Roll-Dependent Modulation of the Subjective Visual Vertical: Contributions of Head- and Trunk-Based Signals

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Tarnutzer AA, Bockisch CJ, Straumann D. Roll-dependent modulation of the subjective visual vertical: contributions of head- and trunk-based signals. J Neurophysiol 103: 934–941, 2010. First published December 16, 2009; doi:10.1152/jn.00407.2009. Precision and accuracy of the subjective visual vertical (SVV) modulate in the roll plane. At large roll angles, systematic SVV errors are biased toward the subject’s body-longitudinal axis and SVV precision is decreased. To explain this, SVV models typically implement a bias signal, or a prior, in a head-fixed reference frame and assume the sensory input to be optimally tuned along the head-longitudinal axis. We tested the pattern of SVV adjustments both in terms of accuracy and precision in experiments in which the head and the trunk reference frames were not aligned. Twelve subjects were placed on a turntable with the head rolled about 28° counterclockwise relative to the trunk by lateral tilt of the neck to dissociate the orientation of head- and trunk-fixed sensors relative to gravity. Subjects were brought to various positions (roll of head- or trunk-longitudinal axis relative to gravity: 0°, ±75°) and aligned an arrow with perceived vertical. Both accuracy and precision of the SVV were significantly (P < 0.05) better when the head-longitudinal axis was aligned with gravity. Comparing absolute SVV errors for clockwise and counterclockwise roll tilts, statistical analysis yielded no significant differences (P > 0.05) when referenced relative to head upright, but differed significantly (P < 0.001) when referenced relative to trunk upright. These findings indicate that the bias signal, which drives the SVV toward the subject’s body-longitudinal axis, operates in a head-fixed reference frame. Further analysis of SVV precision supports the hypothesis that head-based graviceptive signals provide the predominant input for internal estimates of visual vertical.

INTRODUCTION

Gravity perception, as measured by the subjective visual vertical (SVV) or by the subjective visual horizontal (SVH), is subject to varying precision (i.e., the degree of reproducibility) and accuracy (i.e., the degree of veracity) of adjustments depending on the subject’s whole-body roll orientation relative to gravity. Errors and trial-to-trial variability in sensory-guided movements can be due to noisy sensory signals, imperfect central processing and integration of multiple signals, and motor output constant errors and variability. For example, the variability of velocity profiles of smooth-pursuit eye movements is dominated by errors in sensory estimation (Osborne et al. 2005). Sensory signals integrated to estimate self-orientation in space include inputs from the otolith organs, the semicircular canals (SCCs), muscle and joint proprioceptors, skin pressure sensors, truncal somatosensors in the kidneys, mechanoreceptors in the walls of large vessels, and vision (for reviews, see Angelaki et al. 2009; Green and Angelaki 2007). Most psychophysical studies assessing verticality perception relied on the SVV, in which subjects are asked to adjust a luminous line along perceived vertical. In the head-upright position, this task can be performed very accurately within ±2° (Friedmann 1970; Howard 1982), but in tilted whole-body roll orientations systematic misjudgments are observed. At roll angles <60°, several authors (Howard 1982; Van Beuzekom and Van Gisbergen 2000; Wade and Curthoys 1997) reported variable, small overcompensation of whole-body roll (E-effect; Mül ler 1916). For angles ≥60°, subjects undercompensate whole-body roll (A-effect; Aubert 1861), showing errors ≤40° that peak between 90 and 130° roll (Tarnutzer et al. 2009b; Van Beuzekom and Van Gisbergen 2000). Finally, at roll angles >135–150°, a shift from undercompensation back to overcompensation has been described (Kaptein and Van Gisbergen 2004). SVV adjustments in various roll positions modulate not only in terms of accuracy, but also in terms of precision. Trial-to-trial SVV variability is minimal in the upright position and increases with increasing head roll, peaking around 120 to 150° (Lechner-Steinleitner 1978; Schoene and Udo de Haes 1968; Udo de Haes 1970), and decreases to intermediate values in upside-down orientation (Tarnutzer et al. 2009b).

Distinguishing the contribution of the different noisy sensory systems involved in estimating self-orientation may be complicated. Whereas the contribution of some sensors (e.g., vision and the SCC) can be eliminated experimentally, inputs from other sensors (proprioception and trunk-based somato-sensors) are difficult to minimize. In most previous studies the head- and trunk-longitudinal axes were aligned and roll tilted relative to gravity by the same angle. Therefore a differential assessment of both head-based (otolithic and SCC) and trunk-based (proprioceptive, truncal-graviceptive) inputs was impossible (e.g., Bisdorff et al. 1996; Kaptein and Van Gisbergen 2004; Mittelstaedt 1992; Van Beuzekom and Van Gisbergen 2000; Wade and Curthoys 1997). To overcome this limitation, Guerra and colleagues (1998) studied the contribution of head-only tilt to verticality perception by comparing the SVV during either head-on-trunk roll (up to ±28°) while sitting upright or whole-body roll. Errors in SVV were increased for whole-body roll compared with head-on-trunk roll when the trunk remained upright; based on multiple regression analysis, however, head roll was identified to be the major contributor to the errors observed in whole-body roll (Guerra et al. 1998).

To model both the A-effect and the E-effect and SVV trial-to-trial variability, Mittelstaedt (1983) assumed an imbalance of the otolithic signal due to an unequal number of utricular...
and saccular afferents (Rosenhall 1972). More recently, Eggert (1998), De Vrijer et al. (2008, 2009), and Tarnutzer et al. (2009b) showed that the A-effect and E-effect could be reproduced using a Bayesian framework instead. Bayesian modeling allows the integration of distinct sensory signals to optimize performance in the context of optimal observer theory (Knill and Pouget 2004; Kording and Wolpert 2004; Laurens and Droulez 2007). Here an accurate, but noisy otolith input is combined in a statistically optimal manner with prior knowledge about the subject’s roll orientation. Prior knowledge drives the estimate of vertical toward the subject’s body-longitudinal axis because it is based on the assumption that small body roll angles are most likely. This approach results in noise reduction at small roll angles, but it has the downside of causing systematic errors at larger roll angles (De Vrijer et al. 2008).

Both the idiotropic vector model of Mittelstaedt (1983) and its reinterpretation in terms of optimal perception using Bayesian modeling (De Vrijer et al. 2008, 2009; Eggert 1998; MacNeillage et al. 2007; Tarnutzer et al. 2009b) assume that verticality perception is optimized for small head-roll angles and that the CNS makes a basic a priori assumption that the head is mostly oriented near upright. These theories predict that estimates of visual vertical are most precise when the head-longitudinal axis is aligned with the gravity vector and that the function characterizing systematic SVV errors will be head-roll dependent rather than trunk-roll dependent, with a minimum at zero head roll. None of these theories makes the a priori assumption that SVV variability and SVV errors will be minimal with the trunk near upright. Whether assumptions of a head-fixed prior (or idiotropic) and an optimally tuned verticality perception along the head-longitudinal axis are reasonable, however, could not be tested in previous SVV experiments in which the head- and trunk-longitudinal axes were aligned. Dissociating the head- and trunk-longitudinal axes could therefore be used to test the validity of current theories about the origin of the roll-dependent modulation of SVV accuracy and precision (De Vrijer et al. 2008; Dichgans et al. 1974; Mittelstaedt 1983; Van Beuzekom and Van Gisbergen 2000). Whereas Guerraz et al. (1998) provided evidence in favor of a head-fixed reference frame of the prior, it remains unclear whether internal estimates of visual vertical are optimally tuned along head upright or along trunk upright.

Here we studied the individual contributions of vestibular (head-based) and extravesitular (trunk-based) inputs to gravity perception both in terms of accuracy and precision using SVV adjustments in the roll plane. By restraining the head roll tilted relative to the trunk by a constant angle, the reference frame of the head-based contributing signals is shifted by the head-roll angle relative to the reference frame of the trunk-based input. This dissociation between head and trunk roll allows investigation of both the main reference frame of the graviceptive sensors involved and of the putative prior added by the CNS. As we aligned the turntable-fixed luminous line either with the head-longitudinal axis or with the trunk-longitudinal axis, both precision and accuracy of arrow adjustments could be compared while keeping sensory input from neck proprioceptors constant.

**Methods**

**Subjects**

We studied 12 healthy human subjects (5 women and 7 men, 26 to 42 yr old). Two participants were familiar with the experimental protocol and 10 were naïve. Informed consent was obtained after a full explanation of the experimental procedure. The protocol was approved by a local ethics committee and was in accordance with the ethical standards established in the 1964 Declaration of Helsinki for research involving human subjects.

**Experimental setup**

All experiments were run on a turntable with three servo-controlled motor-driven axes (Acutronic, Bubikon, Switzerland). The intersection of the interaural axis and the nasooccipital axis was in the center of rotation of the three turntable axes. Subjects were secured with a four-point safety belt and vacuum pillows were placed on both sides of the chest and hips. While viewing straight ahead, subjects rolled their head as much as possible to the left side, i.e., counterclockwise (CCW) as seen from behind. A thermoplastic mask (Sinmed, Reeuwijk, The Netherlands) that tightly covered the head was applied and attached to the base plate behind the subject’s head. Care was taken to minimize any additional yaw movement of the head in this maximal CCW position. When the mask hardened after a few minutes, the mask restrained the head in a stable and comfortable roll-tilted position. On average, the head-longitudinal axis was roll tilted relative to the trunk-longitudinal axis by $-28^\circ$ ($\pm5^\circ$; $\pm1$SD). Subjects with myopia were allowed to wear their glasses on top of the mask. Note that according to the right-hand rule clockwise (CW) head roll is positive and CCW head roll is negative. To keep the number of trials within an acceptable limit, we studied only head-on-trunk roll tilts in the CCW direction. Likewise, we did no tests with the head and trunk aligned (referred to as “whole-body roll tilts”) because numerous studies have already provided normative data on whole-body roll-angle–dependent errors in SVV (De Vrijer et al. 2008; Friedmann 1970; Howard 1982; Kaptein and Van Gisbergen 2004; Tarnutzer et al. 2009b; Van Beuzekom and Van Gisbergen 2000) and SVH (Betts and Curthoys 1998; Hafstrom et al. 2004; Wade and Curthoys 1997).

To assess the SVV, we used a line with an arrowhead. Such a polarized stimulus has the advantage that it allows a more precise instruction of the task without influencing the accuracy of SVV adjustments (Kaptein and Van Gisbergen 2005). The arrow was projected onto the center of a sphere in front of the subject. The subject’s eyes were 1.5 m away from the center of the sphere; the line (500 $\times$ 3 mm; height $\times$ width) subtended 9.5$^\circ$.

**Experimental paradigm**

Subjects adjusted the SVV while positioned in six different roll orientations. To compare vestibular and extravestibular contributions to verticality perception, the same roll positions ($0^\circ$, $\pm75^\circ$) were applied relative to the trunk-longitudinal axis (angle $\beta$; Fig. 1, A–C) and relative to the head-longitudinal axis (angle $\gamma$; Fig. 1, D–F).

Within a single session lasting about 75 min, a total of 240 trials in six different turntable roll orientations (three relative to trunk-longitudinal; three relative to head-longitudinal) were recorded in three blocks. The turntable roll position was adjusted before each trial using a constant turntable acceleration of $10^2$/s$^2$ followed by a constant deceleration of $10^2$/s$^2$. We decided to use accelerations and decelerations of $10^2$/s$^2$ since values in this range reflect a compromise between keeping the repositioning time as short as possible and minimizing discomfort of the subject by applying high accelerations and decelerations. These acceleration and deceleration values, however, are well above the detection threshold of the semicircular canals (0.05$^2$/s$^2$; Diamond et al. 1982; Shimazu and Precht 1965) and thus will lead to SCC stimulation during the
Results

SVV Errors

Single-trial arrow roll orientations relative to earth-vertical in all different trial types studied are plotted against time in Fig. 2 for a typical subject. Traces are shown starting from when the arrow was projected to the moment when the subject confirmed the completion of the arrow adjustment by button press. For trials with the trunk (Fig. 2A) or the head (Fig. 2D) upright, adjustments yielded few or no errors of the arrow relative to earth-vertical. In trials with 75° CW or 75° CCW roll tilts (either in a trunk- or in a head-fixed reference frame), however, adjustments resulted in systematic errors consistent with roll undercompensation in all four trial conditions (Fig. 2, B, C, E, and F).

Individual average SVV errors of all 12 subjects are plotted against head roll in Fig. 3A, whereas in Fig. 3B the same data are plotted against trunk roll. It took subjects on average 1.5 s (±0.2 s; ±1SD) to complete the different trial types. The direction of arrow rotation did not significantly (two-way ANOVA, P > 0.05) influence the final arrow roll orientation; therefore trials with CW and CCW arrow rotations were pooled for further analysis. For comparison, overall average (±1SD, n = 7 subjects) SVV adjustments in various (15° steps) whole-body roll positions with the head- and trunk-longitudinal axis along earth-vertical (D) adjust the arrow along the subjective visual vertical (SVV). Six different roll angles were tested: trunk-longitudinal axis offset relative to earth-vertical (A); head-longitudinal axis offset relative to earth-vertical (B, C); subject’s head-longitudinal axis offset relative to earth-vertical (D) indicated by the angle β by ±75° (B, C); subject’s head-longitudinal axis offset relative to earth-vertical (indicated by the angle γ) by ±75° (E, F).

Turntable and arrow roll positions were digitally recorded at 200 Hz. Data points were considered as outliers if they were distant from the average by >2SDs. In total, 4.2% of all data points were identified as outliers and were discarded before statistical analysis. The average errors relative to the desired arrow roll angle and both the intra- and interindividual SDs of adjusted angles were calculated. In the following, we will use the term “trial-to-trial variability” whenever we refer to SDs within single subjects. To obtain sample averages of SVV errors (±1SD) and SVV variability (±1SD) for statistical analysis, we pooled individual averages of given trial types (Fig. 3), although there was some variation of the head-on-trunk roll angle among subjects (±5°, ±1SD). Six different average head-roll orientations relative to earth-vertical were tested: 103° left ear down (LED), 75° LED, 28° LED, upright, 47° right ear down (RED), and 75° RED.

Statistical analysis was performed using ANOVA (Minitab, State College, PA). Tukey’s correction was used to compensate for multiple comparisons. In some sections, the statistical analysis was based solely on paired t-tests. Holm’s correction was applied whenever multiple t-tests (number of tests = m) were performed (Aickin and Gensler 1996; Holm 1979). This method uses an adapted level of significance after performing the null hypothesis on the smallest P value (α = α/m) with Bonferroni correction. For the second smallest P value the level of significance is thus α = α/(m − 1) and so on. P values were multiplied according to the denominator defined by Holm’s correction, keeping the level of significance unchanged for all statistical tests (i.e., P = 0.05).

A quadratic function was fit to SVV errors in both head- and trunk-fixed reference frames using standard MATLAB programs. To determine the head- and trunk-roll angle associated with the highest SVV precision, an inverse Gaussian function was fit to the SVV variability data. To estimate the confidence intervals (CIs) of the parameters of the fit (offset and SD), we used bootstrapping with 1000 resamples of the observed data set, each of which was obtained by random sampling with replacement from the original data set (Efron 1979). From the resamples obtained, fitting was done and the bootstrap CI at a level of 95% was calculated.
nal axes aligned (data from Tarnutzer et al. 2009b) are also shown. These data were obtained using the same experimental equipment and a similar experimental protocol. The SVV errors with the head- and trunk-longitudinal axes aligned (Tarnutzer et al. 2009b) more closely resemble the SVV errors when the axes are misaligned when referenced to a head-fixed frame (Fig. 3A), compared with when they are referenced to a trunk-fixed frame (Fig. 3B).

In a head-fixed reference frame (Fig. 3A), SVV errors were small and not significantly different from zero (0.9 ± 1.4°, t-test, P > 0.05) in a head-upright position. SVV errors increased with increasing head- or trunk-roll angle. These errors, however, were significantly different from zero (t-test, Holm corrected, P ≤ 0.05) only at 103° LED (−18.7 ± 7.3°), 75° LED (−4.8 ± 5.2°), and 75° RED (6.4 ± 10.1°), consistent with roll undercompensation (A-effect). SVV errors at 28° LED, i.e., trunk-upright position in a trunk-fixed reference frame (−1.7 ± 3.0°), showed only a trend toward significance (P = 0.07) and errors at 47° RED (−2.1 ± 7.5°) were not significantly different from zero (P > 0.1). In a trunk-fixed reference frame (Fig. 3B), the SVV errors were of identical size, but shifted along the x-axis by the head-on-trunk roll angle. The accuracy of SVV adjustments was determined by comparing the absolute SVV errors and was found to be significantly higher (P < 0.05, paired single-sided t-test) with the head-longitudinal axis along vertical than with the trunk-longitudinal axis parallel to gravity.

To determine the reference frame of the bias signal, SVV errors relative to head-upright and trunk-upright positions were analyzed for an effect of the tilt direction \( \theta \). Depending on the reference frame of the bias signal—being head- or trunk-fixed—the symmetry of SVV under- and overcompensation for CW and CCW roll tilts is better along the head- or along the trunk-upright position. Linear regression analysis (using the standard MATLAB function regress.m) was used to fit a quadratic function (see Eq. 1) to the individual average SVV errors for both CW and CCW roll tilts (including upright position) separately, after reversing sign of SVV adjustments obtained in CCW roll positions and to test for statistically significant differences between the two fits

\[
y = B_1 + B_2 \theta + B_3 \theta^2 + B_4 \phi + B_5 \phi \theta + B_6 \phi^2 \theta
\]

As shown in Fig. 4A, SVV errors obtained in CW and CCW roll positions relative to head upright were in a similar range. This was reflected in the statistical analysis with parameters \( B_4 \), \( B_5 \), and \( B_6 \) not being significantly different from zero (ANOVA, \( P > 0.05 \)). When comparing CW and CCW roll positions relative to the trunk-upright position (Fig. 4B), however, SVV errors were clearly distinct, depending on the tilt direction, yielding larger errors for CCW roll tilts. Statistical analysis of the fitted quadratic functions indicated that the two fits obtained in the trunk-fixed reference frame were significantly different (ANOVA, \( P < 0.001 \))—i.e., that parameters \( B_4 \), \( B_5 \), and \( B_6 \) were different from zero. These findings suggest that the bias signal is rather coded in a head-fixed than in a trunk-fixed reference frame.

In line with these findings, the absolute values of SVV errors for trials with roll tilts of ±75° relative to head upright (i.e., 75° RED vs. 75° LED) did not differ significantly (paired t-test, \( P > 0.05 \)). By contrast, referencing absolute SVV errors in a trunk-fixed frame yielded significantly larger SVV errors for trials with −75° trunk roll (equal to 103° LED head roll) compared with trials with +75° trunk roll (equal to 47° RED head roll) (paired t-test, \( P < 0.001 \)). These observations confirm symmetry of SVV errors relative to head upright and therefore also favor a head-fixed reference frame of the bias signal.

**Trial-to-trial variability**

Individual trial-to-trial variabilities in the different roll positions are depicted both in a head-fixed (Fig. 5A) and in a trunk-fixed (Fig. 5B) reference frame. The direction of arrow rotation did not significantly affect precision of adjustments (two-way ANOVA, \( P > 0.05 \)); therefore CW and CCW trials were pooled for further analysis. Trial-to-trial variability was significantly smaller in a head-upright orientation than that in
In case of predominantly head-based graviceptive sensors (being coded in a head-fixed reference frame), the observed modulation of SVV variability should correlate better with head roll relative to earth-vertical than with trunk roll relative to earth-vertical. In case of predominantly trunk-based graviceptive sensors (being coded in a trunk-fixed reference frame), better correlations of variability modulation are expected with trunk-roll orientation relative to earth-vertical. To determine the head-roll (Fig. 5A) and trunk-roll (Fig. 5B) orientation where trial-to-trial variability was minimal, an inverse Gaussian function (Eq. 2) was fitted to the individual average variability values in all roll positions

\[ y = d - ae^{-(x-b)^2/2c^2} \]  

(2)

Fitting yielded a minimal SVV variability of 2.1° at a roll orientation of −2.5° relative to the head-upright position. In a trunk-fixed reference frame, roll orientation with minimal SVV variability (again reaching a value of 2.1°) was offset 26.2° relative to the trunk-upright position. Whereas the 95% CI of head-roll orientations with minimal variability included head-upright position (range of 95% CI in a head-fixed reference frame: −11.8° to 5.0°), the 95% CI of trunk-roll orientations...
assumption that small body roll angles are most likely. Current SVV models consider the bias signal to be head-roll dependent rather than trunk-roll dependent and assume maximal performance of internal estimates of vertical at zero head roll (De Vrijer et al. 2008, 2009; Tarnutzer et al. 2009b). Since in most previous studies the head- and trunk-longitudinal axes were aligned, the reference frame of the bias signal and its orientation with optimal performance (head vs. trunk) could not be determined. We therefore evaluated whether the bias signal used in modeling errors of visual vertical adjustments (De Vrijer et al. 2008, 2009; Eggert 1998; Mittelstaedt 1983; Tarnutzer et al. 2009b) was coded in a head-fixed or in a trunk-fixed reference frame and determined in which roll direction estimates of visual vertical were optimally tuned. To dissociate the head- and trunk-longitudinal axis—and thereby shift the orientation of the head-fixed otolith organs relative to earth-vertical compared with trunk-fixed gravity-sensing organs—each subject’s head was kept in a roll-tilted position relative to the trunk.

Reference frame of the graviceptive sensory systems and of the bias signal

The roll-dependent decay in precision of SVV estimates (De Vrijer et al. 2008; Kaptein and Van Gisbergen 2005; Lechner-Steinleitner 1978; Mittelstaedt 1983; Schoene and Udo de Haes 1968) has previously been associated mainly with the properties of the otolith organs (nonuniform distribution of otolith afferents in the roll plane, nonlinear firing rates), being optimally tuned along the whole-body upright position (Tarnutzer et al. 2009b). Such an eminent role in verticality perception, however, can be assigned only to the otolith organs, provided there is clear experimental evidence for a modulation of SVV accuracy and precision in a head-fixed reference frame.

Statistical analysis of adjustment errors made by our healthy subjects in CW and CCW roll-tilted positions showed symmetry (i.e., nonsignificant differences) only relative to head upright, but not relative to trunk upright, yielding SVV errors of significantly different size. These findings support a head-fixed bias signal. Significantly more accurate and precise SVV adjustments were noted in a head-upright position compared with that in a trunk-upright position (see precision data in Fig. 5), indicating that the graviceptive sensors are performing optimally when the head-longitudinal axis is aligned with gravity. Our observations regarding SVV accuracy confirm previous work by Guerraz et al. (1998) that identified head roll as the major contributor to the errors in the whole-body roll condition. Compared with Guerraz et al. (1998) we extended the range of head-roll angles studied and also determined the frame of reference of optimal performance—i.e., highest precision—of the involved sensory systems. Our findings indicate that for internal estimates of visual vertical both its precision and the centrally added bias signal are coded in a head-fixed reference frame, yielding optimal performance when the head is upright. We therefore propose that head-based sensors such as the maculae contribute most to the perception of visual vertical.

Compared with SVV adjustments in various whole-body (head- and trunk-longitudinal axis aligned) roll positions (Tarnutzer et al. 2009b), the modulations in accuracy and precision in this study (with the head roll tilted relative to the trunk) were

### DISCUSSION

Theories addressing the origin of the systematic, roll-angle-dependent errors (A-effect and E-effect) of subjective visual vertical (SVV) have proposed computational strategies that use prior knowledge in terms of a bias signal (De Vrijer et al. 2008, 2009; Eggert 1998; Mittelstaedt 1983; Tarnutzer et al. 2009b). This bias drives the estimate of visual vertical toward the subject’s body-longitudinal axis because it is based on the
similar only when using a head-fixed reference frame. For trunk-fixed reference frames minimal SVV variability was shifted CW by about 26° relative to trunk-upright and did not match with the results from the whole-body roll-tilt adjustments taken for comparison. This suggests that for trials with the head- and trunk-longitudinal axes aligned, the graviceptive sensory input is rather coded in a head-fixed reference frame than in a trunk-fixed reference frame.

Neck proprioceptive input, which has previously been shown to influence the SVV (Wade 1968, 1970; Wetzig and Baumgarten 1990), does not explain the differences observed when either using a head- or a trunk-fixed reference frame since the head-on-trunk roll angle was kept constant all the time. Furthermore, neck stimulation by providing trunk-only roll (while keeping the head upright) in healthy normal subjects was not found to systematically influence the subjective visual horizontal (De Graaf et al. 1992).

Internal estimates of gravity require multisensory integration

The assumption of a head-fixed bias signal, based on theoretical considerations in both the idiotropic vector model (Mittelstaedt 1983) and the Bayesian models of verticality perception (De Vrijer et al. 2008, 2009; Eggert 1998; Tarnutzer et al. 2009b), is supported by our findings. Dissociating head- and trunk-based sensory input integrated for internal estimates of the direction of gravity underlines the eminent role of the vestibular organs in sensing gravity (Jaggi-Schwarz and Hess 2003; Miller 2nd et al. 1968; Pavlou et al. 2003; Schoene and Udo de Haes 1968). This, however, does not suggest that internal estimates of vertical are solely derived from head-based sensory systems. Clearly, verticality perception remains the result of a multisensory integration of various sensory input signals within parietotemporal cortical areas (Angelaki and Cullen 2008; Brandt and Dieterich 1999; Green and Angelaki 2007) and relevant contributions by extravestibular and neck-based and trunk-based sensors (e.g., truncal somatosensors, skin pressure sensors, muscle and joint proprioceptors, and kidney and vessel-wall graviceptors) have been described (Anastasopoulos et al. 1999; Bisdorff et al. 1996; Mittelstaedt 1992, 1996; Wade 1970; Yardley 1990). Vestibular cues, however, may play a central role in countervailing visually and proprioceptive-mediated biases on the perception of verticality as proposed by Bronstein et al. (1996). Both vestibular and extravestibular sensory deficits may result in changes in perceived visual vertical: bilateral vestibular loss leads to a shift from E-effects to A-effects at small roll angles (Graybiel et al. 1968) and to an increase of the A-effect at larger roll angles (Bronstein et al. 1996; Miller 2nd et al. 1968), whereas impaired somatosensory function decreases the A-effect (Anastasopoulos et al. 1999; Bronstein 1999; Yardley 1990). These changes in SVV accuracy are likely related to how the brain weights distinct sensory signals. Various psychophysical studies have shown that humans integrate different sensory cues in a manner consistent with a weighted linear combination of perceptual estimates from the individual cues (Angelaki et al. 2009; Ernst and Banks 2002; Knill and Pouget 2004; Ma et al. 2006); thus the weighting of each cue considered is proportional to the cue’s relative reliability, such that a less-reliable cue is given less weight in perceptual estimates. In the case of a deteriorated signal-to-noise ratio of vestibular cues (e.g., due to a uni- or bilateral vestibular loss), extravestibular (somatosensory and proprioceptive) sensory input is expected to be weighted more strongly by the brain. Along with a reweighting of the sensory cues integrated to estimate the direction of gravity in patients with vestibular deficits, a shift in the reference frame of the bias signal could occur under these circumstances. With extravestibular sensory input—being referenced in a trunk-fixed frame—gaining importance coding of the bias signal could also be shifted to a trunk-fixed reference frame. Experimentally determining the reference frame of the bias signal in patients with vestibular deficits in a way similar to that described here in healthy normal subjects could be used to further address and validate this hypothesis.

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