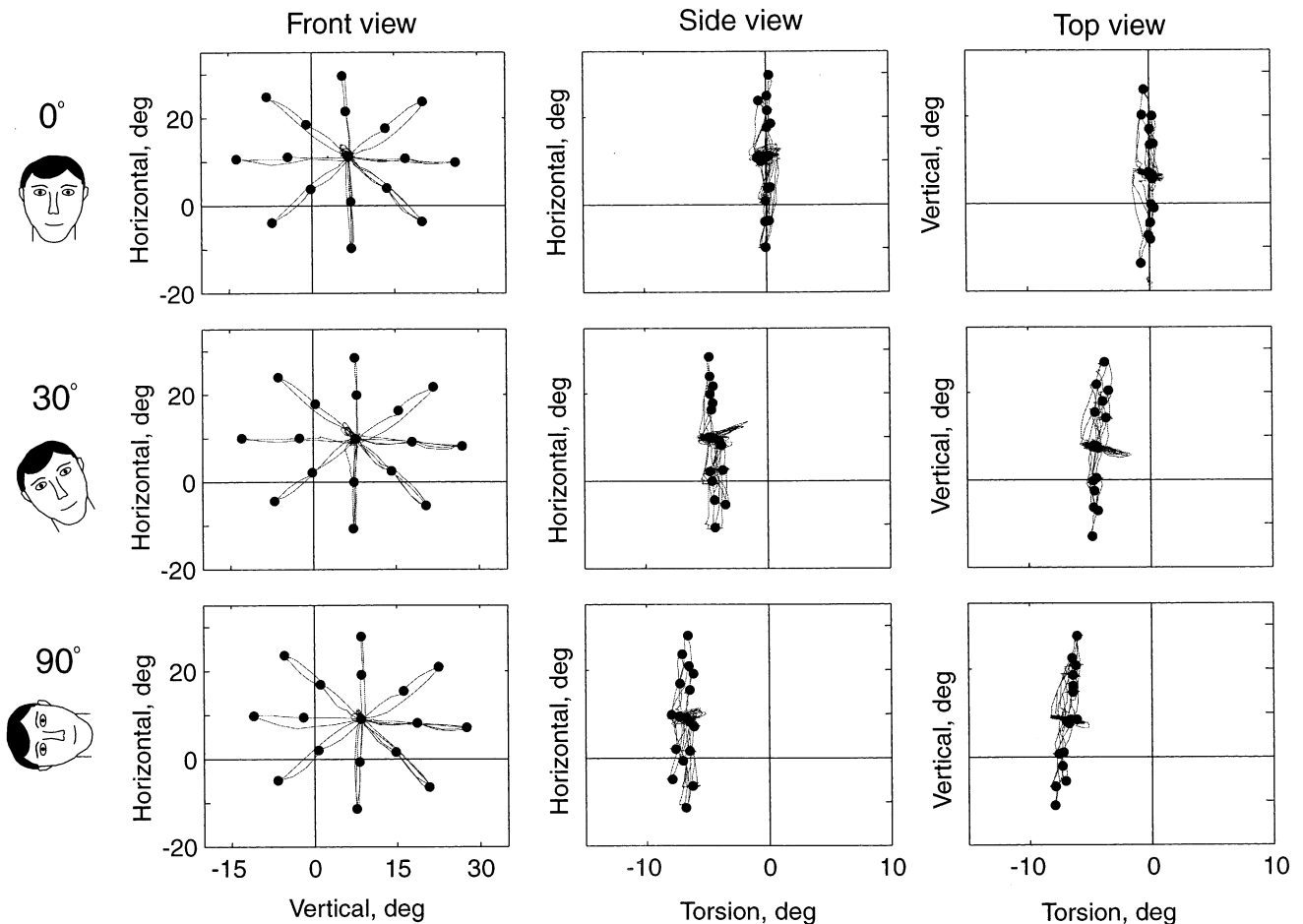


Fig. 1. Eye position and mean fixation points (●) for subject CB when he was tilted right-ear-down. Eye positions are represented in a head-fixed coordinate system, so, for example, 'vertical' eye movements refer to rotations about the interaural axis for all head orientations. For illustration, we chose the reference position such that in the upright position, the plane of rotation vectors is viewed exactly sideways (top row, center and right). Left: front view of rotation vectors, showing vertical and horizontal eye position. Note that the abscissa scale for the front view is different from that for the side and top views. Middle: side view, showing how torsion varies with horizontal eye position ('pitch tilt'). Right: top view, showing the variation of torsion with vertical eye position ('yaw tilt').

Subjects were moved with accelerations of $20^\circ/\text{s}^2$, and eye position recording began 10 s (for chair rotations of 90° or less) or 15 s ($>90^\circ$) after the start of chair movement. We measured eye movements at roll and pitch positions of $0\text{--}360^\circ$, concentrating on positions near upright. Right-ear down and prone corresponds to $+90^\circ$.

To ensure that vestibular canal inputs were not affecting eye movements, we simulated the canal response to the head movements to estimate the maximum velocity transduced by the canals. We assumed a canal time constant of 7 s for all semicircular canals, a head orientation such that Reid's line was 10° nose up with respect to earth vertical, and orientations for the canals as given by Blanks, Curthoys, and Markham (1975). The simulation indicated that the maximum eye velocity transduced by any canal was about $3.8^\circ/\text{s}$ at the beginning of eye position recording. Since all our experiments were done in the light, we expect that this small canal activity was completely suppressed by the constant visual input, and in fact we saw no nystagmus.

2.4. Data analysis

We represent eye positions as 3D rotation vectors in a right handed, head-fixed coordinate system. Positive eye position values indicate clockwise, down, and left from the subject's perspective. We call rotation around the naso-occipital axis 'torsion', and distinguish it from rotation about the line-of-sight. In our usage, *torsion* only corresponds to rotation about the line-of-sight when the eye is looking straight-ahead. Likewise, we refer to rotations about the interaural axis as *vertical* eye movements, and rotations about the axis pointing through the top of the head as *horizontal* eye movements. We use eye position to refer to 3D eye position in head-fixed coordinates, and it should not be confused with *gaze direction* (i.e. the line of sight). The reference position for computing the rotation vectors, corresponding to 0° horizontally, vertically, and torsionally, was always determined by the eye position when the subject was upright and fixating the central target. We removed saccades and movements during blinks, and calculated average eye positions when the subject fixated targets.

A complete description of the effect of gravity on eye position requires determining torsion for all combinations of horizontal and vertical eye position. When the head is upright and stationary and visual targets are a fixed distance from the head, torsion is uniquely specified by horizontal and vertical gaze direction (Donders' Law), and the amount of torsion is given by Listing's Law (Helmholtz, 1867). Listing's Law states that when eye positions are described by rotations from a reference position, all rotation axes lie in a plane. With a suitably chosen reference position (primary

position), this plane is called *Listing's Plane* (LP). Thus, changes in the orientation of LP provide a convenient metric for describing modifications of the global properties of 3D eye positions. (Fig. 1 provides examples of such Listing's planes.) We fit a plane to the rotation vectors describing 3D eye positions collected at each roll and pitch position: $Torsion = intercept + \beta_1 * vertical_eye_position + \beta_2 * horizontal_eye_position$. The intercept describes the translation of the plane of rotation vectors along the torsion axis, and therefore indicates a constant torsional offset. The slope parameters (β_1 , β_2) describe how torsion varies with vertical and horizontal eye position. As planes fit to the mean fixation data showed little difference to planes obtained by taking just saccades or including all eye positions, we report only the fits to the mean fixation data, since these fits are not biased by sample size (fixation duration). The *thickness* of the fitted plane is defined as the standard deviation of the distance of the eye positions from the best-fit plane. To compare how the dependence of torsion on horizontal and vertical eye position changed with head orientation, we subtracted within each subject the slope parameters of the eye position planes when the subject was upright from the measured slope values. Since visual inspection of the data did not reveal any trends towards curvature, and the quality of the plane fits did not suggest so either, we did not investigate higher order fits any further.

We will use the convention introduced by Tweed, Cadera, and Vilis (1990) and refer to planes of rotation vectors describing eye position as 'displacement planes' (DPs), since the rotation vectors making up these planes describe the displacement from the reference position to the current eye position. While the change in the torsional offset of these planes is equivalent to the torsional offset of the corresponding LPs, the change in orientation is half the amount of the orientation change of LP. For a detailed treatment of the differences between DP and LP, see Haslwanter (1995).

2.5. Coil artifacts

In pilot experiments where we attached a search coil to the upper eyelid we sometimes noticed torsion associated with blinks (Fig. 2), such as those reported by Collewijn et al. (1985) and attributed to the contact lens slipping on the eye. Since the contact lens is tightly coupled to the conjunctiva, and the conjunctiva bound tightly only at the limbus and the fornix, the coil can rotate with the conjunctiva relative to the cornea. While torsion often returned to the pre-blink value when horizontal and vertical eye position was stable, offsets were sometimes observed that either did not reset, or reset slowly over hundreds of milliseconds. Collewijn et al. (1985) and Straumann, Zee, Solomon, and Kramer (1996) also observed long-term (e.g. 30 min) drift in

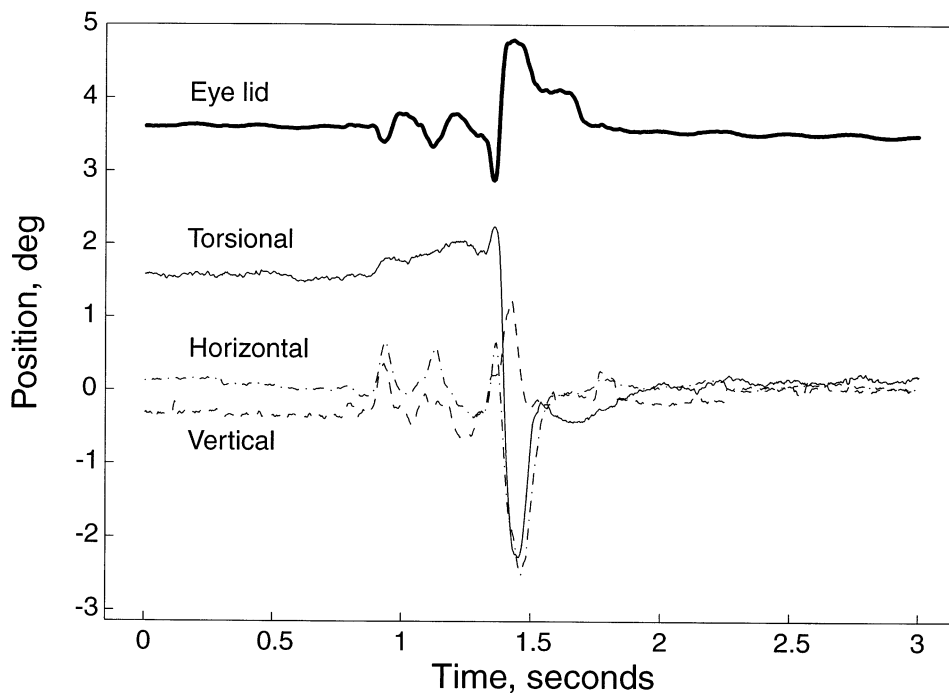


Fig. 2. Coil slippage during a blink. Eye position is shown along with the signal of a search coil attached to the upper eyelid (in arbitrary units). The subject fixated a target approximately straight ahead for 3 s. At about 0.8 s the upper eyelid began to move, as did the eye position signals. Horizontal and vertical eye position returned to their pre-blink values, but torsion retained an offset of about 1.5°.

torsion, which they attributed to coil slippage. While some torsion during blinks probably reflects an actual change in eye position, some might be due to the coil slipping when the upper eyelid pushes on the wire exiting from the contact lens, or on the contact lens itself. We measured reference positions before and after each trial when the subject was upright (about every minute). For these fixations, the torsional standard deviation across subjects was on average 1.3°, which was considerably higher than standard deviations for vertical (0.4°) and horizontal (0.3°) eye position. This result is consistent with our interpretation that coil slippage differentially affects torsion. To reduce these artifacts, we averaged reference positions before and after each trial when calculating rotation vectors. Note that the method used by Steffen, Walker, and Zee (2000), who re-determined the reference position after each eccentric eye movement, cannot be used here, since ocular counterroll moves the eye away from the reference position. Experiments with scleral search coils concentrating on eye velocity are not affected by the problem of coil slippage: the slippage only leads to artifacts during the short period of coil slippage itself, and otherwise leaves eye velocity measurements unaffected.

Coils were always placed with the lead wire exiting nasally. Thus, torsion that rolls the upper pole of the eye nasally moves the lead wire close to the lower eyelid, which could hinder further rotation. We mea-

sured the left eye in half our subjects, and the right eye in the other half, and all our subjects showed less counterroll when rolled towards the side of the measured eye. Using photographic methods that are not subject to these torsion artifacts, Diamond and Markham (1983) found that binocular counterroll when looking straight ahead was conjugate. More recently, they reported that while some torsional disconjugacy can be observed during static roll, the direction of the disconjugacy is random across subjects and repetitions (Diamond & Markham, 2000). (In fact, some of our subjects reported double vision when upside down.) Thus, the consistent asymmetrical counterroll we find suggests that the lower eyelid inhibits coil rotation. Therefore, we concentrated on data when the subject rolls away from the measured eye, and converted the data such that all measured eyes appear as left eyes, and all head rolls appear as right-ear-down.

3. Results

3.1. Change of torsion with head roll

For all subjects and roll angles, eye positions were closely confined to a plane. Plane thickness across all subjects and roll angles averaged 0.4° (range 0.2–0.7°), and we found no trend for the thickness to vary with roll angle.

Fig. 1 shows front, side, and top views of the eye positions for subject CB for roll angles of 0, 30 and 90°, with the mean eye position during target fixation indicated with filled circles. For the figure, the reference position was chosen such that the DPs are seen ‘edge-on’ when the subject was upright (top row), so changes in the orientation and displacement of the plane are easily visualized. (This change of reference position also induces the horizontal/vertical shift of the displayed rotation vectors.) The front view (left) shows horizontal versus vertical eye position. The side view (middle) shows the *pitch tilt* of DP, i.e. how torsion varies with horizontal eye position; and the top view (right) shows the *yaw tilt* of DP, i.e. how torsion varies with vertical eye position. Increasing head roll caused an increase in torsion at all vertical and horizontal eye positions, that is, the plane of rotation vectors shifted along the torsion axis. In this subject small changes in the yaw tilt (right column) also occurred, with torsion varying slightly with vertical eye position as the subject rolled from upright. However, across all subjects we did not find any trend for torsion to vary with either horizontal or vertical eye position at different head roll angles. In other words, we found no

systematic trend for the orientation of DP to vary with head roll angle.

On average, ocular counterroll increased with head roll angle to about 60°, when counterroll was -4.8° (Fig. 3). Torsion was similar at the ear down position (-4.9°), and then returned towards zero as the subject rolled upside-down. For comparison, Fig. 3 also shows the mean counterroll data of four rhesus monkeys recently collected by Cabungcal, Misslisch, Scherberger, Hepp, and Hess (2001).

Force on the (approximately) horizontal utricles varies with the sine of the head roll angle, and force on the (approximately) vertical saccules with the cosine. Therefore, we tried modeling our data as a linear combination of the sine and cosine of the head roll angle, as well as their interaction, since an interaction of the utricular and saccular signal might account for the sharp increase in torsion at small roll angles and the apparent asymmetry around the ear-down position. However, whereas the (utricular) sine component was significantly different from zero (coefficient = 4.35; $t = 8.8$, $P < 0.0001$), the (saccular) cosine (coefficient = -0.17 , $t = 0.5$, $P < 0.59$) and the interaction (coefficient = 1.5; $t = 1.8$, $P < 0.07$) were not.

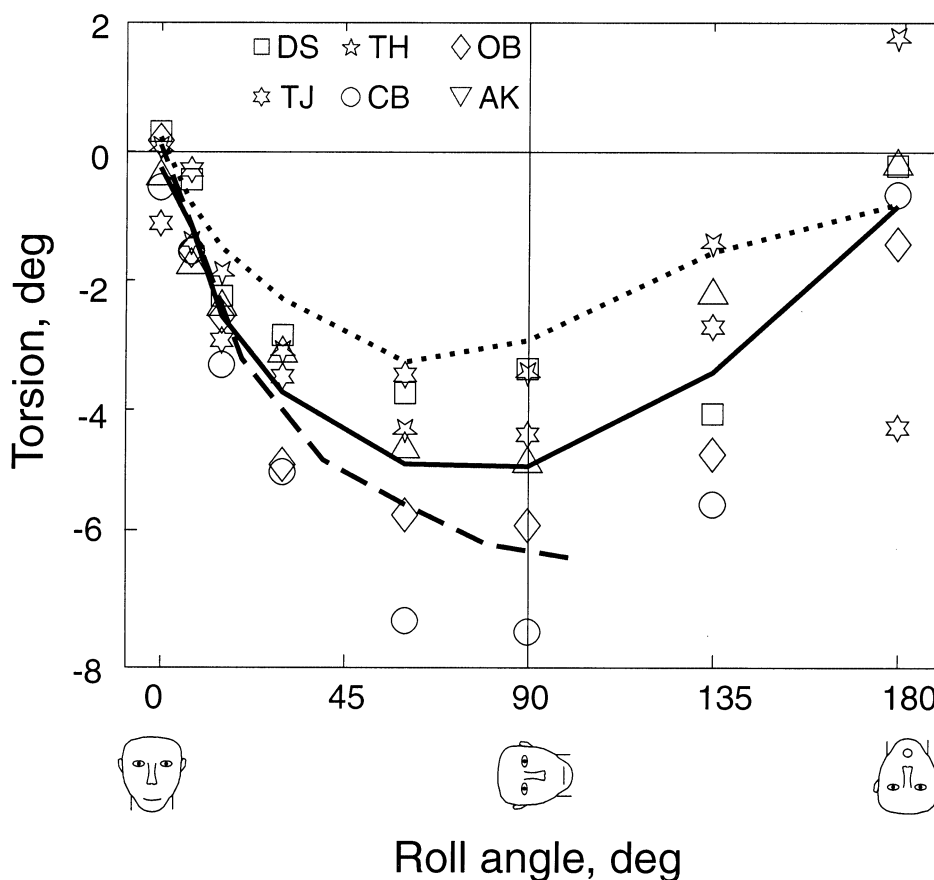


Fig. 3. Change in torsion during head roll (the intercept of the best-fit plane to the rotation vectors). Each symbol represents data from a different subject, and the solid line is their mean. The dotted line is the inverted mean torsion for head roll in the opposite direction. We believe the reduced torsion is an artifact due to the lower eyelid touching the exit wire of the contact lens, thereby limiting rotation of the scleral search coil (see Section 2). The dashed line is data from rhesus monkey (Cabungcal et al., 2001).

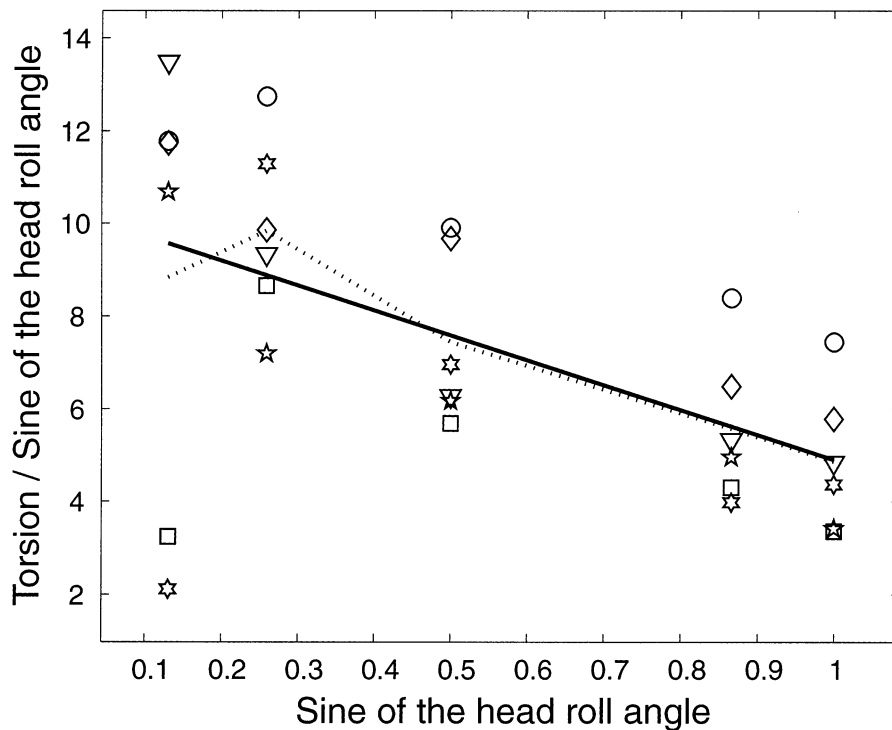


Fig. 4. Torsion gain (torsion/sine of the head roll angle) decreased with the sine of the roll angle. Points are individual subjects (as in Fig. 3), and the dotted line is their mean. The solid line is the best linear fit.

If counterroll were proportional to the force on the utricle, we would expect that torsion gain (torsion/sine of the head roll) would be constant across all head angles. However, we found that torsion gain decreased with the sine of head roll angle (Fig. 4). The slope of the best-fit line of torsion gain versus the sine of the head roll angle was significantly different from zero (slope = -5.4 , $t = 3.8$; $P < 0.001$).

3.2. Change of torsion with head pitch

During static head pitch, the DP thickness also remained small (see, for example, Fig. 5). It averaged 0.4° across all subjects and pitch angles (range 0.2 – 0.8°), and did not vary with head pitch angle.

When the head pitched forward, the eyes rotated counterclockwise when the subject looked left, and clockwise when the subject looked right (Fig. 6). That is, DP tilted backwards. When the head pitched forward 135° and 180° , the slope of DP was on average -0.06 , indicating that torsion changed -0.6° for every 10° of horizontal eye position. This corresponds to a -3.4° change in the orientation of DP. In contrast, torsion did not vary with horizontal eye position when subjects were supine (t -tests with a Bonferroni correction, $P = 0.05/6 = 0.0083$, showed no significant difference for any supine head position; all t s < 3.7 ; all P s > 0.014 , all df s = 5). For comparison, Fig. 6 also shows similar data recently collected in monkey (Cabungcal et al., 2001).

The yaw-tilt of DP changed when the subject was upside-down such that the eyes rotated clockwise when the subject looked down, and counter clockwise when the subject looked up. On average, the maximum yaw-slope was 0.04 (torsion/vertical eye position) at 225° . We fit a 0.5 frequency sine wave to the yaw-tilt data, and the amplitude (0.03), was significantly different from zero ($P < 0.001$). The average torsion (displacement of DP along the nasal-occipital axis) did not vary with head pitch angle.

4. Discussion

4.1. Effect of head roll on 3D eye position

As expected, our study shows that ocular torsion depends on the head roll position. In all orientations, torsion varied uniformly with vertical and horizontal eye position, i.e. there was little change in the orientation of DP. The maximum counterroll was 4 – 5° , and occurred with static head roll between 60 and 90° from upright. Our results are similar to those found in monkey, where there was also no change in the orientation of DP and maximum counterroll was 6.4° (Haslwanter et al., 1992). Maximum counterroll during slow, dynamic head roll ($3^\circ/s$) has a similar magnitude, and also occurs around 60° (Diamond & Markham, 1983). Klier and Crawford (1998), who measured the torsional shift

of LP as subjects actively held their head at 45° , found somewhat larger counterroll (7.4 and 9.5° , for monocular and binocular viewing, respectively). Since we used passive whole-body tilts in our study, this quantitative discrepancy may be caused by the paradigm difference.

The low gain of ocular counterroll is not caused by ocular mechanics, since ocular torsion in dynamic situations can be as high as 15° (Tweed, Haslwanter, & Fetter, 1998). Interestingly, Wade and Curthoys (1997) report that during head roll, subjects make errors in visual but not somatosensory judgments of line orientation that are similar to the amount of ocular torsion. This suggests that torsional extraretinal eye position information is not available for visual perception tasks. Given this deficiency, the low gain of ocular counterroll has the benefit of limiting misperceptions of object orientation, and perhaps perceived direction of motion, during head roll.

Force on the utricle varies with the sine of the head roll angle, and the response of otolith nerve cells is an approximately linear ($\pm 10\%$) function of force acting on the otolith (Fernandez, Goldberg, & Abend, 1972). While force on the saccule varies with cosine of the head roll angle, our analysis suggests that the saccule contributes little to ocular counterroll. We found that ocular counterroll gain was not proportional to the force on the utricle, but decreased by 50% from near upright to ear down. This non-linear behavior may be due to population coding of otolith afferent signals: simulations by Jaeger, Haslwanter, and Fetter (2000), which were based on a finite element model of the utricle and the on-directions of the utricular hair cells, indicated that the absolute change in firing rate per degree of tilt, summed over all hair cells, shows a similar, non-linear behavior, with the maximum change at small tilt angles.

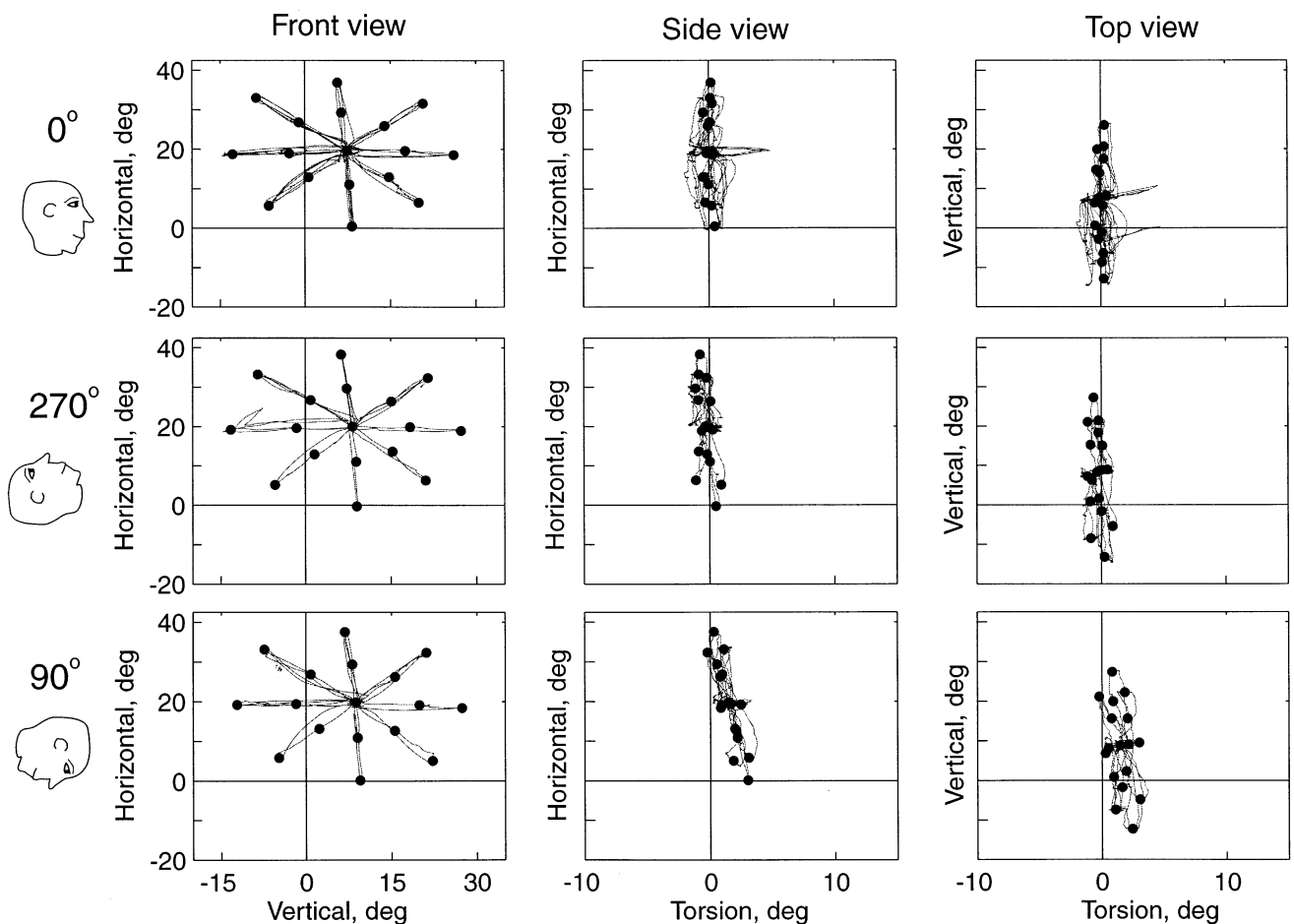


Fig. 5. Eye position during head pitch. Mean fixation points (●) are shown for subject DS when he was upright (top row), supine (middle) and prone (bottom). For illustration we chose the reference position such that in the upright position, the plane of rotation vectors is viewed exactly sideways (top row, center and right). Left: front view of eye positions. Note that the abscissa scale for the front view is different from that for the side and top views. Middle: side view, showing how torsion varies with horizontal eye position ('pitch tilt'). Right: top view, showing the change of torsion with vertical eye position ('yaw tilt').

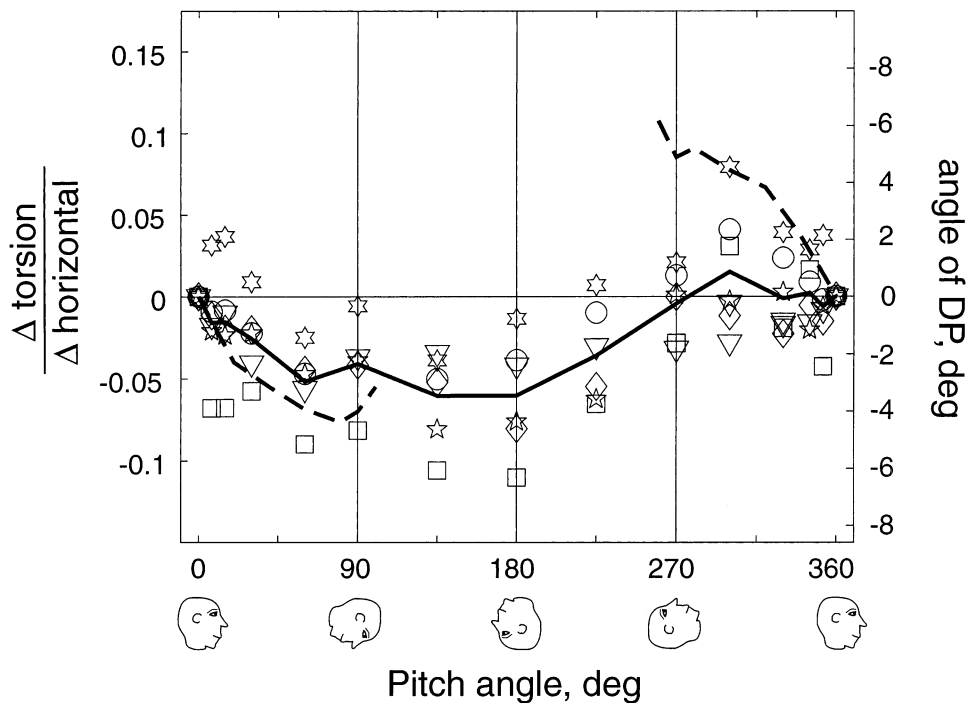


Fig. 6. Torsion changed with horizontal eye position during head pitch. The left ordinate shows the slope of the eye position data ($\Delta\text{torsion}/\Delta\text{horizontal}$), and the right ordinate shows the corresponding pitch angle of DP. Torsion changed during pitch forward, but not pitch backward. Each symbol represents data from a different subject (as in Fig. 3), and the solid line is their mean. Data at 0° is duplicated at 360° . The dashed line is average data from four rhesus monkeys (Cabungcal et al., 2001).

4.2. Effect of head pitch on 3D eye position

We found little change in torsion during supine head pitch. In prone positions torsion increased slightly when the subjects looked right, and decreased when they looked left (e.g. the orientation of DP tilted backwards). The maximum slope change that we found was only -0.06 , which corresponds to a -3.4° tilt of DP. Therefore, for a large 40° eccentric eye position, torsion was only 2.4° different in upright and prone positions.

In contrast to humans, the pitch tilt of DP in rhesus monkeys was modified by both prone and supine head position (Haslwanter et al., 1992; Cabungcal et al., 2001). In monkeys, the maximum change in the pitch plane, about a 7° rotation of DP, occurred when monkeys were supine, and when prone the maximum rotation was about -3° . Thus, even the asymmetry of the monkey response is opposite to what we found in humans.

These species differences are even more pronounced during dynamic otolith stimulation. In monkeys, Hess and Angelaki (1997a,b) have shown that when head orientation is changing with respect to gravity, spatial orientation mechanisms attempt to keep the eyes in the same spatial orientation as when the monkey is upright. This mechanism is more prominent with faster head rotation, and could aid visual object recognition mechanisms that might suffer if images are seen in atypical

retinal orientations. Humans do not show this spatial re-orientating behavior (Haslwanter et al., 1999a). These findings are consistent with the species differences of the 3D VOR when the eyes are in eccentric eye positions: while in monkeys the eyes rotate about the same axis as the head, humans tend to accept a compromise between observance of Listing's Law and an ideal VOR (Misslisch, Tweed, Fetter, Sievering, & Koenig, 1994; Misslisch & Hess, 2000). Monkeys try to stabilize the full retinal image during rotation, while humans appear to follow an apparently simpler strategy of stabilizing only foveal images. We speculate that, compared to monkeys, the small change in 3D eye position that we found during static head pitch in humans likewise reflects the dominance of foveal image processing in humans.

These differences between humans and monkeys in low frequency otolith-ocular responses should not distract from the fact that for higher frequencies, humans also show robust otolith-ocular reflexes that help to compensate for the retinal slip caused by fast linear movements (Baloh, Beykirch, Honrubia, & Yee, 1988; Paige, 1989). Our results, which support the findings by Fetter, Heimberger, Black, Hermann, Sievering, and Dichgans (1996), Haslwanter et al. (1999a) and Haslwanter, Jaeger, Mayr, and Fetter (2000), imply that the low-frequency otolith-ocular reflex shows the most pronounced species differences.

Adult human subjects, who typically are older than monkey subjects both developmentally and chronologically, have usually spent much of their active lives in bright illumination due to artificial lighting, where the visual pursuit system is capable of stabilizing eye position during low frequency head movements. We speculate, then, that the reduced low-frequency otolith-ocular reflexes in adult humans reflect the operation of adaptive mechanisms that have suppressed those reflexes due to lack of use.

Acknowledgements

We thank J. Cabungcal for providing the rhesus monkey data shown in Figs. 3 and 6, Dr O. Bergamin for help with the eye lid coil, A. Züger for technical assistance, and Drs D. Straumann and B.J.M. Hess for valuable comments on the manuscript. Supported by the EMDO-Foundation and by the Koetser Foundation.

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