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RESEARCH ARTICLES

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Direction specific error patterns during continuous tracking of the subjective visual vertical

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Abstract The aim of this study was to characterize the error pattern of continuously tracking the perceived earth-vertical during roll rotations from upright to right or left ear-down and from right or left ear-down to upright. We compared the tracking responses of two paradigms, which either continuously activated the otoliths organs alone (constant velocity tilt) or both the otolith organs and the semicircular canals (constant acceleration tilt). The tracking responses of the subjective visual vertical showed characteristic differences depending on starting position and tilt direction relative to gravity. The error patterns in the constant-velocity and constant-acceleration tilt paradigm were reversed. Estimations during tracking, when otolith information was continuously changing, were more precise compared to estimations following fast tilts to fixed roll tilt positions. We conclude that the central processing underlying these perceptual tracking responses requires, besides the otolith input, information from the vertical semicircular canals.

Keywords Spatial orientation · Semicircular canal-otolith interaction · Somatosensory signals

Introduction

Unbiased perception of verticality represents an important asset in self-orientation and motion in space. Traditionally, estimation of the earth-vertical has been studied by excluding visual cues and significant semicircular canal activation in order to isolate the otolith function (Böhmer and Mast 1999; Mittelstaedt 1983, 1991, 1999; Van Beuzekom and Van Gisbergen 2000; Van Beuzekom et al. 2001). When asked to orient a luminescent bar parallel to the perceived earth vertical in an otherwise dark environment, subjects show characteristic error patterns that usually consist of overestimations of the earth-vertical at smaller tilt angles [E-effect (Müller-effect): Müller 1916] and underestimations at larger angles [A-effect (Aubert-effect): Aubert 1861; for a review see Howard 1982, 1986]. Which factors determine these error patterns as a function of body position has not been clear. Recently, we reported that otolith signals appear to provide the major reference for body tilts in the range up to ~45° based on almost precisely reciprocal error patterns of the visual and postural vertical in this range (Jaggi-Schwarz et al. 2003). Apart from otolith signals somatosensory cues contribute to the perception of the subjective visual vertical (Schöne 1975; Mittelstaedt 1991; Anastostopoulos et al. 1999). These cues appear to preponderate at larger tilt angles (Schöne 1975), where they contribute to the variability of the A-effect, possibly due to adaptation effects (Anastosopoulos et al. 1999). A number of investigators have studied the effect of simultaneous activation of vertical semicircular canals and otoliths on the perception of the vertical (Correia and Guedry 1966; Stockwell and Guedry 1970; Udo de Haes and Schöne 1970). Regarding the role of semicircular canal signals, Guedry and colleagues concluded “subjects are able to accurately estimate visual vertical soon after being tilted without supplementary canal information, but only when tilt is sufficiently slow” (Stockwell and Guedry 1970). Along these lines, we recently reported that fast roll tilts improve the estimations in the tested tilt range of ±90° (Jaggi-Schwarz and Hess 2003), supporting the notion that orientation cues from the otolith organs are centrally more strongly weighted when the vertical semicircular canals are coactivated. In contrast to earlier suggestions, activation of the semicircular canals appears not to be a necessary condition for the development of an E-effect. Overestimations can also be observed during (slow) constant-velocity tilts that minimally activate the semicircular canals (Jaggi-Schwarz et al. 2003).

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In this study we use a paradigm in which subjects had to track the perceived earth-vertical by continuously adjusting a luminescent line during roll tilt. To address the question of the influence of initial position and tilt direction we applied roll rotations from positions close to upright and 90° side-down positions. In close-to-upright positions, the initial estimation error is expected to correspond on average to an overestimation whereas in side-down positions it should correspond on average to an underestimation. By cross-examination of the error patterns for different tilt directions we address specifically the question of whether the tracking errors depended on the previous stimulus history. Furthermore, we combined each of the four different initial conditions with one of two stimulus profiles that activated either the otolith receptors alone or receptors of both the otolith organs and the semicircular canals. To this end we used constant-velocity or small amplitude constant-acceleration tilts. Based on responses to these different stimulus profiles we asked the question of how otolith and semicircular canal signals interact with somatosensory cues in the tracking responses of the subjective visual vertical.

Materials and methods

Subjects

Fifteen subjects (eight males, seven females) between 24 and 38 years of age participated in this study after having given written informed consent according to a protocol approved by the Ethics Committee of the Canton of Zurich, Switzerland. In the medical case history subjects had normal hearing and no otological or neurological disorders.

Experimental setup and protocol

Subjects were comfortably seated on a chair, which was mounted on a 3D turntable with three servo-controlled motor driven axes (Acutronic, Switzerland). The head was positioned at the rotation center and restrained with an individually molded thermoplastic mask (Sinmed BV, Reeuwijk, The Netherlands). The torso was secured with safety belts and evacuation pillows. A laser projector (MVS Lasertechnik, Switzerland), mounted above the subject's head, projected a luminous line of 32 cm length on a tangent screen at a distance of 76 cm in front of the subject. The line was centered at eye level (visual angle: 23.8°, luminance: 20 cd/m^2). Subjects could adjust the angular position of the luminous line by using a rotary knob (angular velocity up to 3,100°/s; used velocity was maximally 34°/s). The angular position of the luminous line and the subject's roll position were continuously recorded, digitalized and fed into a computer. The error in recording the line setting was less than 1° and the subject's roll position was determined with an error of less than 0.1°.

The experimental protocol consisted of eight roll tilts in complete darkness. Subjects were rotated with an acceleration of 10°/s^2 (peak velocity of 10°/s) in complete darkness from upright to the start position, which was either 30° or 110° left or right ear-down. After a delay of 30 s in the dark, the laser line appeared in front of the subject in a random position and the chair started rotating. Throughout the whole tilt range, the subjects had to keep the luminous line aligned to the estimated earth-vertical as accurately as possible.

Four different paradigms were used: (1) in the *up-down constant velocity paradigm* (Fig. 1A), the subjects were tilted at a constant velocity of 0.5°/s (acceleration/deceleration: 0.05°/s^2) from ±30° to ±100°; (2) in the *down-up constant velocity paradigm,* the subjects were tilted at the same constant velocity from ±110° to ±10°; (3) in the *up-down constant acceleration paradigm* (Fig. 1B), the subjects were tilted at a constant acceleration of 3°/s^2 (peak velocity of 20°/s) from ±30° to ±120°; (4) in the *down-up constant acceleration paradigm,* tilts were performed at the same acceleration but from ±120° to ± 30°.

After each protocol, the subject was returned to the initial upright position (ρ=0°) and the room light was switched on for ~10 s for reorientation.

The continuous tracking data exhibited response features comparable with those of previously reported responses after fast tilts (Jaggi-Schwarz and Hess 2000). However, because in the previous work we had only recorded responses following side-down tilts, we decided to supplement these data by recording the luminous line setting characteristics also following roll tilts towards upright starting in 90° side-down positions. For this, the subjects were tilted in the dark with an acceleration of 180°/s^2 (peak velocity: 100°/s) from a left or right ear-down position (ρ=±90° right/left ear-down) towards one out of 15 different more upright positions (±60°, ±50°, ±40°, ±30°, ±20°, ±10°, 0° or upright). Tilt directions and angles varied randomly, but for each subject in the same way.

Data analysis

The tracking error was computed as the angle between the laser line and the earth-vertical (Fig. 2; error angles δ). The tilt direction was taken into account, which means that if the line was tilted between the earth-vertical and the subject we called this underestimation (A-effect) and if it was tilted further to the other side of the earth-vertical it was designated as overestimation (E-effect). The error angles are presented according to the following sign convention: in left ear-down positions, i.e., at negative tilt angles, overestimations were plotted as positive errors and underestimations as negative errors. Similarly, in right ear-down positions, i.e., at positive tilt angles, overestimations were plotted as negative errors and underestimations as positive errors. To compare the results with our previous study (Jaggi-Schwarz and Hess 2003), we evaluated the data at roll tilt angles of 0°, ±10°, ±20°, ±30°, ±40°, ±50°, ±60°and ±90° in the following way: We used bins of 1° centered around the desired tilt angles and averaged all data points within each bin. For

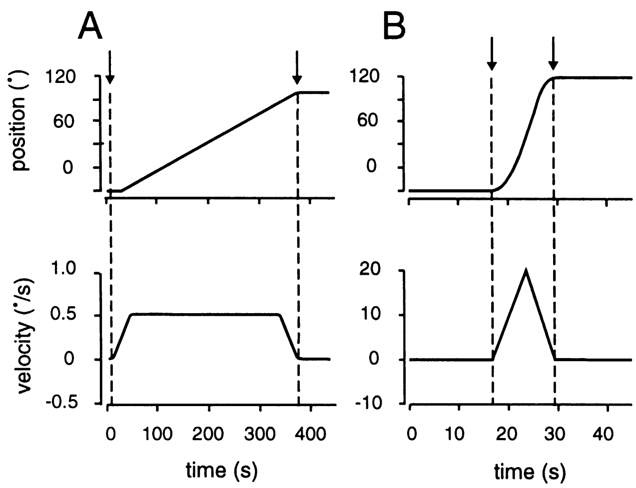


Fig. 1 A Constant velocity profile (−30° to +100°). **B** Constant acceleration profile (−30° to 120°). *Top row* Chair position during up-down motion. *Bottom row* velocity trace. *Arrows* and *vertical dashed lines* indicate onset and stop of chair motion. Note the different scales in **A** and **B**

the upright-position (ρ=0°) we computed the mean of the responses from the up-down and the down-up paradigms.

In the constant velocity paradigms, we separately analyzed the time intervals where the subjects moved the laser line (*adjustment intervals*) from those where they did not move it (*decision intervals*). These intervals were manually selected with a time resolution of about 0.3 s, then we computed the mean interval duration and the position of the laser line in bins of 10°.

Since our data were generally not normally distributed we used the Kruskal-Wallis non-parametric tests for statistical computations.

Results

Examples of individual tracking response of the subjective vertical are shown in Fig. 3. At large tilt angles, all subjects often showed quick and large changes in the tracking error (see arrowheads in Fig. 3A). In line with this observation, subjects reported that the laser line appeared to move rapidly after intervals in which nothing seemed to happen or that the tilt velocity seemed to change. Some subjects also felt tilted in the yaw or pitch plane instead of the roll plane. At closer inspection, the error curves revealed a saccade-like behavior in the constant velocity paradigm (Fig. 3A, B), in contrast to the oscillatory behavior in the constant acceleration error curves (Fig. 3C, D).

The average duration of the adjustment intervals, during which subjects adjusted the laser line, was about 0.99 ±0.26 s (mean ± SD over pooled adjustment intervals from all constant-velocity experiments). The average durations of the decision intervals, where subjects did not adjust the line, was about 2.21±0.73 s. We found that the decision intervals were on average longer at larger than at smaller tilt angles, in particular in the up-down paradigms (Fig. 4A, Table 1).

The average number of readjustments was 7.4±1.6 per bin of 10° and increased at smaller tilt angles (Fig. 4B), which means near upright positions. In the whole tilt range the average number of readjustments was 110.7±23.7.

There was a trend to increasing numbers of readjustments in the up-down and down-up tilts when comparing the first and the last bins (Fig. 4B: significant differences are marked by stars and circles).

Inspection of the averaged response errors revealed the following interesting characteristics: The average initial tracking error at onset of the tilt and tracking task corresponded to the error expected in the respective tilt position: near upright it was close to zero or indicating slight overestimation and in side-down position it was indicating underestimation. The mean error curve of the

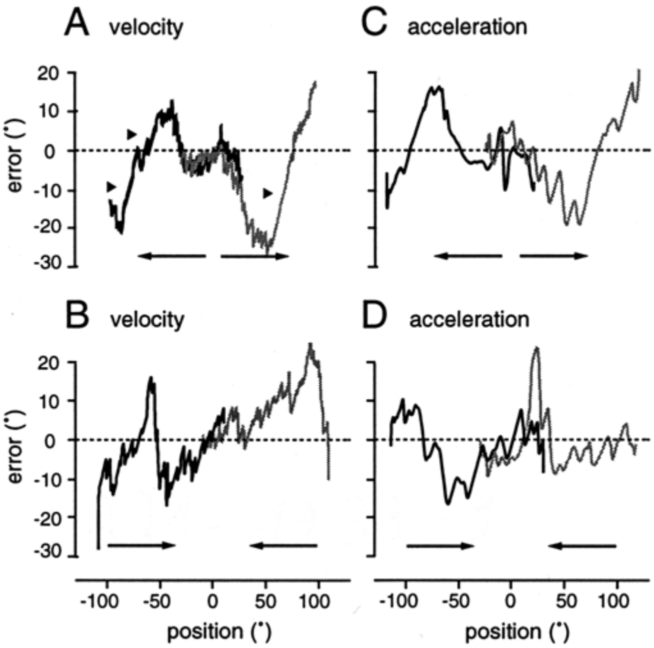


Fig. 3A–D Tracking error curves of one representative subject. **A, B** Constant-velocity paradigm. **A** From upright to left (*black solid line*) and right ear-down (*gray solid line*). **B** From left (*black solid line*) and right ear-down (*gray solid line*) to upright. **C, D** Same as in **A** and **B** but for the constant-acceleration paradigm. *Horizontal arrowheads* denote large changes in the tracking error over short time intervals in **A**; similar brisk adjustments also occurred in **B, C** and **D**. The *horizontal arrows* mark the direction of the roll tilts. Starting position: around upright (±30°) or ear-down (±110°/±120°). Negative tilt angles denote left ear-down positions; positive tilt angles denote right ear-down positions. Positive errors correspond to overestimations in left ear-down positions and underestimations in right ear-down positions

Table 1 Kruskal-Wallis test for the duration of decision intervals in the different constant velocity tilt paradigms. For larger tilt angles the duration of decision intervals was longer than for smaller ones, primarily in the up-down paradigms.*Asterisks* indicate significant differences

Decision interval durations	*P*value
Up-down to the right	0.0113*
Up-down to the left	0.0004*
Down-up to the left	0.0952
Down-up to the right	0.1323

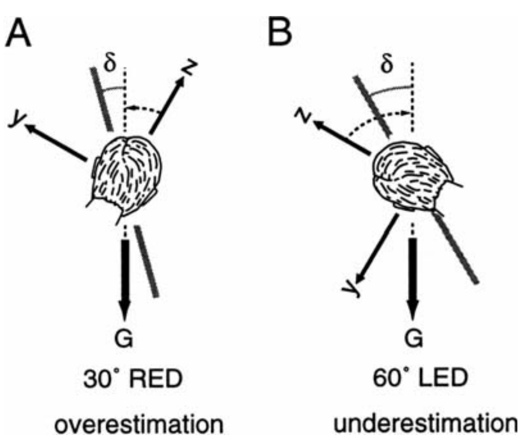


Fig. 2A, B Estimation of earth-vertical in the luminous line paradigm. **A** Overestimation (E-effect) of the direction of earth-vertical by δ, in a subject in 30° right ear-down (RED, back view). **B** Underestimation (A-effect) of the direction of earth-vertical by δ, in a subject in 60° left ear-down (LED) (*solid thick gray lines* luminous line, *dotted black lines* earth-vertical, *G* gravity)

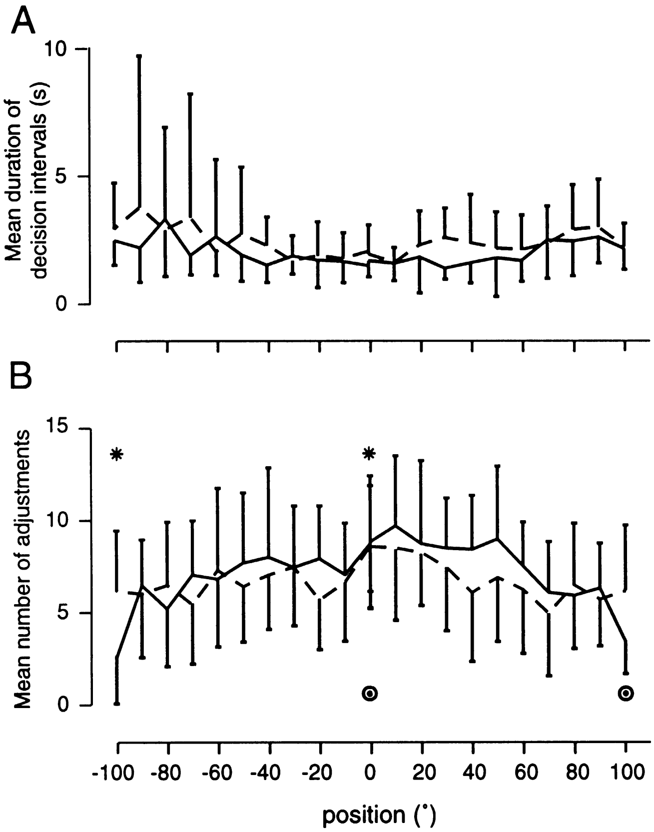


Fig. 4 Mean duration of decision intervals **(A)** and mean number of adjustments **(B)** per 10° bins (*solid black lines* up-down constant velocity paradigms, *dashed black lines* down-up constant velocity paradigms, *stars and circles* indicate significant differences between the first and last 10° bins in the down-up velocity paradigm)

up-down velocity and the down-up acceleration paradigms showed clear E- and A-effects (Figs. 5A: black solid line, 5B: black dashed line). But there was no E-effect in the mean error curve of the down-up velocity and the up-down acceleration paradigms (Figs. 5A: gray solid line, 5B: gray dashed line). The standard deviations were small at smaller tilt angles and increased for larger ones.

Up-down and down-up mean error curves of the constant velocity paradigms (Fig. 5A) significantly differed from each other at 0° and +30 to +60° (Kruskal-Wallis-test: $p<0.05$), whereas in the accelerations paradigm (Fig. 5B) the difference was significant at all tilt angles (Kruskal-Wallis test: $p<0.05$). Also comparisons between the two different paradigms (Fig. 5C, D) showed significant differences in the mean error curves. The up-down mean error curves (Fig. 5C) significantly differed at –60° to –20° and +20° to +90° tilt angles (Kruskal-Wallis test: $p<0.05$) and the down-up mean error curves (Fig. 5D) were significantly different at –30°, −10°, 0° and +30° to +60° tilt angles (Kruskal-Wallis test: $p<0.05$).

The most striking result was the similarity between the responses obtained from the constant-velocity down-up/constant-acceleration up-down tracking paradigms and the fast tilt paradigm (Fig. 5A: constant-velocity down-up tracking: gray solid line; Fig. 6A: constant-acceleration up-down tracking: black solid line, fast down-up tilt paradigm: black dashed line). Also the constant-velocity up-down/constant-acceleration down-up tracking and the fast up-down error curves showed a remarkable similarity on average (Fig. 5A: constant-velocity up-down tracking: black solid line; Fig. 6B: constant-acceleration down-up tracking: black solid line; fast up-down tilt paradigm: black dashed line).

Discussion

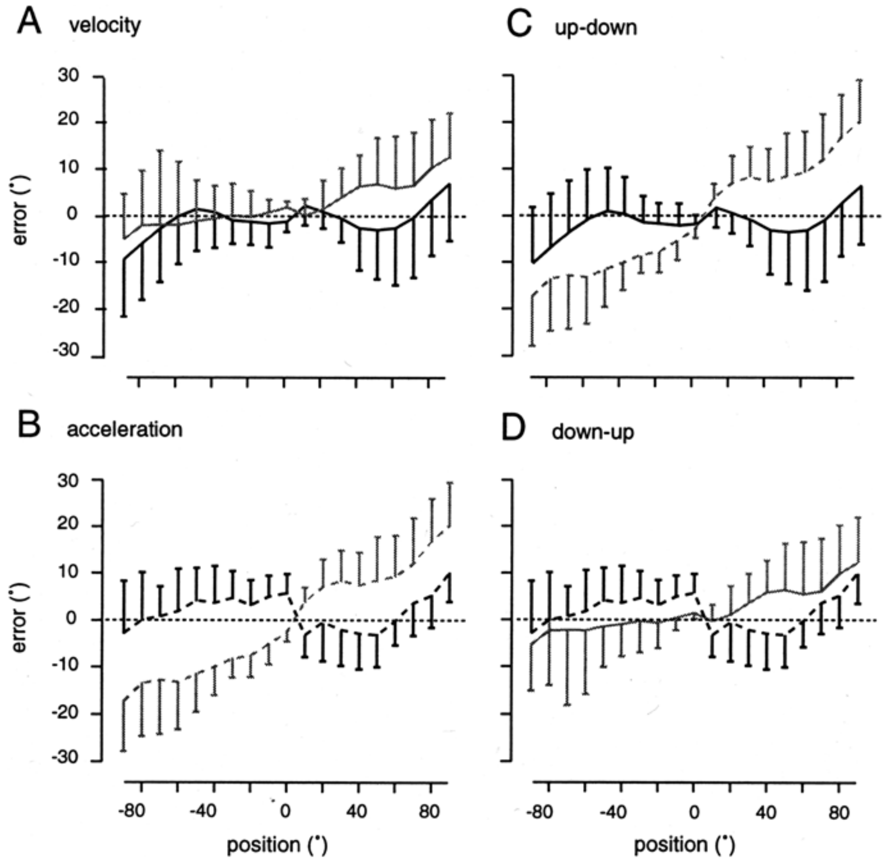
Our results clearly demonstrate that the error patterns of tracking responses do not simply reflect the initial error but that they are strongly modulated by head position, tilt direction and acceleration profile. In general the error patterns depended on both the direction and the motion characteristics. We found that the down-up constant-acceleration paradigm showed similar response characteristics as the fast up-down tilt paradigm and vice versa, suggesting that it is the direction of acceleration rather than the motion direction relative to gravity that determines the error profile.

Individual response patterns

The quick and large tracking movements at larger tilt angles in the constant velocity paradigms (see arrowheads in Fig. 3) matched the subjects' reports that the luminous line appeared to remain earth-vertical for a certain time, but then suddenly sloped at a large angle. This rivaling sensation, which could reflect visual motion adaptation (McGraw et al. 2002), probably prompted subjects to massively readjust the laser line. Another reason for the jerky tracking behavior could be that in ear-down positions the subject's sensitivity to estimating the earth-vertical direction decreased due to adaptation of somatosensory cues, which resulted in increasing standard deviations. The verbal reports support the notion that the subjects experienced an increasing uncertainty in estimating the earth-vertical in ear-down positions. For example, some subjects reported illusionary sensations of forward or backward rather than roll tilt. We assume that this disorientation is due to failing integration of the different sensory signals and/or somatosensory adaptation processes (Anastosopoulos et al. 1999; Jaggi-Schwarz et al. 2003). Accordingly, the decision interval significantly increased at larger tilt angles, particularly in the up-down tracking paradigms (Fig. 4A; Table 1). In the down-up tracking direction, the decision intervals did not change much over the tilt range (Table 1) presumably because, when the paradigm started in side down position, somatosensory adaptation was likely rather small. The numbers of readjustments per 10° bin decreased with increasing tilt angle (Fig. 4B). However, there was no correlation between amplitudes of readjustments and tilt angles.

There could be several reasons for the interesting jerky or saccade-like appearance of the tracking error in the velocity paradigms (Fig. 3A, B). First, the central process

Fig. 5A–D Mean error curves of the subjective visual vertical during different roll tilts. **A** Constant velocity paradigms (*solid black line* roll tilt from upright to ear-down position, *solid gray line* roll tilt from ear-down to upright position). **B** Constant acceleration paradigms (*dashed gray line* roll tilt from upright to ear-down position, *dashed black line* roll tilt from ear-down to upright position). **C** Comparison between constant velocity (*solid black line*) and acceleration (*dashed gray line*) upright-to-ear-down tilts. **D** Comparison between constant velocity (*solid gray line*) and acceleration (*dashed black line*) ear-down-to-upright-tilts



of updating self-orientation in space is probably discontinuous (Schall 2003; Van Rullen and Koch 2003). Second, the central decision-making process, which is bound to underlie the adjustments of the subjective vertical during the very slow constant velocity tilt, is probably also a discontinuous process. Finally, the jerky behavior could be provoked by a certain discrepancy between the high angular sensitivity of the device controlling the laser line and the relative imprecision of estimates of the earth-vertical (large standard deviation). The oscillatory rather than jerky behavior of the acceleration error curve could result from the necessity of deciding relatively quickly about the location of the subjective vertical during the accelerating change in orientation.

Average response patterns

Interestingly, not only the mean error curves of the constant velocity and acceleration paradigms showed characteristic differences, but also the two tilt directions (Figs. 5, 6). It should be mentioned that subjects always thought to react belatedly during the acceleration paradigm. Accordingly the tracking error should always show an A-effect, which was, however, only true for the up-down, but not for the down-up, direction.

The mean error curves of the up-down constant-velocity and down-up constant-acceleration paradigms were strikingly similar to those of the fast tilt paradigm, which we used in an earlier study (Jaggi-Schwarz and Hess 2003). Similarly, the down-up constant-velocity and the up-down constant-acceleration error curves minimally differed on average from the curve of the fast upward tilt paradigm.

Tentative explanations of the different response characteristics

First, we will compare the impact of the two rotation directions on the error patterns. Although the up-down and down-up error curves of the constant-velocity paradigm (Fig. 5A) did not significantly differ from each other (exceptions were at tilt angles 0° and +30° to +60°; Kruskal-Wallis test: $p<0.05$), the shapes look different. In the up-down paradigm (Fig. 5A: black solid line), the mean error curve shows small E- and A-effects in contrast to the down-up paradigm, which shows mainly an A-effect (Fig. 5A: gray solid line). In the up-down acceleration paradigm, there is only an A-effect (Fig. 6A: black solid line), whereas in the down-up paradigm there is a significant E-effect followed by an A-effect (Fig. 6B: black solid line). Notice the considerable hysteresis in the error patterns, indicating that it depends on whether a given position has been approached from an upright or side-down position. Interestingly, this hysteresis is much more pronounced during the relatively fast constant-acceleration than during the slow constant-velocity tracking paradigm, where it is significant only in one tilt

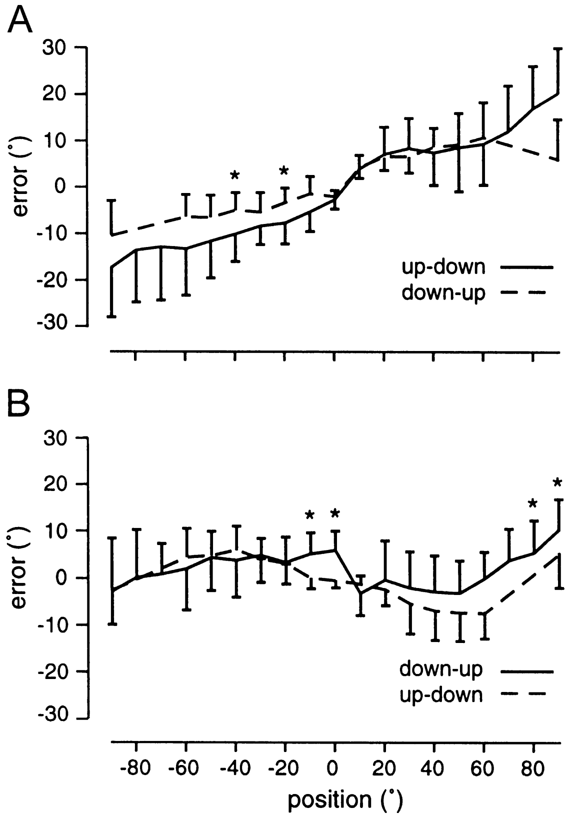


Fig. 6A, B Comparison of error patterns obtained with the tracking and fast tilt paradigms. **A** Error patterns of constant-acceleration up-down tracking (*solid black line*) and fast down-up tilt paradigm (*dashed black line*). **B** Error pattern of the constant-acceleration down-up tracking (*solid black line*) and the fast up-down tilt paradigm (*dashed black line*). *Stars* indicate significant differences between the curves. Data of the fast tilt paradigm are from Jaggi-Schwarz and Hess (2003)

direction. Activation of the vertical semicircular canals is apparently the major reason for the observed hysteresis in the constant-acceleration paradigms in contrast to static tilt paradigms where the effect of a preceding tilt on the subjective visual vertical has been linked to adaptation effects in the somatosensory system (Schöne and Lechner-Steinleitner 1978). Similar adaptation effects could be responsible for the asymmetric hysteresis observed in the constant-velocity paradigm.

Assuming linear superposition of the effects caused by semicircular canal activation, it should be possible to estimate the semicircular canal influence by taking the algebraic difference between the constant-velocity (interaction of otolith + somatosensory cues) and the constant-acceleration error profiles (interaction of otolith + semicircular canals + somatosensory cues). This procedure is perhaps justifiable if adaptation of somatosensory cues during the course of tilting is negligible. In doing so one would reach the conclusion that semicircular canal activation is biasing the perception of the visual vertical towards underestimation, particularly at larger tilt angles (compare error curves in each of Fig. 5C, D). A tilt-dependent semicircular canal effect has been described previously by Udo de Haes and Schöne (1970).

Pavlou et al. (2003) found similar differences when they measured the subjective visual vertical during whole body yaw rotation about an earth-vertical axis. Their subjects had to pitch the head in straight on, up and down positions to vary the concomitant vertical canal activation. Depending on the head position, the otoliths were statically activated to a variable degree. These authors concluded that the different amount of concomitant vertical canal activation consistently influenced the perception of the visual vertical. In our experiments, the sole difference between the up-down and down-up rotations in the acceleration paradigms was the starting position (±20° or ±110°) and the direction of otolith and canal activation. Therefore, the simultaneous activation of the vertical semicircular canals appears to be responsible for the different shapes of the error curves. If a subject rotates from a right ear-down position upwards (i.e., leftward), the hair cells of the anterior and posterior vertical canals on the left side, i.e., those in the upper lying ampullae relative to gravity, will be excited, whereas those of the lower lying ampullae on the right side will be inhibited. The opposite activation pattern occurs if the subject rotates downwards. For example, if the upper ampullary hair cells are activated while gravity is directed towards the inhibited lower ones, the subject moves upwards. Associated with this activation pattern, the subjective vertical showed alternating E- and A-effects (Fig. 6B). However, if gravity is directed towards the activated lower ampullae, the subject moves downwards. In this case, the tracking error curve showed only A-effects (Fig. 6A). The same is true for other head positions. In our previous fast tilt study (Jaggi-Schwarz and Hess 2003), we observed a similar response behavior when we tilted subjects from upright into different roll positions. In this case, gravity was always directed towards the activated vertical canals when the rotation stopped. Interestingly, the shape of the mean error curve was similar to the one shown here for the down-up paradigm. The difference between these two paradigms was that in the fast tilt paradigm, the subjective vertical was estimated after the rotation stopped (i.e., following an angular deceleration), while there was no change in the direction of acceleration or velocity in the constant acceleration paradigm. To verify our hypothesis that the vertical canals are important for monitoring the tilt direction relative to gravity, we tested the error response behavior in an analogous fast tilt paradigm in an upward direction. According to the hypothesis, the mean error curve should then show the same or a similar profile as in the up-down constant-acceleration paradigm. And, indeed, the two error curves were similar in shape (Fig. 6A). Our results reveal a similar mechanism of otolith-canal interaction as described by Guedry (1992), who found that the perception of rotation on the centrifuge depended on the relative direction of linear and angular acceleration. In our case, too, not only the otolith but also the canal signals, which are taken into account in the computation of motion relative to gravity, influence the perceptual responses reported here.

Interestingly, the average constant-velocity error curves showed characteristics opposite those of the constant-acceleration paradigm (Fig. 5C, D). While constant-velocity up-down tracking showed minimal errors in the range of –60° to 40°, the constant-acceleration tracking exhibited a significant undershooting in the whole tilt range (compare gray dashed line and black solid line in Fig. 5C). Similarly, in the down up tracking paradigms constant-velocity tracking led to undershooting in the same tilt range where the constant-acceleration tracking evoked overshooting (compare gray solid line and black dashed line in Fig. 5D). Moreover, when the semicircular canals were not activated, up-down tracking resulted in a small-amplitude oscillating pattern around zero that tended towards a clear A-effect only at the largest tilt angles (Fig. 5A: black solid line), whereas the down up tracking exhibited a predominant A-pattern (Fig. 5A: gray solid line). The long duration for completing a full 90° tilt represents a principal difficulty for a more conclusive interpretation of the error patterns of the constant-velocity paradigms. In contrast to the fast tracking responses it is likely that somatosensory cues had a more variable impact on the slow tracking responses due to their liability to adaptation. The different shapes of the error curves suggest that body position and motion direction relative to gravity are important determinants. These factors also play a role in the vestibular modulation of autonomic reflexes, for example in the regulation of blood pressure (Kaufmann et al. 2002; Ray and Carter 2003). Under static conditions, the initial body position is particularly relevant for the different initial tracking error in the up-down versus the down-up tilt paradigms. We have previously hypothesized that the postural and/or righting reflexes, which tend to keep the head upright, could bias the internal reference frame due to a mismatch between reafferent signals from the neck muscles and the actual head movement. If this hypothesis is true, the bias is likely to depend also on initial head and body position since it is known that the utricles generate asymmetric postural reactions, whereas the saccules operate in symmetric fashion (Uchino et al. 1996, 1997). But, why do these error patterns reverse when the semicircular canals are coactivated? The simplest answer would be that this is by coincidence. However, our results suggest that it is the semicircular canal activation, which triggers postural reflexes in the same direction in the continuous up-down/down-up tracking paradigms as in the fast down-up/up-down tilt paradigms, that causes the observed reversal (Cohen 1974; Goldberg and Fernandez 1975; Wilson 1975; Wilson and Melvill-Jones 1979; Fuchs 1989).

Since in the velocity paradigm only the otoliths were activated, one would expect to find similar results to one of our previous reports, where subjects estimated the vertical in a self-controlled tilt paradigm using very slow tilt velocities (Jaggi-Schwarz et al. 2003). Surprisingly, this is not the case. In comparison with the tilt paradigm, continuous tracking of the subjective vertical is found to be more precise, even though it is asymmetric. One explanation for this rather unexpected finding is that continuous updating of the position by the otoliths facilitated the estimation of the subjective vertical. Whether this is due to a continuous activation of phasic otolith units during the tilt remains to be seen.

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References

Anastasopoulos D, Bronstein A, Haslwanter T, Fetter M, Dichgans J (1999) The role of somatosensory input for the perception of verticality. Ann N Y Acad Sci 871:379–383

Aubert H (1861) Eine scheinbare bedeutende Drehung von Objekten bei Neigung des Kopfes nach rechts oder links. Arch Pathol Anat 20:381–393

Böhmer A, Mast F (1999) Assessing otolith function by the subjective visual vertical. Ann N Y Acad Sci 871:221–223

Cohen B (1974) The vestibulo-ocular reflex arc. In: Kornhuber HH (ed) Handbook of sensory physiology, vol 6. Vestibular system, part 1: basic mechanism. Springer, Berlin, pp 497–540

Correia MJ, Guedry FE (1966) Modification of vestibular responses as a function of rate of rotation about an earth-horizontal axis. Acta Otolaryng (Stockh) 62:297

Fuchs AF (1989) The vestibular system. In: Patton HD, Hille B, Scher AM, Steiner RL (eds) Textbook of physiology. Saunders, Philadelphia, p 583

Goldberg JM, Fernandez C (1975) Vestibular mechanism. Ann Rev Physiol 37:129–162

Guedry FE (1965) Orientation of the rotation-axis relative to gravity: its influence on nystagmus and the sensation of rotation. Acta Otolaryngol (Stockh) 60:30

Guedry FE (1992) Perception of motion and position relative to the earth. An overview. Ann N Y Acad Sci 656:315–328

Haustein W (1989) Considerations on Listing's law and the primary position by means of a matrix description of eye position control. Biol Cybern 60:411–420

Howard IP (1982) Human visual orientation. Chap. 10: Visual orientation to gravity. Wiley, New York, pp 412–442

Howard IP (1986) The perception of posture, self motion, and the visual vertical. In: Boff KR, Kaufman L, Thomas JP (eds) Handbook of perception and human performance. Wiley, New York, pp 1–50

Jaggi-Schwarz K, Hess BJM (2003) Influence of dynamic tilts on the perception of earth-vertical. Exp Brain Res 149:340–350

Jaggi-Schwarz K, Ortega M, Hess BJM (2003) Reciprocal error behavior in estimated body position and subjective visual vertical. Exp Brain Res 150:122–125

Kaufmann H, Biaggioni I, Voustianiouk A, Diedrich A, Costa F, Clarke R, Gizzi M, Raphan T, Cohen B (2002) Vestibular control of sympathetic activity. An otolith-sympathetic reflex in humans. Exp Brain Res 143:463–469

McGraw PV, Whitaker D, Skillen J, Chung STL (2002) Motion adaptation distorts perceived visual position. Curr Biol 12:2042–2047

Mittelstaedt H (1983) A new solution to the problem of the subjective vertical. Naturwissenschaften 70:272–281

Mittelstaedt H (1991) The role of the otoliths in the perception of the orientation of self and world to the vertical. Zool Jb Physiol 95:419–425

Mittelstaedt H (1999) The role of the otoliths in perception of the vertical and in path integration. Ann N Y Acad Sci 871:334–344

Müller GE (1916) Über das Aubertsche Phänomen. Z Sinnesphysiol 49:109–246

Pavlou M, Wijnberg N, Faldon ME, Bronstein AM (2003) The effect of semicircular canal stimulation on the perception of the visual vertical. J Neurophysiol 90:622–630
Ray CA, Carter JR (2003) Vestibular activation of sympathetic nerve activity. Acta Physiol Scand 177:313–319
Schall JD (2003) Neural correlates of decision processes: neural and mental chronometry. Curr Opin Neurobiol 13:182–186
Schöne H (1975) The “weight “ of the gravity organ’s signal in the control of perceptual and reflex type orientation at different body positions. Fortschr Zool 23:274–285
Schöne H, Lechner-Steinleitner S (1978) The effect of preceding tilt on the perceived vertical. Hysteresis in perception of the vertical. Acta Otolaryngol 85:68–73
Stockwell CW, Guedry FE (1970) The effect of semicircular canal stimulation during tilting on the subsequent perception of the visual vertical. Acta Otolaryngol 70:170–175
Uchino Y, Sasaki M, Sato H, Imagawa M, Suwa H, Isu N (1996) Utriculoocular reflex arc of the cat. J Neurophysiol 76:1896–1903
Uchino Y, Sato H, Sasaki M, Imagawa M, Ikegami H, Isu N, Graf W (1997) Sacculocollic reflex arcs in cats. J Neurophysiol 77:3003–3012
Udo de Haes HA, Schöne H (1970) Interaction between statolith organs and semicircular canals on apparent vertical and nystagmus. Acta Otolaryngol 69:25–31
Van Beuzekom AD, Van Gisbergen JA (2000) Properties of the internal representation of gravity inferred from spatial-direction and body-tilt estimates. J Neurophysiol 84:11–27
Van Beuzekom AD, Medendorp WP, Van Gisbergen JA (2001) The subjective vertical and the sense of self orientation during active body tilt. Vision Res 41:3229–3242
Van Rullen R, Koch C (2003) Is perception discrete or continuous? Trends Cogn Sci 7:207–213
Wilson VJ (1975) The labyrinth, the brain, and posture. Am Sci 63:325
Wilson VJ, Melvill-Jones G (1979) Mammalian vestibular physiology. Plenum Press, New York, p 221