Gravity Modulates Listing’s Plane Orientation During Both Pursuit and Saccades

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Hess, Bernhard J.M. and Dora E. Angelaki. Gravity modulates Listing’s plane orientation during both pursuit and saccades. J Neurophysiol 90: 1340–1345, 2003; 10.1152/jn.00167.2003. Previous studies have shown that the spatial organization of all eye orientations during visually guided saccadic eye movements (Listing’s plane) varies systematically as a function of static and dynamic head orientation in space. Here we tested if a similar organization also applies to the spatial orientation of eye positions during smooth pursuit eye movements. Specifically, we characterized the three-dimensional distribution of eye positions during horizontal and vertical pursuit (0.1 Hz, ±15° and 0.5 Hz, ±8°) at different eccentricities and elevations while rhesus monkeys were sitting upright or being statically tilted in different roll and pitch positions. We found that the spatial organization of eye positions during smooth pursuit depends on static orientation in space, similarly as during visually guided saccades and fixations. In support of recent modeling studies, these results are consistent with a role of gravity on defining the parameters of Listing’s law.

INTRODUCTION

The torsional orientation of the eyes during visually guided eye movements depends on gaze direction in space. The underlying relationship when the head remains stationary relative to the visual environment and maintains a constant orientation relative to gravity is known as Listing’s law (Ferman et al. 1987; Helmholz 1867; Tweed and Vilis 1987). It implies that there exists a unique ocular orientation, called primary eye position, from which any other accessible eye positions at a constant vergence angle can be reached by a combination of horizontal and vertical rotations. Eye positions with zero torsion lie in a plane, called Listing’s plane. Saccadic, fixation, and smooth pursuit eye positions have all been shown to be confined to this plane (Crawford and Vilis 1991; Haslwanter et al. 1991, 1992; Tweed and Vilis 1987; Tweed et al. 1992).

When statically tilted away from the upright orientation, primary position and Listing’s plane during saccades and fixations were shown to change in both humans and monkeys (Bockisch and Haslwanter 2001; Crawford and Vilis 1991; Furman and Schor 2003; Haslwanter et al. 1992; Suzuki et al. 1997). Specifically during static roll tilts, a constant amount of torsion is added to all eye positions, resulting in a shift of Listing’s plane along the torsional axis. Similarly, during static pitch tilts, there is a corresponding upward or downward rotation of Listing’s plane. In both cases, the direction of shift or rotation, amounting to only about 10% of the tilt, is in opposite direction to the static tilt, such that Listing’s plane does not remain fixed in head coordinates. Other eye movement systems, such as smooth pursuit, have been shown to follow Listing’s law (Haslwanter et al. 1991; Tweed et al. 1992). Although these effects of head position on Listing’s plane orientation hold true for saccadic eye movements with or without visual guidance, it is presently unknown whether the same relations also hold true for smooth pursuit eye movements. Since burst neurons, whose firing rates reflect this gravity-dependent modulation (Scherberger et al. 2001), do not modulate during smooth pursuit eye movements, such information is important for understanding these otolith-dependent effects and the neural organization of 3D eye movements in general. The aim of this work was to study the 3D ocular orientation during smooth pursuit eye movements as a function of static head orientation relative to gravity.

METHODS

Animal preparation and eye movement recording

Data were obtained from two rhesus monkeys (Macaca mulatta), which were chronically prepared with scleral dual-search-coils for three-dimensional (3D) eye movement recordings and skull bolts for restraining head motion during the experiments. Details of fabrication and implantation of the dual-search coil have been reported elsewhere (Hess 1990). The dual coil was implanted on the left eye of one animal and the right eye of the other animal. All surgeries and animal handling were in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and were approved by the Veterinary Office of the Canton of Zurich. 3D eye position was measured with a two-field search coil system (Eye Position Meter 3000, Skalar, Delft, The Netherlands). The search coil signals were calibrated as described in Hess et al. (1992). In brief, an in vitro calibration prior to implantation yielded the coil sensitivities and the angle between the two search coils. The orientation of the dual coil on the eye was determined from the four coil output signals during fixation of a series of vertically arranged target lights relative to straight ahead. Horizontal, vertical, and torsional eye positions were digitized at a sampling rate of 833 Hz and stored on a computer for off-line data analysis. Eye positions were expressed as rotation vectors, \( \mathbf{E} = \tan(\psi/2)\mathbf{u} \), where \( \mathbf{u} \) is a unit vector pointing along the axis of rotation that brings the eye from the reference position to current.

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position, and \( \rho \) is the angle of rotation about \( \mathbf{u} \) (Haustein 1989). 3D eye positions were expressed relative to a right-handed coordinate system. A positive torsional, vertical, or horizontal eye position component \( (E_{\text{tor}}, E_{\text{ver}}, E_{\text{hor}}) \) corresponded to a clockwise, downward, or leftward rotation of the eye (from the subjective viewpoint). Listing’s plane and primary eye position were determined from spontaneous eye movements in the light with the head upright and stationary. All rotation vectors in tilted head orientations were expressed relative to primary position that was calculated in an upright position as the unique eye orientation with gaze direction normal to Listing’s plane (see Data analyses).

**Experimental protocols**

During the experiments, animals were seated in a primate chair with their head restrained in a position of 15° nose-down relative to the stereotaxic horizontal (defined as “upright” position) to place the lateral semicircular canals approximately earth-horizontal. The animals were placed inside the inner frame of a superstructure consisting of two motor-driven gimbaled axes. The effects of static changes in head orientation relative to gravity on visually guided saccades and smooth pursuit eye movements were studied while the monkey was sitting inside a sphere, which completely surrounded the animal (inner diameter, 80 cm). The inner wall of the sphere was covered with a random dot pattern. Using the outmost gimbaled axis of the superstructure, the animal could be tilted relative to earth-vertical without changing its orientation relative to its visual surround (i.e., the optokinetic sphere).

The experimental protocols consisted of the following two visual stimulation protocols that were each tested with the animal in upright, 30°, and 90° left or right ear-down position as well as in 30° and 90° nose up and nose down position. 1) Projection of a laser spot at random locations on the inner wall of the sphere to elicit visually guided saccades. Data were also collected during spontaneous saccades that typically occurred over a range of approximately 35° × 35° (re: straight ahead). 2) Projection of a horizontally or vertically oscillating laser spot at various elevations and eccentricities relative to straight ahead (0°, ±10°, ±15°) at frequencies and amplitudes of 0.1 Hz, ±15° (corresponding to ±9.4°/s) or 0.5 Hz, ±8° (corresponding to ±25.1°/s). Trained animals maintained their eye position within a 2° behavioral window for fluid reward. Due to the eccentric mounting of the system (35 cm up and 15 cm forward relative to the center of the optokinetic sphere) the projected laser spot moved only approximately on iso-elevation and iso-azimuth curves. As a result, target movement during vertical pursuit generated large vertical but also small horizontal eye movements (Fig. 1A and 1B).

**Data analyses**

At the beginning of each experimental session, primary position was determined from spontaneous eye movements while the animal was looking around in the normally lit laboratory, as follows. First, a planar surface was fitted to the pooled eye positions by minimizing the least-squares error according to the equation: \( E_{\text{p}} = a + bE_{\text{tor}} + cE_{\text{ver}} \), where \( E_{\text{tor}} \), \( E_{\text{ver}} \), and \( E_{\text{hor}} \) denote the torsional, vertical, and horizontal components of the eye position vector \( \mathbf{E} \). From the best fit plane parameters \( a, b, \) and \( c \), primary eye position, \( \mathbf{P} \), was determined as the rotation vector: \( \mathbf{P} = [a, c, -b] \), where \( t \) denotes transpose (Hess and Angelaki 1997a,b, 1999). Note that in upright the \( x \)-component of primary eye position is zero for gaze in reference direction (i.e., \( a = 0 \): the best fit plane passes through the origin of the coordinate system).

Data collected in tilted head orientations were then expressed relative to upright primary position (Listing’s coordinates) (i.e., relative to an orthogonal coordinate system whose first axis was aligned with primary gaze direction). For this, we left-multiplied all eye position vectors, \( \mathbf{E} \), with the inverse of primary eye position: \( \mathbf{E}' = \mathbf{P}^{-1} \cdot \mathbf{E} = (\mathbf{P}^{-1} + \mathbf{E} + \mathbf{P}^{-1} \cdot E) / (1 - \mathbf{P}^{-1} \cdot \mathbf{E}) \), where “\( \cdot \)” denotes the cross product and “\( \circ \)” denotes the scalar product. For pursuit analyses, only the slow-phase portions where the eye followed the motion of the target were included. For the saccade/fixation protocols, the whole data set (including both saccades and fixations) was included in the analyses. Subsequently, eye positions in each tilted head orientation were fitted separately for pursuit and saccades/fixations with planar surfaces. The parameter “\( a \)” then described the torsional offset of these best fit planes, while “\( b \)” and “\( c \)” described the temporal and forward-backward tilt of the best fit plane relative to upright Listing’s plane. The “thickness” of the best fit planes was...
characterized by the torsional SD of eye positions relative to the plane. This torsional SD was computed as

\[
\text{SD}_\text{tor} = \sqrt{\frac{1}{N-3} \sum (E_{\text{tor}} - a - b E_{\text{ver}} - c E_{\text{hor}})^2},
\]

where \(N\) = number of points of pooled saccades or smooth pursuit traces. For a more direct comparison between saccades and pursuit, we also computed the thickness of the best fit planes to saccades in a restricted oculomotor range, namely to all saccades in a disc of radius \(15^\circ\) centered in the oculomotor range. Specifically, we computed the center coordinates as \(y_m = 1/N \sum E_{\text{ver}}\) and \(z_m = 1/N \sum E_{\text{hor}}\) and collected all saccades such that \(R_i = \sqrt{(E_{\text{ver}} - y_m)^2 + (E_{\text{hor}} - z_m)^2} \leq 15^\circ\) (for \(i = 1\) to \(N\)).

Presented data were collected during 20 experimental sessions for each animal. Statistical comparisons were based on analyses of covariance (ANCOVA) with tilt angle as a covariate.

RESULTS

The main finding of this study was that pursuit eye movements exhibited the same spatial characteristics versus head orientation relative to gravity as those described for the saccadic system (Haslwanter et al. 1992). In the following we compare the spatial organization of horizontal and vertical smooth pursuit eye movements with those of saccadic eye movements that have been obtained in the same animal under identical experimental conditions. For an easy comparison, all eye movements were expressed in Listing’s coordinates relative to primary position, which was obtained on each experimental day from visually guided saccadic eye movements in upright orientation (see METHODS).

Figures 1 and 2 illustrate the 3D organization of smooth pursuit eye movements in tilted roll and pitch head orientations, respectively. In both plots, the top traces show torsional, vertical, and horizontal eye position as a function of time during 0.1 Hz pursuit centered at three different directions of gaze. During horizontal pursuit (Figs. 1A and 2A), gaze direction pointed straight ahead, as well as \(15^\circ\) upward and downward. During vertical pursuit (Figs. 1B and 2B), gaze pointed straight ahead, as well as \(15^\circ\) to the left and to the right. Thus each plot in Figs. 1, A and B, and 2, A and B, consisted of nine different traces, corresponding to three gaze directions \(\times\) three head orientations (upright and left/right side-down or supine/prone). Torsional eye position, although negligible in upright orientation, increased its amplitude in side-down positions (Fig. 1, A and B). Specifically during horizontal smooth pursuit, there was a positive torsional shift in left side-down positions and a negative torsional shift in right side-down positions (Fig. 1A). Similarly, during vertical smooth pursuit, a similar torsional shift was also observed in the respective roll head orientations (Fig. 1B).

The change in the 3D organization of smooth pursuit eye movements in upright versus tilted head orientations became more apparent when the same data were now plotted in spatial coordinates (Fig. 1, C and D). Specifically, Fig. 1C plots eye positions in the sagittal (horizontal-torsional) plane, whereas Fig. 1D plots eye positions in the horizontal (vertical/torsional) plane (see cartoon drawings). For these spatial orientation plots, we have combined data during both horizontal and vertical smooth pursuit eye movements at all different vertical and horizontal eccentricities. All upright smooth pursuit eye positions have been shown in yellow, whereas left and right side-down data have been plotted in blue and green, respectively. To quantify any changes in plane orientation, these 3D eye positions were fitted with planar surfaces (solid lines in Fig. 1, C and D). Although in tilted head orientations eye positions still exhibited a small (<1°) torsional SD relative to the fitted planar surface, a clear change in the orientation of this plane (including both a torsional shift, Fig. 1C, and a temporal rotation; Fig. 1D) was apparent. In fact, these changes in plane
orientation were very comparable to those during visually guided saccades/fixations under identical experimental conditions (Fig. 1, C and D, insets on the right).

Changes in eye position plane orientation, although typically smaller, were also obtained when the animal was tilted in the pitch plane (Fig. 2). In this case, rather than a torsional shift (Fig. 1), there was a small but systematic pitch tilt in the 3D plane of eye positions during smooth pursuit. This tilt was most apparent in the sagittal plane view (Fig. 2C). For clarity due to the small effects, responses obtained in the upright position have not been illustrated in the spatial plots. These observations for static pitch tilts were similar to those during saccades and fixations (Fig. 2, C and D, insets on the right; see also Haslwanter et al. 1992).

Data from both animals have been summarized in Fig. 3. Because there was no difference in the spatial organization of 3D eye positions during pursuit at 0.1 and 0.5 Hz ($R_{3,56} = 1.5$, $P > 0.05$), data were combined. The spatial orientation and thickness of the 3D planes as a function of tilt angle were described by four parameters, including the torsional shift, the temporal tilt angle (i.e., yaw-plane rotation), the forward/backward tilt angle (i.e., pitch-plane rotation), and the torsional SD (Fig. 3, A–D). There were no significant differences in the torsional shift, temporal tilt, or forward/backward tilt as a function of tilt angle for smooth pursuit and visually guided saccades ($R_{3,121} = 0.8$, $P > 0.05$; Fig. 3, compare open with solid circles, respectively). A significant correlation between the torsional shift of the planes and tilt angle was only observed for roll tilts (pursuit: $r = 0.95$, saccades: $r = 0.97$; Fig. 3A).

The temporal tilt angle of the fitted planes (parameter $b$; see METHODS) was also found to vary as a function of roll (but not pitch) tilt (pursuit: $r = 0.87$, saccades: $r = 0.73$; Fig. 3C). In contrast, the forward/backward tilt of the fitted planes (parameter $c$; see METHODS) exhibited a systematic dependence on pitch (but not roll) tilt angle (pursuit: $r = 0.73$, saccades: $r = 0.94$; Fig. 3D).

When considering the whole range of saccadic eye movements recorded, smooth pursuit planes exhibited a smaller torsional SD compared with saccade/fixation data ($F_{1,123} = 81.6$, $P < 0.05$; Fig. 3B, compare open with solid circles, respectively). This difference was due to the large eccentricities ($\pm 35^{\circ}$) used for saccades compared with pursuit ($\pm 15^{\circ}$), as this difference was no longer present when displacement planes for saccades/fixations were restricted to a similar oculomotor range ($\pm 15^{\circ}$ relative to straight ahead; $F_{1,123} = 2.9$, $P > 0.05$; Fig. 3B, solid triangles).

DISCUSSION

We have shown that ocular torsion during smooth pursuit eye movements exhibits the same dependence on head orientation in space as during visually guided saccades and fixations. In particular, a change in the roll orientation of the head shifted torsional eye position in the same way during smooth tracking movements as during saccades. Similarly, a change in pitch head orientation resulted in a small but significant pitch (forward/backward) tilt of the eye position planes during both smooth pursuit and saccadic eye movements. In both cases, the
change in Listing’s plane orientation was in the opposite direction of the tilt and tended to compensate for the change of head orientation in space. These shifts/rotations in the orientation of Listing’s plane during smooth pursuit eye movements exhibited a sinusoidal dependence on tilt angle, as previously shown for saccadic eye movements (Hashwanter et al. 1992). Although clearly present, these effects were rather small, typically compensating for <10% of the head tilt.

In addition to the torsional shift, there was also a significant change in the temporal (yaw) tilt of Listing’s plane as a function of roll tilt. Orienting gaze shifts have been studied mostly in the horizontal plane as a shift in the beating field of vestibular or optokinetic nystagmus (“Schlagfeldverlagerung”) in the direction of the ocular quick phases (man: Jung and Mittermaier 1939; monkey: O-Uchi et al. 1981; Solomon and Cohen 1992a,b; cat: Chun and Robinson 1978; Vidal et al. 1982; pigeon: Gioanni 1988; rat: Maier and Dieringer 1993). Whether the small but significant conjugate rotation of Listing’s plane toward the contraversive side, which we observed here in static side-down positions, can be interpreted in this context is not clear because primary gaze tends to move away from the direction in which one would fall. Thus the gravity-driven modulation of Listing’s plane in the yaw plane appears not to follow the principle that subjects tend to orient gaze toward the direction of (loco-) motion (Chun and Robinson 1978).

In recent years, there is growing evidence that the visuomotor control of 3D eye orientation is implemented downstream of the superior colliculus (Hepp et al. 1993; Van Opstal et al. 1991). Visual and eye movement related signal processing in many cortical areas as well as in the superior colliculus seem to be organized in retinal coordinates and 3D eye/head coordination, including torsional eye movements and Donder’s law are implemented downstream of the superior colliculus (Klier et al. 2001, 2003). Burst neurons in the midbrain have been reported to change their firing rates as a function of static head position (Scherberger et al. 2001). Recent models of the otolith effects on the static orientation of the eyes have suggested a direct involvement of the velocity-to-position neural integrator (Crawford et al. 1999; Glasauer et al. 2001). The present results, showing similar gravity dependence for pursuit and saccades, are consistent with this notion. Although the neural networks for integration of eye velocity signals, including the nucleus prepositus hypoglossi, the interstitial nucleus of Cajal, and the paramedian tract neurons (Cannon and Robinson 1987; Crawford 1994; Crawford et al. 1991; Fukushima 1991; Godaux and Cheron 1996; Kaneko 1997; Nakamagoe et al. 2000) are extensively interconnected with the vestibular nuclei (see Buettner-Ennever 1989, 1999 for review), the details of these interactions and computations are still missing.

The functional significance of this small but systematic shifts and tilts of Listing’s plane as a smooth function of the head roll and pitch angles remains unknown, although it has been postulated that it merely represents a vestigial remnant of ocular counterrolling and counterpitching that is large in lateral-eyed species (Vilis 1993). This hypothesis arises from the fact that ocular counterrolling is small in humans (Collewijn et al. 1985; Diamond and Markham 1981, 1983; Diamond et al. 1982; Hannen et al. 1966; Markham and Diamond 2001; Miller and Graybiel 1971) but large in lateral-eyed species (Baarsma and Collewijn 1975; Barmack and Pettorossi 1988; Dickman and Angelaki 1999; Hess and Dieringer 1990, 1991).

The findings reported here that not only saccades but also pursuit eye movements are modulated by head orientation relative to gravity further raises the question of why these static otolith-driven orientation reflexes have not been completely eliminated during evolution, if of no functional role (Vilis 1993). Notably, during movement, the systematic shifts and rotations of 3D eye position planes of visually guided saccades as a function of head orientation in space not only persist but are also much larger than those observed under static conditions (Hess and Angelaki 1997b). In addition, these shifts/rotations of 3D eye position planes were reported to increase as a function of tilt movement frequency not only during visually guided saccades but also during smooth pursuit eye movements as well (Hess and Angelaki 2002). We have previously proposed that the low gain changes in the 3D organization of eye positions under static tilt conditions might represent the low-frequency tail of a functionally relevant vestibular mechanism that subserves orientation constancy with respect to earth-vertical during motion. Accordingly, under static tilt conditions, otolith-driven 3D eye position changes contribute only minimally to the spatial constancy of retinal images, which is then mainly guaranteed by visually driven mechanisms. In contrast, during mid- and high-frequency rotations when visually driven mechanisms are less effective, a vestibularly driven orientation mechanism appears to exist that maintains the coordinates of Listing’s plane largely invariant with respect to earth-vertical. This hypothesis remains to be tested in future studies.

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DISCLOSURES

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