Effect of Semicircular Canal Stimulation on the Perception of the Visual Vertical

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INTRODUCTION

Various sensory inputs, in particular visual, proprioceptive, and vestibular inputs, are used to determine the orientation of the body with respect to gravity. The ability to set a luminescent bar to earth vertical in the absence of external visual information depends primarily on proprioceptive and vestibular cues, the latter usually equated with the tonic afferent input from the otolith organs and central graviceptive pathways (Brandt and Dieterich 1994; Miller and Graybiel 1966). In the upright position, stationary normal subjects are able to set a luminescent bar with great accuracy to within a mean deviation of ±2° of the true gravitational vertical (Friedman 1970). As a result, clinical studies emphasize that greater than average tilts of the subjective visual vertical (SVV) are a sensitive tool for detecting an imbalance in otolith function (Böhmer and Mast 1999; Gresty et al. 1992; Halmagyi and Curthoys 1999; Tabak et al. 1997; Vibert et al. 1999).

Early experiments, however, have been neglected. For instance, Holst and Grisebach (1951), Udo de Haes and Schöne (1970), and Stockwell and Guedry (1970) all noted that the SVV was affected by stimulation of the vertical (anterior and posterior) semicircular canals (SCCs) during roll plane rotation. More recently, observations on the subjective visual horizontal (SVH) during centrifugation in a free-swinging gondola also found a tilt of the SVH (Tribukait 1999). In this study, the recorded SVH offset was induced during centrifuge acceleration, thereby suggesting that the vertical SCCs may have played a role in the formation of the SVH.

However, several studies have investigated the role of the SCCs in visual verticality. For example, Holst and Grisebach (1951), Udo de Haes and Schöne (1970) and centrifugation studies (Tribukait 1999) is that both involve combined SCC and otolith stimulation. Therefore the specific contribution of the SCCs to the perception of verticality cannot be clearly deduced.

The purpose of this study is therefore to examine the effect of SCC stimulation on the SVV during earth-vertical yaw axis angular acceleration when otolith interaction is minimal. In two studies by Curthoys and coworkers (Smith et al. 1995; Wade and Curthoys 1997), consistent ocular torsional changes during yaw angular acceleration, and a significant correlation between SVH settings and torsional eye position, were reported. These studies, however, did not assess a distinct contribution of the vertical or horizontal SCCs. Therefore the origin of the SVV tilt induced by yaw rotation and, more generally, the role of the vertical SCC in visual verticality perception remains unclear.

METHODS

Experiment 1: SVV following yaw axis acceleration

Eight healthy normal individuals (6 males, 2 females; mean age: 27.5 yr; range: 21–36 yr) with no evidence of vestibular disturbance participated in the study, which was approved by the local ethics committee.

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committee. Subjects were seated on a motorized Bárány chair (combined control from Contravez-Goerz, CA, and Acutronic Schweiz AG, Switzerland) fitted with head, foot, and armrests and a safety belt. The SVV apparatus was attached to a chair-mounted framework, supporting a 40-cm-long bar with a 1-mm-wide luminescent strip. This bar could be rotated in the frontal plane and was centered at eye level, 48 cm in front of the subject (Fig. 1A). The framework could be vertically adjusted 13 cm to place the bar closer to primary gaze for each head position. Rotation of the bar was controlled by a wheel located near the subject’s right hand via a pulley system. The orientation of the bar was measured using a potentiometer.

SVV procedure

Subjects were instructed to close their eyes, offset the luminescent bar by a random large amount, clockwise or counter-clockwise, then open their eyes and reset the bar to their perceived gravitational vertical. A pushbutton, in the subject’s left hand, was used to signify satisfaction with the adjustment. A pilot study indicated that the average SVV measured using this procedure was the same as that measured with the experimenter offsetting the bar while the subject’s eyes were closed. Experiments were conducted in a dark room, and the subject was observed with an infra-red camera.

Stimuli

The SVV was measured under a static condition, during clockwise (rightward) and counter-clockwise whole body yaw rotations about an earth-vertical axis and during the postrotatory periods. Rotations were velocity steps of 60-s constant velocity at 90°/s and acceleration/deceleration periods of 2 s.

In the static condition, subjects repeated the SVV procedure six times. In the rotation conditions, subjects were instructed to repeat the SVV procedure continuously, throughout the yaw rotation and during a 60-s postrotatory period. For each rotation and postrotatory period, an average of eight settings was obtained from each subject. Subjects completed one rotation and postrotatory period for each direction, clockwise and counterclockwise.

Head positions

Subjects were rotated about an earth-vertical axis with different head positions to vary the relative amount of horizontal and vertical SCC stimulation. The static and rotation conditions were repeated with four different pitch positions: head “normal” (HN) with the subject looking straight ahead in a comfortable position; head up (HU) with the occiput pitched backward ca 30° from the normal position; head down (HD) with the nose pitched downward ca 30° from the normal position; and head further down (HFD) ca 40° from the normal position (Fig. 1B). The degree of tilt in HU and HFD was limited by the comfortable range of motion that could be achieved by subjects. A rigid arc-shaped metal head restraint placed against the occiput and a chin rest, both appropriately padded, secured the head in each pitch position. The head was located at the center of chair rotation for maximal SCC and minimal otolith stimulation.

To measure changes in the head angle accurately, a rigid plastic rod was attached with surgical tape to the subject’s head throughout the experiment. This rod represented a line from the superior border of the external auditory meatus to the outer canthus of the eye (Reid’s plane). The orientation of this line with respect to the gravitational horizontal was measured using a large protractor with an attached spirit level. The head angle was measured before and at the end of rotation in each head position. In HN, the anterior end of the plastic rod was ~10° above horizontal. The order in which the different head positions were used and the initial rotation direction in each head position were randomized between subjects.

For each head position, an estimate of the relative magnitude of stimulation of the horizontal, anterior, and posterior canal planes was calculated using the average planar equations from Blanks et al. (1975). The efficiency of canal stimulation was calculated from the projection of the canal plane onto the stimulus (earth-horizontal) plane for each individual’s measured head position. The planar equations given by Blanks et al. (1975) are referenced to the Reid stereotaxic coordinate system in which the inferior margin of the orbits and the center points of the two external auditory canals lie in the horizontal plane. The general form of these planar equations is \( ax + \beta y + \gamma z = 0 \). When the subject’s head is pitched by \( \theta \) degrees from the Reid reference position (positive for forward pitch), then the efficiency of canal stimulation by earth-horizontal yaw acceleration is given by \( -a \sin \theta + \gamma \cos \theta \). Peak efficiency, or optimal plane of stimulation, is obtained when the canal plane lies closest to the earth-horizontal plane; zero stimulation occurs when the canal plane is vertical, and a sign reversal indicates a reversal in the stimulation direction of the canal.

Data analysis

The orientation of the bar, the push-button signal and chair velocity were recorded at a sampling frequency of 50 Hz. The SVV values were taken as the angular deviations of the luminescent bar from true gravitational vertical at the times indicated by the push-button signal. Tilt of the top of the luminescent bar to the subject’s right was indicated as a positive value and a tilt toward the left negative. For each subject, in each head position, the average SVV during the static condition was used as a baseline for the subsequent rotational SVV.
values. Data points occurring during the 2-s periods of acceleration were discarded.

Supplementary experiments

EXPERIMENT 2: SIMULTANEOUS SVV AND EYE-MOVEMENT RECORDINGS AFTER HN YAW ANGULAR ACCELERATION. In a separate session, four of the subjects were rotated in the HN position, while wearing a three-dimensional (3D) video-oculography mask (SensoMotoric Instruments, Berlin, Germany) fixed with heavy-duty occipital bands and a two-way adjustable helmet. The video-oculography system consisted of a free-field-of-view mask and a battery-powered video recorder, to tape high-quality images of the subject’s right eye, at 25 frames/s. The tape recording was analyzed off-line using field sampling (alternate analysis of odd and even lines in the video image), to give horizontal, vertical, and torsional eye position at 50 Hz. Spatial resolution was 0.1° for the torsional channel and <0.03° for horizontal and vertical eye position. During these experiments, the subjects were asked to keep their eyes open all the time and to continuously adjust the luminescent bar to subjective verticality.

EXPERIMENT 3: EFFECT OF VERTICAL EYE POSITION ON THE SVV AFTER HN YAW ANGULAR ACCELERATION. In Experiment 1, the center of the luminescent bar was at eye level during the HN condition. However, due to mechanical limitations of the framework, the center of the bar remained below primary gaze in the HD condition and above primary gaze in the HD and HFD conditions. As a supplementary experiment, the effect of vertical eye position on SVV measurements was investigated by repeating the static and rotation conditions in the HN position with the subject’s eyes in normal primary gaze (eyes normal, EN), with eyes looking up (EU), or with eyes down (ED).

Eight subjects (6 males, 2 females; mean age: 27.5 yr, range: 21–41 yr), three of whom had also participated in Experiment 1, were seated on the Barány chair. Seat height was adjusted for each individual so that primary gaze was at the same level for all subjects. The subject always fixated the center of the luminescent bar, which was positioned straight-ahead (EN), 19 cm (21.5° above (EU), or 40 cm (39.8°) below (ED) the primary gaze direction. The eye deviations in the EU and ED conditions were specified to match the average deviations from primary gaze that were present during the HD and HU conditions, respectively, in Experiment 1. During these trials, participants were asked to keep their eyes open and to use the adjustment wheel to continuously maintain the luminescent bar at their perceived vertical.

For the vertical eye position experiments, the continuous SVV responses to the four rotational stimuli were normalized in polarity for the static values. In the HN and HU positions, rotation to the left and the cessation of rotation to the right both produced a right (positive) SVV tilt, whereas yaw rotation to the right and the cessation of yaw rotation to the left both produced a negative SVV tilt. However, SVV tilt direction was typically reversed in the HFD position (25 of 32 test trials) compared with that in the HN, HU, and HD positions (Fig. 2; NB: a trial is a single rotation or postrotatory period). Tilts of the SVV in all rotations mostly occurred during the initial 5 s of each stimulus, reaching peak values within 20 s and then decaying (Fig. 3). It should be noted that SVV settings were always in the direction opposite to that expected if the SVV tilts were due to the slow phase torsional vestibuloocular reflex (VOR; see DISCUSSION).

At the end of each 60-s window (per- and postrotatory period) an average tilt of 1°, with respect to the static value, remained in all head positions.

The magnitude of the SVV rotational response (for each subject, in each head position) was quantified by averaging all SVV settings occurring within the first 20 s of each stimulus (after reversing the sign of the right rotation and left stop responses). Individual subjects made, on average, 2.6 SVV settings within the first 20 s of each stimulus, giving a total of 83 responses for each head position (8 subjects, 4 stimuli). One-factor repeated-measures ANOVA showed a significant effect of head position on tilt of the SVV ($P < 0.01$). Bonferroni post hoc comparisons showed a significant difference for SVV tilt ($P \leq 0.04$) among all head positions with the greatest differences ($P < 0.01$) found between HU (mean SVV tilt: $3.0 \pm 0.4°$) and HD (0.4 ± 0.2°), between HU and HFD ($-0.7 \pm 0.3°$), and between HN (1.9 ± 0.3°) and HFD (Fig. 4).

There was a significant dependence of the SVV on the direction of the rotational stimulus in both HN and HU positions ($P < 0.01$), but there was no significant dependence in the HD and HFD positions. For HN and HU, Bonferroni post hoc comparisons showed significant differences when right rotation or left stop were compared with left rotation or right stop ($P < 0.01$), but there was no difference between right rotation and left stop responses or between left rotation and right stop responses. The statistical differences found in HN and HU relate to response polarity (sign) but not magnitude of tilt,

RESULTS

Experiment 1: SVV following earth-vertical, yaw axis angular acceleration

Inspection of raw records for HN and HU showed that yaw rotation induced a tilt of the SVV settings in the opposite direction to rotation. During stopping, the direction of the SVV tilt reversed. The SVV tilt was larger with HU, not discernible with HD, and often reversed in polarity during HFD. Detailed analyses now follow.

Under static conditions, the mean value of the SVV tilt was not significantly dependent on head position, although the combined signed average for all subjects showed a slightly greater tilt of the SVV in HFD ($1.6 \pm 0.9°$; mean ± SE) than in the other three head positions ($0.7 \pm 0.7°$ in HN and $1.1 \pm 0.7°$ in HU and HD).

The rotational stimuli evoked SVV tilt with respect to the static values. In the HN and HU positions, rotation to the left and the cessation of rotation to the right both produced a right (positive) SVV tilt, whereas yaw rotation to the right and the cessation of yaw rotation to the left both produced a negative SVV tilt. However, SVV tilt direction was typically reversed in the HFD position (25 of 32 test trials) compared with that in the HN, HU, and HD positions (Fig. 2; NB: a trial is a single rotation or postrotatory period). Tilts of the SVV in all rotations mostly occurred during the initial 5 s of each stimulus, reaching peak values within 20 s and then decaying (Fig. 3). It should be noted that SVV settings were always in the direction opposite to that expected if the SVV tilts were due to the slow phase torsional vestibuloocular reflex (VOR; see DISCUSSION).

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which was similar for both left and right per- and postrotary periods.

Figure 5 illustrates the relationship between the mean SVV tilt and SCC efficiency as defined in METHODS. The degree of SVV tilt was smallest in the HD position, where the estimated magnitude of posterior and anterior canal stimulation was low (average efficiencies of 0.14 and −0.17, respectively) but the horizontal canal stimulation was near its peak (average efficiency of 0.96). The degree of SVV tilt tended to increase as the head was pitched backward and the vertical canals were brought progressively into the earth-horizontal plane. Because the geometrical relations between all canals are anatomically fixed, increasing activation of one pair of canals, e.g., the posterior canals, is associated with decreasing activation in a different pair, e.g., the horizontal canals. Thus for HN, canal stimulation increased for the posterior canal (average efficiency: 0.54) and remained high for the horizontal and low for the anterior canal (average efficiencies: 0.78 and 0.47, respectively). In the HU position, the average efficiencies of the posterior and anterior canals reached 0.78 and 0.47, respectively, but the horizontal efficiency was reduced to 0.34. A Spearman correlation of the magnitude of SVV tilt versus the degree of canal efficiency indicated a strong positive correlation for the posterior canal (rho = 0.79), a weaker correlation for the anterior canal (rho = 0.34), and a strong negative correlation for the horizontal canal (rho = −0.80). Thus as can be seen in Fig. 5, the largest SVV tilts occurred for head positions with the strongest posterior and weakest horizontal canal stimulation, whereas the smallest SVV tilts occurred for

FIG. 2. A and B: comparison of subjective visual vertical (SVV) in A (HU) and B (head furthest down (HFD)) for an individual subject. Each point has been referred to the static baseline and represents 1 setting of the luminescent bar during left rotation (△) and stop (○), right rotation (■) and stop (▲) stimuli. Note the reversal in SVV settings for identical per- and post rotary conditions in HU and HFD. Data points have been fitted with a 3rd-order polynomial trendline so as to portray the effect more clearly.

FIG. 3. Time constant of SVV response decay. Mean ± SE of SVV tilts in the HU condition for 5-s bins combining all rotational stimuli, normalized for direction in all subjects. The time constant of decay of the response (30 s) was measured as the time required for the peak SVV tilt value (3.3°) to decrease to 37% of its peak value (1.2°).

FIG. 4. The effect of head position on SVV tilt. Mean ± SE of the rotationally induced SVV tilt in the various head positions during the 1st 20 s of stimulation.

FIG. 5. The relationship among SVV, SCC efficiency, and head position. Each dot represents the mean SVV tilt (right y axis), normalized for polarity, for 1 subject in 1 of the four head positions (HU, HN, HD, or HFD). There are 32 data points but some dots are not visible due to overlapping. The x axis represents the pitch angle of the head relative to the Reid reference position. The lines represent the canal efficiencies (left y axis) over the range of head positions, for the horizontal (HC), posterior (PC), and anterior (AC) canals (taken from Blanks et al. 1975) not line fits to the SVV data points. As the head is tilted back the efficiency of both AC and PC increases, efficiency of HC decreases and SVV tilt increases. However, note that the SVV tilt data are close to 0 for head positions in which the PC efficiency is close to 0 (HD, circa 20°). The signs of the efficiencies indicate the stimulation direction of the canal and have been normalized for positive efficiencies in the HN position.
head positions in which stimulation of the posterior canal was minimal but stimulation of the horizontal canal was strongest. Also the pitch angle of the head at which the zero crossing of the SVV tilt occurred (at about $+20^\circ$, Fig. 5) seemed to correspond most closely with the zero crossing of the canal efficiency plot for the posterior canal. Note that over this range of head angles ($0^\circ$–$40^\circ$), the efficiency of the horizontal canal remains essentially constant. For anterior canal stimulation, the weaker correlation is due to the fact that the magnitude of anterior canal stimulation in the HN and HD positions is fairly similar (although the direction of the stimulation is reversed), but the SVV tilt is much larger in the HN position (Fig. 5). A change in sign of the canal efficiency indicates a reversal in the stimulation direction for the canal and, for the posterior canal, this corresponded to the reversal of the SVV tilt.

Given that the SCCs are generally seen as acting in pairs, it is important to explain how the analysis deals with this fact. The horizontal SCCs on the right and left sides of the head are symmetrically placed about the sagittal plane. Because our experiments only involve different pitch head positions and rotational stimulation in the earth-horizontal plane, the projections of the canal planes onto the plane of stimulation or in other words the “efficiency” of canal stimulation will be identical for the right and left sides. Depending on the direction of chair rotation, one side will produce an ON response and the other side will produce an OFF response, but the strength of the combined response depends on the canal efficiency; similarly for the posterior canal pair and the anterior canal pair.

A time constant for the decay phase of the SVV response was estimated using data from the HU condition because this condition induced the largest tilts. The signs of the right rotation and left stop responses were reversed then the data from all of the subjects and the four stimuli were averaged in 5-s bins. The mean peak SVV response was $3.3^\circ$ (at 15–20 s after acceleration; see Fig. 3). The time constant for the decay of this response was taken as the time required for the average response to decrease to 37% of its peak value and was measured to be 30 s.

Experiment 2: simultaneous SVV and eye-movement recordings following HN yaw angular acceleration

The rotational stimuli produced nystagmic responses and torsional deviation of the eyes. Yaw rotation to the left and the cessation of yaw rotation to the right both induced a left-beating horizontal nystagmus and torsional deviation of the eyes to the right (top of the eye tilting toward the subject’s right shoulder). Stimuli in the opposite direction (yaw rotation to the right and the cessation of yaw rotation to the left) induced a right-beating horizontal nystagmus and torsional deviation of the eyes to the left. Torsional nystagmus was less consistently observed. All of the eye-movement responses decayed during the constant velocity phase of the stimulus. The torsional eye movement responses (4 subjects $\times$ 4 stimuli) were averaged to produce a “mean” response in which the torsional eye position reached a peak $\sim$ 6 s after the onset of the stimulus. The averaged torsional response remained fairly steady for $\sim$ 5 s and then decayed in an approximately exponential fashion with a time constant of 23 s. Figure 6 illustrates one subject’s responses to the initiation and cessation of yaw rotation to the left [NB: the additional small up-beating nystagmus observed is a common occurrence in $\sim$ 1/3 of normal subjects and is tilt sensitive (Bisdorf et al. 2000; Kim et al. 2000)].

The continuous SVV measured during the 3D video-oculography recordings was in accordance with the SVV data obtained during HN stimulation in Experiment 1. In Experiment 2, simultaneous 3D video-oculography and SVV recordings showed that the SVV tended to follow the torsional eye position; all individual data are shown in Fig. 7. A normalized cross-correlation of torsional eye position and SVV angle was calculated for each 120-s trial; the mean peak correlation value (excluding left rotation data for subject S3 due to the erratic SVV settings and excessive blinking) was 0.83. The individual correlation coefficients of torsional eye position with SVV angles were 0.87 (S1), 0.84 (S2), 0.92 (S3), and 0.77 (S4). SVV settings lagged torsional eye position by an average of 3.5 s, the delay allowing for all the preceding perceptual and manual processes involved in the task. We measured the ratio of peak change in SVV angle with respect to peak change in torsional eye position. The mean change in SVV tilt was 76% of the torsional eye position change, with individual values of 69% for S1 and S2 and 80 and 84% for S3 and S4, respectively.

Surprisingly, both the ocular tilt and SVV settings were in a direction opposite to the direction of yaw acceleration, i.e., an opposite direction to that which may have been expected from the slow phase torsional VOR (see discussion). For this reason, the individual eye-movement recordings were visually inspected. Clear torsional nystagmic patterns were identified in 3/4 subjects. In 50% of the trials, the net change in ocular torsional position was due to fast phase activity rather than to the slow phase component of the torsional VOR (Fig. 6).
However, in the remaining cases, the net torsional deviation could not be confidently ascribed to clearly defined slow or fast phase eye movements.

Experiment 3: effect of vertical eye position on the SVV following HN yaw angular acceleration

This was a control experiment to see whether SVV recordings in Experiment 1 might have been influenced by different vertical eye positions. As expected, the rotational SVV response in this experiment, with continuous visual vertical adjustment, was generally similar to that recorded in the original HN experiment (Experiment 1). The mean peak tilt of the SVV in the EN condition was 2.6 ± 0.4°. The response was similar in the EU condition (mean peak tilt: 2.7 ± 0.5°). However, in the ED condition the average peak SVV tilt was reduced to 1.4 ± 0.6°.

Repeated measures ANOVA indicated a statistically significant effect of eye position on SVV tilt (P = 0.04) but further analysis with Bonferroni post hoc comparisons failed to indicate any significant mean differences between various eye positions. Static averages showed no significant difference between eye positions.

In none of the three experiments did subjects volunteer illusions of body tilt. Four additional subjects were separately rotated while viewing the static luminous line placed vertically in the four head positions and were specifically asked to report any body tilt sensations. All responses were always negative.

Discussion

These experiments investigated the effect of SCC stimulation on the SVV. The topic has not only physiological but also clinical implications because the clinical literature tends to view abnormal tilts of the SVV as a selective indication of otolith (graviceptive) system disease (Böhmert and Mast 1999; Brandt and Dieterich 1994; Gresty et al. 1992; Halmagyi and Curthoys 1999; Tabak et al. 1997; Vibert et al. 1999). First we will discuss the effect of rotation on the SVV and then the relation between the SVV and eye movements.

Subjective visual vertical and vertical semicircular canal activity

In these experiments, SCC stimulation was delivered by on-axis angular rotation about an earth-vertical axis. In this way, there was no net stimulus delivered to the otoliths. Thus the differences in SVV tilt due to rotation with the head in different positions (HN, HU, HD, HFD) relate to the variable proportion of stimulation given to the horizontal or vertical SCCs.

Most previous work on the effect of SCC stimulation on the SVV involved roll plane rotation around an earth-horizontal axis (Holst and Grisebach 1951; Stockwell and Guedry 1970; Udo de Haes and Schöne 1970) or centrifugation (Tribukait 1999), which stimulated not only the SCC but also the otoliths. Tribukait (1999) influenced the subjective visual horizontal by centrifugation with a free-swinging gondola so that the subject’s main longitudinal body axis aligned itself with the net gravitational vector. [NB: for simplicity, we will consider that subjective horizontal and vertical are equivalent although dissociation between these two measurements can occur (Betts and Curthoys 1998; Pettorossi et al. 1998)]. It was argued that the actual body tilt with respect to earth-vertical could only be sensed by the vertical SCC and that there was no roll stimulus to the otolith organs. However, Tribukait (1999) admitted that
some subjects correctly perceived that they were tilted with respect to earth vertical and that the magnitude of the visual tilt was a function of the g levels attained. In view of these two factors, namely tilt perception and g-level dependence, how much of the visual tilt observed could be attributed to the vertical SCCs in these experiments is not clear. The experiments by Curthoys and coworkers (Smith et al. 1995; Wade and Curthoys 1997), with yaw rotation in the normal upright position (i.e., no otolith stimulus) produced a bias in torsional eye position that correlated closely with the rotationally induced tilts of the visual horizontal. The effect was attributed to SCC stimulation and “cross-coupling of the horizontal head-velocity signal to a torsional eye position integrator,” but the specific possibility that the vertical SCCs could have induced the ocular or SVH tilt was not raised.

Our experiments were based on the hypothesis that SVV tilt during earth-vertical axis yaw rotation is due to vertical SCC stimulation. This was confirmed by the existence of a positive correlation between vertical SCC stimulation and mean SVV tilt as indicated by Fig. 5. When the head was pitched back (HU), both vertical SCC stimulation and SVV tilt were greater than for any other head position tested. When the head was tilted forward (HD), vertical SCC stimulation was minimal and there was no measurable effect of rotation on the SVV. Had the SVV tilt been mediated by horizontal canal activity, then the effect would have been larger in this particular head position because the horizontal canal planes were closely aligned with the rotational plane. Moreover, even in HFD where the horizontal canals continued to experience strong stimulation in the same rotational direction, the tilt of the SVV was reversed with respect to HN or HU as expected if the vertical canals mediated the observed effects (Fig. 5). Although both anterior and posterior canals are contributory, the reversal in SVV tilt responses coincided with the change in the direction of posterior SCC stimulation, and, in fact, correlation analysis showed that SVV tilt was more strongly associated with posterior rather than anterior SCC stimulation.

**Ocular movements and subjective visual vertical**

Several aspects deserve discussion: whether the SVV effects described could be an artifact related to vertical eye position, the relation between torsional eye position and the SVV, including the polarity and the duration of the rotationally induced SVV tilt.

**VERTICAL EYE DEVIATION.** During Experiment 1, the subjects’ eyes were not in primary gaze for all head positions tested, so it was important to ensure that our results were not due to varying vertical eye position. The rotational SVV responses in the supplementary eye positions experiment (Experiment 3) were similar to those recorded in Experiment 1 but with rotationally induced SVV tilts being smaller with ED than with EN and EU. This trend was statistically significant with the ANOVA \( (P = 0.04) \) but post hoc Bonferroni comparisons failed to confirm significant differences between SVV values in the different eye positions. Because ED in the original experiment was adopted during HU, the results of the eye-position experiment indicated that, if anything, the effect observed during the HU condition could have been underestimated. Our experiments with the normal head position (HN) kept the eyes around primary gaze thus vertical ocular deviation was never an issue. It may be worth mentioning that convergence is not a confounding issue either due to the fact that nasion-target distance was kept constant in all conditions.

**TORSIONAL EYE POSITION.** 3D video-oculography showed that SVV settings and torsional eye position followed a similar temporal and directional pattern with torsional deviation of the eyes and SVV tilt occurring in the same direction for identical stimulation, with a similar time constant and a mean peak correlation coefficient of 0.83. An amplitude comparison showed that 76% of the torsional change is reported by subjects as SVV tilt or, in other words, that only 24% of ocular tilt is not reported by subjects as SVV tilt.

These findings confirm those of Wade and Curthoys (1997), but a limitation present in their experiment, namely the technical impossibility of obtaining simultaneous ocular and SVV recordings, was overcome in the present study. This allowed us to cross-correlate the two measurements and measure the average delay between torsional eye position changes and SVV settings, which was found to be \( \sim 3.6 \) s. In agreement with Wade and Curthoys (1997), we conclude that ocular torsional position plays a critical role in SVV tilt perception and that both are influenced not only by otolith (Brandt and Dieterich 1994; Miller and Graybiel 1966; Mittelstaedt 1992) but also by vertical SCC activity. During body tilt, somatosensory input also plays a role in the perception of the SVV (Anastasopoulos and Bronstein 1999; Bronstein 1999).

One should not conclude, however, that all rotationally induced SCC effects on tilt perception relate to changes in ocular torsional position. Recently, Merfeld et al. (2001) conducted human centrifuge experiments and observed changes in the time course of visual (SVV) and somatosensory tilt perception, according to the presence or absence of earth-vertical yaw rotational cues. Clearly, yaw effects on the somatosensory task cannot be ascribed to ocular torsional changes. Unfortunately, the possibility that yaw rotation effects on tilt perception may be due to vertical SCC activation was not considered nor were torsional eye movements recorded. This consideration, however, may be of value in interpreting some differences between two sets of similar experiments in the literature (Merfeld et al. 2001; Seidman et al. 1998). In these experiments, subjects were centrifuged with the head in the upright position with the variable radius (or dynamic-radius) technique. Essentially, subjects are initially rotated on axis and then, when all canal effects are extinguished, linearly displaced to the eccentric position. In doing so, subjects are exposed to the centrifugal acceleration without further canal signals and accordingly report body and visual tilt. In the Merfeld et al. (2001) experiment, subjects were displaced laterally along the interaural axis, and the subjective tilt reported was in the roll plane. In the Seidman et al. (1998) experiments, subjects were displaced in the fore-aft axis, and so the tilt experienced was in the pitch plane. Whereas the findings in these two experiments are overall in agreement, it is not clear why the development of the tilt illusion was considerably slower in the fore-aft displacement experiments. We would suggest that the addition of roll-motion cues arising from activation of the vertical SCCs during head-upright rotation (as discussed in this study) may facilitate the development of the tilt illusion in the roll plane but not in the pitch plane. We are, however, skeptical of our own suggestion. One would expect that centrifugation in the

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side-on position should produce larger/faster tilt illusions when subjects face the direction of motion than when they are moving backward on the basis that in the facing motion position, vertical SCCs and otolith input would signal roll-motion and roll-tilt outward congruently. For instance, clockwise rotation facing motion will deliver a leftward roll-motion stimulus to the vertical canals and a re-orientation of the gravito-inertial vector interpreted as left tilt. When backing the direction of motion, canal cues remain identical but the tilt effect is inverted, so creating otolith-canal directional conflict. Thus one would expect better tilt perception while facing motion, but actually the opposite is the case (Merfeld et al. 2001). On the basis of this finding, our suggestion that differences in the time course of the pitch and roll tilt illusions during centrifugation are due to co-planar vertical SCCs cues in the roll plane is less likely to be appropriate. Repeating the side-on centrifugation experiments with different head positions as in our study could help settle this problem.

POLARITY OF THE ROTATIONALLY INDUCED TILT OF THE SVV. Although it can be concluded that the SVV tilt observed is due to vertical SCC stimulation, attention should be drawn to the polarity of such tilt. With the head in HN or HU positions, chair rotation to the right stimulates the vertical SCC as in roll motion to the left. If the SVV effect followed the slow phase torsional VOR, the expected SVV tilt would be in the opposite direction to that of roll stimulation, i.e., SVV tilt to the right during chair rotation to the right. However, this is not the case. Our results show that the SVV settings are tilted in the same direction as the angular acceleration to the vertical SCC and so, unexpectedly, cannot be explained by the slow phase of the torsional VOR. Although Wade and Curthoys (1997) recorded the same polarity that we did, the observation was not discussed. We believe that the unexpected polarity of SVV and ocular tilts results from an “anticompensatory” ocular torsional deviation. This term was coined by Melvill Jones (1964) as he observed that during fast head rotations the predominant deviation of the eyes within the orbit was not in the expected, compensatory, slow phase direction of the VOR but in the opposite, anticomparnsatory direction. Such deviation of the eyes is brought about by the fast phase components of vestibular nystagmus and is particularly noticeable during high-velocity, sustained head rotations (Melvill Jones 1964). The saccadic origin of this anticomparnsatory eye deviation was observed in half of the Experiment 2 trials (Fig. 6), but, in the rest of the trials, characterization of the eye movements was difficult, a fact also discussed by Melvill Jones (1964). These anticomparnsatory gaze shifts have since been observed with optokinetic (Hood and Leech 1974), vestibular (Barnes 1979; Melvill Jones 1964), and cervical (Bronthoy and Hood 1986) stimuli and so appear to be a general property of the oculomotor system that allow the eyes to “... automatically thrown into the position which will most quickly pick up the new point of interest” (Melvill Jones 1964). It is possible that the predominantly saccadic basis for this torsional eye deviation was not observed in the experiments by Smith et al. (1995) and Wade and Curthoys (1997) due to the low video rate used (6 Hz). The sample rate we used (50 Hz) is an improvement, but definitive identification of fast or slow phase components underlying the anticomparnsatory torsional deviation would require even faster sampling rates.

DURATION OF THE SVV AND OCULAR TORSIONAL RESPONSES. The time constant of decay of the SVV tilt and the ocular torsional position deviation were unusually long. The mean time constant for the decay of the response in our experiments was 30 s for the SVV and 23 s for torsion, and it was common to observe that by the end of the 60-s window there were often ocular and SVV tilts remaining of ~1° (see Fig. 3). Both Tribukait (1999) and Smith et al. (1995) also reported long-lasting effects, much longer in duration than the expected time constant of the horizontal (~16 s) (Benson 1968; Cohen et al. 1981; Okada et al. 1999) and torsional (~5 s) (Jäuregui-Renaud et al. 2001; Seidman and Leigh 1989) VOR responses. VOR time constants generally represent the progressive decay in slow phase velocity. Our experiments, however, show that the SVV tilts are mediated by an anticomparnsatory, probably fast phase-mediated, torsional ocular deviation. As such, the duration and time constant of the response is not dictated by the dynamics of the slow phase mechanisms. Pursuit or saccadic eye movements can correct position biases in the vertical or horizontal planes of the oculomotor system, but a positional bias in the torsional oculomotor system cannot be corrected in this way due to absence of any tangible pursuit or voluntary saccades in this plane. Accordingly, any position bias such as the one induced by our rotational stimuli is likely to last until new stimuli induce torsional VOR activity. We do not know whether spontaneous drifts or occasional “spontaneous” torsional saccades can occur to reset torsional eye position to normal.

In summary, these experiments show that SCC stimulation consistently influences the perception of the SVV. These effects are mediated by the vertical, particularly posterior, SCCs. The SVV tilts fall changes in ocular torsional position that are due to an anticomparnsatory eye deviation rather than the slow phase torsional VOR. The strong warning to the clinical community is that, in light of these findings, it is incorrect to interpret lesion-induced tilts of the SVV as a result of damage only to otolith receptors and pathways.

DISCLOSURES

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