Static roll-tilt over 5 minutes locally distorts the internal estimate of direction of gravity

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Tarnutzer AA, Bockisch CJ, Straumann D, Marti S, Bertolini G. Static roll-tilt over 5 minutes locally distorts the internal estimate of direction of gravity. J Neurophysiol 112: 2672–2679, 2014. First published September 3, 2014; doi:10.1152/jn.00540.2014.—The subjective visual vertical (SVV) indicates perceived direction of gravity. Even in healthy human subjects, roll angle-dependent misestimations, roll overcompensation (A-effect, head-roll > 60° and <135°) and undercompensation (E-effect, head-roll < 60°), occur. Previously, we demonstrated that, after prolonged roll-tilt, SVV estimates when upright are biased toward the preceding roll position, which indicates that perceived vertical (PV) is shifted by the prior tilt (Tarnutzer AA, Bertolini G, Bockisch CJ, Straumann D, Marti S. PLoS One 8: e78079, 2013). Hypothetically, PV in any roll position could be biased toward the previous roll position. We asked whether such a “global” bias occurs or whether the bias is “local”. The SVV of healthy human subjects (N = 9) was measured in nine roll positions (−120° to +120°, steps = 30°) after 5 min of roll-tilt in one of two adaptation positions (±30°) and compared with control trials without adaptation. After adapting, adjustments were shifted significantly (P < 0.05) toward the previous adaptation position for nearly roll-tilted positions (±30°, ±60°) and upright only. We computationally simulated errors based on the sum of a monotonically increasing function (producing roll undercompensation) and a mixture of Gaussian functions (representing roll overcompensation centered around PV). In combination, the pattern of A- and E-effects could be generated. By shifting the function representing local overcompensation toward the adaptation position, the experimental postadaptation data could be fitted successfully. We conclude that prolonged roll-tilt locally distorts PV rather than globally shifting it. Short-term adaptation of roll overcompensation may explain these shifts and could reflect the brain’s strategy to optimize SVV estimates around recent roll positions. Thus postural stability can be improved by visually-mediated compensatory responses at any sustained body-roll orientation.

perception; gravity; adaptation; subjective visual vertical

VARIOUS SENSORY SIGNALS, INCLUDING those from the vestibular organs (utricle, saccule, semicircular canals), skin proprioceptors, vision and joint receptors, are computationally combined within the central nervous system in a weighted fashion to obtain an optimal internal estimate of the direction of gravity (Angelaki et al. 2009). Perceptual estimates of spatial self-orientation relative to gravity provide a straightforward means to quantify graviception at the level of the cortex. Due to its widespread availability and easy-to-understand task, visual line adjustments, termed “subjective visual vertical” (SVV), are most frequently used to assess graviception. Behavioral studies investigating prolonged roll-tilt reported concomitant drifts of the SVV (Lechner-Steinleitner 1978; Schoene and Udo de Haes 1968; Wade 1970) and a bias (i.e., deviations of perceived SVV) upon return to upright position (Day and Wade 1966), termed posttilt bias. In a recent study (Tarnutzer et al. 2013), we noted this bias to be usually toward the direction of previous roll-tilt (termed “adaptation position”) and to decay exponentially (time constant about 70 s). We favored central mechanisms to explain the posttilt bias and proposed a perceptual shift of perceived vertical toward the recent (roll-tilted) position based on prior knowledge. This concept describes a strategy relying on the assumption that an earth-vertical (upright) position is most likely and therefore assumes that the subject’s recent whole body orientation was approximately parallel to gravity. Accordingly, this prior knowledge is combined with sensory input in a Bayesian framework to estimate the most likely roll position (Kording and Wolpert 2004; Laurens and Droulez 2007; MacNeilage et al. 2007). As a result, the perceived direction of gravity will be shifted toward the body-longitudinal axis. With regards to the SVV, this may, in addition to the reported posttilt bias when returning upright, also lead to a bias for subsequent SVV measurements obtained in roll positions distinct from upright. Specifically, we asked how such a bias in perceived vertical would affect SVV adjustments in the entire roll plane. Resulting from the concept of prior knowledge, the bias would drive adjustments toward the previous roll-tilt position, increasing or decreasing the roll-dependent SVV errors, termed A-effect [i.e., roll undercompensation for roll angles > 60° and < 120–135° (Aubert 1861)] and E-effect [i.e., roll overcompensation for roll angles < 60° or > 120–135° (Mueller 1916)]. Theoretically, such a bias could affect SVV adjustments within the entire roll plane (“global” bias), either by shifting estimates by an offset of constant size or by combining roll-dependent and roll-independent shifts (resulting in a roll angle-dependent size of the bias). Alternatively, a more locally pronounced effect could be imagined (“local” bias), affecting mostly roll positions adjacent to the roll-tilt position kept for a prolonged period of time. By exploring the bias at different whole body roll-tilt angles, we aimed to elucidate the mechanism behind the drift of the SVV adjustments observed during and after prolonged roll tilts.

MATERIALS AND METHODS

Nine healthy human subjects (4 women; aged 27–45 yr; mean age ± 1 SD: 34.9 ± 5.7 yr) were studied. Written, informed consent of all subjects was obtained after a full explanation of the experimental procedure. The protocol was approved by the local ethics committee (Ethics Committee Neurology, University Hospital Zurich) and was in...
accordance with the ethical standards laid down in the 2013 Declaration of Helsinki for research involving human subjects.

**Experimental setting.** All recordings were performed on a three-axis motor-driven turntable (Acutronic, Jona, Switzerland). Subjects were secured with a four-point safety belt with the head restrained in natural straight-ahead position with a thermostatic mask. Since the otolith organs, which have the greatest contribution to verticality estimation, are situated in the head, the subjects’ orientation in the roll plane will be referred to as head-roll orientation, although roll movements on the turntable were whole body. SVV measurements were obtained in nine different head-roll orientations (upright, ±30°, ±60°, ±90°, ±120°). Each position was selected once during both the control condition and the test condition, and a series of adjustments was obtained. Each series of adjustments in a given head-roll orientation shall be called a “run”. Positions were reached by turntable movements with 10°/s constant acceleration and deceleration. This acceleration was chosen as a compromise between keeping the reporting 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 semi-circular canals (SCC) [0.05°/s² (Diamond et al. 1982; Shimazu and Precht 1965)] and the perceptual thresholds (Lewis et al. 2011). Therefore, the motion parameters of the turntable applied here stimulate the SCCs and affect errors in the SVV (Jaggi-Schwarz and Hess 2003; Pavlou et al. 2003). To minimize effects of SCC stimulation, the first trial after any chair movement was delayed by 5 s. For such static SVV adjustments, we have previously checked for postrotatory torsional ocular drift and nystagmus to quantify the contribution of SCC stimulation after the movement and showed that average torsional eye velocity at the time subjects confirmed arrow adjustments was small (0.10 ± 0.06°/s) (Tarnutzer et al. 2009a).

A remote control box allowed the subjects to rotate an arrow (covering the central 9.5° of the binocular visual field) projected by a laser on a sphere 1.5 m in front and to confirm adjustments. Myopic subjects wore their contact lenses or their glasses (on top of the mask).

**Experimental paradigm.** All participants completed two 75-min sessions, which used different adaptation positions. Note that, for each session, only one adaptation position was studied and that the order of the two sessions was random. All sessions consisted of a first part with nine “control runs” and a second part with nine “test runs”. Within these two parts, the order of control (first part) and test (second part) runs was also random. All trials were collected in complete darkness (except for the luminous arrow used to indicate perceived vertical). In each run, five consecutive SVV adjustments were obtained without any turntable movements in between single SVV trials. To study effects of static prolonged roll-tilt on the perception of vertical, two different roll-tilted “adaptation” positions were selected: +90° and −90°. For each test run, the subject was brought from the upright position to the adaptation position. Within each session, this adaptation position was fixed. The subject then waited in this static, roll-tilted position for 5 min in complete darkness. Subjects were reminded to stay awake; however, no specific tasks or measurements were applied during the dark period. The duration of resting in a static roll-tilt position was limited to 5 min. The choice of this time length was based on previous observations reporting that adaptation mechanisms in the SVV occurred mostly during the first 3–5 min (Schöne and Udo de Haes 1968; Wade 1970). After this period of adaptation, the subject was brought back to the starting roll orientation, represented by the arrow. The first SVV adjustment in the measurement position started 5 s after the turntable came to a full stop. The starting roll orientation of the arrow was random within the entire 360° roll plane. Adjustment time for single SVV trials was limited to 5 s, and consecutive trials were presented to the subject with a 2-s delay. This time limit to complete the task ensured that subjects spent about equal time on the task in all conditions, which reduced potential time-dependent differences in arrow adjustment variability (Tarnutzer et al. 2012b). Completion of each trial was confirmed by the subject pushing a button. Prior to data collection, 5 to 10 training trials were run in each subject. Before subjects started with the second part of the session, i.e., the nine test runs, the control runs were applied. They were brought from upright position to one of the nine measurement positions and, as in the test runs, five SVV adjustments were obtained in succession. At the end of each control or test run, the subject was brought back to the starting (upright) position, and the room lights were briefly turned on, terminating visual adaptation to the dark and allowing the subjects to relax. In each session, a total of 90 SVV adjustments were obtained (18 runs times 5 SVV adjustments per run).

Based on our observations after adapting at ±90°, we repeated this paradigm in all subjects with an adaptation position of ±45°. For this additional data collection, all other parameters of the paradigm were identical to the measurements after adapting at ±90°.

**Definition of terms frequently used.** Clockwise (CW) shifts relative to the earth-vertical axis (as seen by the subject) have positive signs and counterclockwise (CCW) shifts have negative signs. We will use the term trial-to-trial variability to refer to the within-subject median absolute deviation (MAD) of SVV adjustments. In relation to trial-to-trial variability, the term precision reflects the inverse, i.e., the degree of reproducibility. Accuracy, on the other hand, is defined as the magnitude of the median adjustment error.

**Data analysis.** We defined the normal range of SVV values according to previous publications, i.e., SVV within ±2.5° of true earth-vertical when sitting or standing upright (Brandt et al. 1994; Perrenou et al. 2008). As our data were not normally distributed (using the Jarque-Bera hypothesis test of composite normality, jbtest.m, Matlab 7.0), median (±1 median absolute deviation or MAD) values were provided when pooling individual data points. For both the ±45° and the ±90° adaptation position sessions, results after adapting in those positions and results from the control data sets were pooled each for further analysis as no statistically significant (P > 0.05) differences were noted.

To evaluate the potential impact of the 5-min adapting periods, individual median adjustment errors of both the control and the test conditions were compared using paired t-tests. Holm’s correction was applied whenever multiple t-tests (number of tests = m) were performed [see (Tarnutzer et al. 2012a) for detailed explanation]. We assessed the adjustment time (showing no significant differences between the control and test conditions).

We also evaluated the amount of drift over the five SVV adjustments in each chair position and calculated the difference between the first and the fifth SVV adjustment (ΔSVV). Paired t-tests were then applied to assess differences in the ΔSVV between the control and the test conditions.

In a second step, we fit a descriptive model to the adjustment errors to further understand the mechanisms behind the shifting pattern observed.

**Descriptive model of the A- and E-effect.** The following descriptive model based on two parts was used to generate the pattern of roll angle-dependent over- and undercompensation characteristic to the SVV:

$$\text{Err} = \left( k_1 a \right)^3 + k_2 a + k_3 \left( e^{-\frac{a - C}{2\sigma^2}} - e^{-\frac{-a - C}{2\sigma^2}} \right) \quad (1)$$

where α is the tilt angle at which the median adjustment error Err was recorded. The first and second addend, i.e., the sum of a cubic and a linear function, represent roll overcompensation (increasing with the roll angle) and eventually are responsible for generating the A-effect. The third addend, the difference of two Gaussian functions, accounts for the local roll overcompensation (as observed for the E-effect). Its width was determined by the parameter σ of the Gaussian functions and the distance between their two centers 2 * C. k₁ and k₂ scaled the relative contribution of the two monotonic functions to allow for the variability of the behaviors observed in the nonlinear growth of A-effect, while k₃ scaled the third function.
SHIFTS IN PERCEIVED VERTICAL AFTER PROLONGED ROLL

RESULTS

Impact of adapting on adjustment errors. SVV adjustments in a single subject before and after adapting at +90° (right ear down) are illustrated in Fig. 2. In this subject (S2), on the side of the adaptation position, the E-effect at +30° was lost and SVV adjustments at +60° (being accurate in the control condition) were shifted by almost 20° toward the adaptation position, resulting in an A-effect both at +30° and +60°. Adapting at +90° also had an (although smaller) impact on subsequent SVV adjustments in left ear-down positions in this subject (i.e., on the side contralateral to the previous roll-tilt), similar to that for right ear-down (i.e., on the side of previous roll-tilt) adjustments, after adapting the E-effect at −30° was lost and the A-effect at −60° and −90° became larger.

Comparing the control and the test conditions for the two sessions, including all subjects studied, a gap between overall median SVV adjustments before and after adapting at ±90° (see Fig. 3, A and B) was noted at roll angles smaller than the adapting angle (i.e., 30° and 60° roll-tilt) on the same side as the adaptation position. Noteworthy, no shifts occurred when obtaining the SVV adjustments at the position of adapting (±90°).

Statistical analysis (paired t-tests) did not yield any significant differences between adjustment errors after adapting at +90° or at −90° (P > 0.05). Therefore, for further analysis, results after adapting in those two positions were pooled (after mirroring the results from the −90° adapting session both along the x-axis and the y-axis), doubling the sample size. By analogy, since no statistically significant differences in adjustment errors were found in the control conditions obtained before adapting in either session, the same procedure was also performed with the control data sets from the two sessions.

Adapting at ±90° significantly changed adjustment errors (Fig. 4), shifting the SVV for measurements obtained on the side of adapting. This was indicated by the gap between the control and test trials on the ipsilateral side, at angles smaller than the adaptation position, i.e., at 30° (−4.3 ± 2.9° vs. 5.1 ± 3.1°, P < 0.001) and 60° (−1.4 ± 3.6° vs. 12.4 ± 6.9°, P < 0.001). Integrity of adaptation was confirmed by statistical analysis (paired t-tests) that showed a statistically significant difference between a test and control condition for the two aforementioned adjusted roll angles (P < 0.05).

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Fig. 1. Graphical representation of the role of the different parameters in the proposed model. A: output of Eq. 1 (black solid line) is the sum of two elements. The first element of Eq. 1, generating roll undercompensation (gray dotted line), is only determined by the scaling factor $k_1$. The second element, generating local roll overcompensation (gray dotted line), is determined by the distance $2\sigma + C$ between the centers of two identical Gaussian functions with width $\sigma$, summed with opposite signs and scaled by $k_2, k_3$; the parameter $d$ shifts the center of the Gaussian functions in the second element of Eq. 2 (light gray dotted line) with respect to the one in the first element of Eq. 2 (dark gray dotted line). By summing the shifted function generating local roll overcompensation (i.e., an E-effect) with the unchanged function yielding roll undercompensation (i.e., an A-effect), the output of the second line of Eq. 2 (solid black line in B) differs from the output of the first line of Eq. 2 (solid black line in A), therefore accounting for intrasubject differences in manifestation of the E-effect. The output of the fitting function, together with the specific role of the parameters, is depicted in Fig. 1.

Individual median adjustment errors from test (ErrTest) and control (ErrCont) runs acquired at a single roll angle were fitted together using the following set of equations, derived from Eq. 1:

\[
\text{ErrTest} = (k_1\alpha)^2 + k_2\alpha + k_3\left[\frac{e^{-\frac{C+\alpha}{2\sigma^2}} - e^{-\frac{-\alpha}{2\sigma^2}}}{2\sigma^2} \right]
\]

\[
\text{ErrCont} = (k_1\alpha)^2 + k_2\alpha + k_3\left[\frac{e^{-\frac{C-d}{2\sigma^2}} - e^{-\frac{-\alpha-d}{2\sigma^2}}}{2\sigma^2} \right]
\]

(2)

The only difference between the two equations is the displacement parameter $d$, which allowed the center of local roll overcompensation to shift along the tilt angle (while the sum of the monotonic functions was kept fixed). Best fit values of parameters were obtained by least square minimization of a unique error calculated over both the test and control runs. Therefore, the same values for all of the parameters were used by both equations, except $d$, were applied. This approach allowed a different center of the function generating local roll overcompensation compared with that generating global roll undercompensation and avoided the high number of parameters causing overfitting of the difference observed between test and control runs. This difference, which is the focus of the present study, was indeed only characterized through a single parameter ($d$).

Equation 2 was fit to median adjustment errors from each pair of test and control runs acquired for each adaptation position, both pooling all subjects and on a single-subject basis. The quality of the fit was assessed calculating the $r^2$ value.

Individual median adjustment errors (±1 MAD) were calculated for both sessions in all subjects.

Fig. 2. Subjective visual vertical (SVV) adjustments relative to true earth-vertical (indicated by the dashed horizontal line) are plotted against head roll orientation in a single subject (S2) for both the control condition (light gray circles, interconnected by a dashed line) and the test condition after adapting at +90° (dark gray squares, interconnected by a solid line). For each head roll orientation tested, a series of five SVV adjustments (sorted from left to right according to their order of recording, i.e., with the first trial the leftmost and the last trial the rightmost) were obtained before moving the turntable back upright for a brief break with the lights on.
of a cubic and a linear function) and roll overcompensation at larger head-roll angles (represented by a mixture of Gaussian functions) (see Eq. 2 in the materials and methods section). The data were pooled with respect to symmetric adaptation positions (right ear down and left ear down), and median curves across subjects were calculated, as presented above. The $r^2$ value of the fit of Eq. 2 to the median curves was 0.99 for both fitting control and test data. The group fits are shown in Fig. 5. Compared with the control trials, the value of the displacement $d$ of the mixture of Gaussian functions generating local roll overcompensation (i.e., an E-effect, located usually near upright) was 89.2° when fitting the test data, closely matching the roll angle of the adaptation position.

To further investigate whether a shift of the mixture of Gaussian functions describes the effect of adaptation on SVV adjustments, we fit the single-subject data, pooling again the data obtained from the two symmetric adaptation positions as above. The mean $r^2$ was 0.96 ± 0.04 after adapting at ±90° and 0.97 ± 0.03 for the respective control trials. The distribution of displacement values $d$ showed one outlier (defined as deviating more than 2 standard deviations than the mean of all other values), with a value of 9.5°. After removing this outlier, the mean individual $d$ value was 86.9 ± 17.6°.

Follow-up measurements with an adaptation position of ±45°. Comparing the control and the test conditions for the two sessions, including all subjects studied, a gap between overall median SVV adjustments before and after adapting at ±45° (see Fig. 6, A and B) was noted at roll angles larger than the adaptation angle (i.e., 60° and 90° roll-tilt) on the same side as the adaptation position. As for the ±90° adaptation position sessions, results after adapting in those two positions and results from the control data sets were pooled each for further analysis as no statistically significant ($P > 0.05$) differences were noted. In this pooled data, verticality perception was found to be significantly shifted on the side of adapting, but at angles larger than the adaptation position, i.e., at 60° (6.0 ± 3.5° vs. −4.5 ± 8.7°, $P < 0.001$) and 90° (13.8 ± 3.3° vs. 7.7 ± 4.8°, $P < 0.001$) (Fig. 6C). As for ±90°, returning upright after adapting at ±45° resulted in a significant shift of verticality perception toward the previous

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**Fig. 3.** Overall median adjustment errors [±1 median absolute deviation (MAD)] relative to true earth-vertical are plotted against head roll orientation for the two sessions with adapting at +90° (A) and −90° (B) in all nine participants. Both the test condition after adapting (black squares, interconnected by a solid line) and the control condition (obtained immediately after roll-tilting the subject; gray circles, interconnected by a dashed line) are shown for comparison. The dotted horizontal line indicates true earth-vertical orientation, and the dashed vertical line indicates the adaptation position.

**Fig. 4.** For both statistical analysis and improved visualization of the impact of prolonged static roll on verticality perception, adjustment errors from the two sessions at ±90° were pooled after mirroring the data from the −90° adapting session. This was done for the test and the control data separately. In the pooled data (i.e., after adapting at ±90°), significant shifts of SVV adjustments relative to the control condition were found in head roll positions nearby, as indicated by the * ($0.05 > P$ value $> 0.01$) and the ** ($P$ value $< 0.01$). The horizontal dashed line indicates perfect earth-vertical judgments; the vertical dashed line refers to the adaptation position.
adaptation position (control vs. after adapting; \(0.7 \pm 1.2^\circ\) vs. \(1.9 \pm 1.8^\circ, P = 0.001\)). Trial-to-trial variability increased with head-roll angle in both sessions without significant differences between adapting at \(+45^\circ\) and at \(-45^\circ\) and between the control and the test trials (paired t-test, Holm’s corrected). Therefore, results from the two sessions were pooled (after mirroring all values for LED adapting relative to the \(y\)-axis). This same procedure was made for the control trials.

Model fitting (as described above) was also obtained for these additional data sets. For the median curves, the \(r^2\) value was 0.97 after adapting at \(+45^\circ\) and 0.95 for control data. (The value of the displacement \(d\) of the function representing local roll overcompensation along the tilt angle was \(34.9^\circ\).) As for sessions with adaptation positions of \(\pm 90^\circ\), we fitted individual data before and after adapting at \(\pm 45^\circ\). Mean individual \(r^2\) values confirmed a good quality of the fit \((0.89 \pm 0.13\) and \(0.93 \pm 0.07\) for test and control trials, respectively); however, the values of \(d\) were not normally distributed (Lilliefors test, \(P = 0.009\)). One subject did not show roll overcompensation (not even in the control runs) and almost no difference between test and control runs. Accordingly, the fit provided a value of 0 to the scaling factor \(k_3\) of the mixture of Gaussian functions in this subject. Since no measure of shift can be obtained, the subject was not considered for further analysis. In the remaining eight subjects, we used a \(k\)-means clustering approach (Matlab function kmeans.m) to the displacement \(d\), which resulted in two subgroups: three subjects showed a clear shift toward the adaptation position (median \(d \pm 1\) MAD; \(42.7^\circ \pm 6.9^\circ\)) and five showed no shift \((8.0^\circ \pm 2.7^\circ\)).

**DISCUSSION**

The perception of earth-vertical is influenced by the subject’s recent head-roll orientation relative to gravity. Overall, the pattern of changes observed are consistent with a “local bias” or distortion of the internal estimate of direction of gravity, being most prominent at roll-tilt angles close to the preceding adaptation position. This effect was symmetric, i.e., did not depend on the direction of roll-tilt when adapting. Plainly, the behavior of this local bias speaks against a simple addition/subtraction of a constant offset from the internal estimate of direction of gravity. We rather hypothesize that it is the result of a more complex, most likely central mechanism.

 Virtually all sensory systems show adaptational mechanisms (Gillespie and Muller 2009; Series et al. 2009). The goal of adaptation will depend on the context and may aim at improving the discriminability around the adapter (Abbonizio et al. 2002). Systematic biases in the estimation of orientation, contrast and direction of subsequent stimuli after prolonged exposure to a visual stimulus of a particular orientation are examples of such processes (Clifford 2002; Hamnett et al. 1994; Levinson and Sekuler 1976). Adaptation may also improve rebalancing bilateral sensory input, as in the case of prolonged vestibular stimuli, such as constant-velocity rotation or caloric irrigation. Reversal of nystagmus during constant-velocity rotation with slow phases pointing into the opposite direction after the original nystagmus stops (Furman et al. 1989; Leigh et al. 1981) likely reflects an adaptive mechanism (Leigh and Zee 2006). In the following sections, we will discuss how such adaptational changes in our experimental paradigm can be interpreted and modeled.

*Simulating the experimental data.* To elucidate such a mechanism, a descriptive model was introduced. We allowed the...
function representing local roll overcompensation, usually centered at upright position, to shift within the roll plane. We could fit the SVV pattern after adapting at ±90° with high reliability at the group ($r^2 = 0.99$) and the individual subject (mean $r = 0.97$) level. Differences in adjustment errors before vs. after adapting were described by variations of one parameter only: the displacement of the center of the function representing local roll overcompensation along the roll plane. Our modeling results show that a shift in the distribution of this function toward the previous adaptation position explains the error pattern observed best. Such a shift allows hypothesizing a potential role of local roll overcompensation as a short-term adaptation mechanism to optimize estimates around the most recent (presumably upright) position.

According to Bayesian theory, both sensory input and an internal bias constructed from previous experience (“prior knowledge”) are combined to solve a specific task, such as estimating direction of gravity (Kording and Wolpert 2004; Laurens and Droulez 2007; MacNeilage et al. 2007). As a result, the posterior distribution will be shifted toward the most commonly experienced earth-vertical, i.e., the head position. Bayesian models describing adjustment errors with this approach have proven successful in the past (De Vrijer et al. 2008; Eggert 1998; Tarnutzer et al. 2009b).

This raises the question whether existing SVV models may be suitable to simulate the adaptational changes observed in our experimental paradigm. When evaluating previously published Bayesian SVV models from De Vrijer et al. (2008, 2009), Clemens (2011) and our own group (Tarnutzer et al. 2009b), they had two major shortcomings: first, these models do not reproduce the experimentally observed E-effect at small roll angles; instead a slowly increasing A-effect is generated. To simulate a shift in the E-effect usually centered on upright is, therefore, not possible with these models. Second, none of these Bayesian SVV models was designed to take into account adaptational changes of sensory (e.g., otolith, proprioceptive, or visual) input. The second limitation was also true for the idiotropic vector model by Mittelstaedt (1983), while this model reliably generated an E-effect at small roll angles. Taken together, neither previously published Bayesian SVV models nor Mittelstaedt’s SVV model were suitable for fitting the pre- and postadaptation data obtained here.

In previous models, an E-effect was predicted only when assuming that it originates from the otolith signal (Mittelstaedt 1983), a notion conflicting with detailed modeling of otolith responses (Tarnutzer et al. 2009b). Our current modeling results, moreover, suggest that the E-effect might be caused by a local compensatory mechanism that can shift to a different roll-tilt angle. We hypothesize that this mechanism might reflect a strategy that avoids undercompensation of the SVV for roll angles near the most recent sustained stable head-roll position.

Based on this hypothesis, we propose that, when remaining in a static roll-tilted position for a certain time, this mechanism stops affecting the roll angles around upright and appears around the current (roll-tilted) position, making it the new internal reference position. We did not observe significant SVV shifts when remaining at the preceding adaptation position (±90°). This might underline the hypothesis that the previous adaptation position becomes the new reference position. In upright position, this strategy results in an estimated visual vertical parallel to true vertical, while, when applied to a different reference position, it preserves the perceived visual vertical predicted by the Bayesian optimal observer theory. Noteworthy, perceived vertical at this position will likely differ from the true vertical, as it is biased by undercompensation normally occurring at ±90°. Although preserving a wrong vertical when roll-tilted, this strategy could be considered good by the central nervous system since, besides working perfectly when upright, it always counteracts undercompensation of the visual vertical, making the subject more stable against perturbations (Fig. 7). Undercompensation, if not compensated tightly, impairs postural stability and increases the risk for falls. However, preventing undercompensation might be obtained at the cost of roll overcompensation (E-effect) at small angles.

Even if the bias seems to be largest and significant only for nearby head-roll angles, we also observed a significant bias toward the previous adaptation position when returning upright. This is consistent with observations by others (Day and Wade 1966) and our own group (Tarnutzer et al. 2013). We propose that this posttilt bias might be related to central adaptation shifting local roll overcompensation toward the previous roll-tilted position. This effect will be smaller for more remote roll-tilt positions. The significant changes noted in upright position may be related to higher signal-to-noise ratio of sensory input when near upright compared with roll-tilted positions.

Fig. 7. Graphical representation of the local compensatory behavior of the proposed Gaussian function. A: when upright, the local function shifting estimates toward roll overcompensation (dotted black line) at small roll angles are normally centered at 0° and counteract the increasing roll undercompensation (dashed black line) within the range $r$ of small roll angles around upright. This results in a tendency for the estimate of vertical (gray solid line) within the range $r$ to be biased toward roll overcompensation while roll undercompensation is avoided, consistent with an E-effect. B: after adapting in a roll-tilted position (+90° chosen here for illustration), the local Gaussian function facilitating roll overcompensation is now shifted and counteracts the growth of roll undercompensation within the range $r$ centered at 90° in this example. The resulting estimate of vertical will, therefore, be more stable around the new estimate of vertical than previously for roll-tilt of 90°, as indicated by the almost flat part of the gray solid line around 90° to the positive slope of the A-effect at the same angle.
The descriptive model, its relation to previous SVV models and the possible role of oculor counterroll. The approach to simulate SVV adjustments as proposed here should be considered a descriptive model only, focusing on the overall pattern of perceptual errors in this task. Its strength is combining functions that can be modified independently and, therefore, to isolate the features accountable for the changes observed after adaptation. By modeling such changes with a single parameter, it allows a simple parameterization of the effect we aimed to study. Obviously, our model does not reach the level of granularity of other SVV models and, more importantly, does not embed any functional interpretation of the parameter describing the adaptation. However, it demonstrates that implementing a mechanism that optimizes estimates around the perceived vertical position and allowing it to shift along the roll plan describes our data well. Therefore, it raises the question whether current SVV models may be modified in such a way that they can simulate the postadaptation data.

A possible answer to such questions comes from observing the effect that the head-fixed prior has on SVV adjustments, according to an optimal observer model (Tarnutzer et al. 2009b). As any good prior, it decreases the variability of the estimated vertical, but it also causes the adjustments to be invariably biased toward the current head position, which means undercompensation of the SVV in every roll-tilt condition. This implies that the visual horizon roll-tilts with the subjects, reducing the potential benefits from visually-mediated compensatory responses to stability. Since postural stability strongly depends on vision (Ray et al. 2008), it could be hypothesized that a risk factor corrects the Bayesian optimal observer estimate. Risk-dependent reweighting of optimal behavior is often observed when different risks are associated with different outcomes (Braun et al. 2011). The E-effect might result from a strategy aimed at reducing the risk of imbalance. Indeed, by locally counteracting underestimates of the visual vertical, it might reinforce visually mediated compensation of small roll around any sustained body position.

Noteworthy, previous SVV models and our descriptive model do not take into account the potential impact of oculor counterroll (OCR). This otolith-ocular reflex partially compensates for head roll and was proposed to cause the E-effect because of the brain being unaware of OCR (Wade and Curthoys 1997). Pansell et al. (2005) reported drift in torsional eye position during prolonged static roll and initial OCR overshooting or undershooting when returning back upright. After 20 s, OCR was again close to baseline. Potentially, the shift in SVV adjustments after prolonged roll could be related to an initial bias in torsional eye position when reaching the measurement position. Assuming such an effect of OCR on the SVV, two predictions can be made. 1) An offset in OCR results in a shift of SVV adjustments at any subsequent roll position. 2) With the dynamics of OCR described (returning to baseline within 20 s), drift in adjustment errors over this time span is significantly larger in the test than in the control runs. Both predictions were not true for our experimental data, as changes in SVV occurred only for roll positions nearby the adaptation position and as drift was similar for control and test runs. We, therefore, consider a relevant contribution of OCR to the local SVV bias as unlikely.

Additional data, adapting at ±45°. While adapting at ±90° resulted in consistent changes of SVV adjustments, findings after adapting at ±45° varied considerably among individuals. Overall, adjustments at nearby larger (±60 and ±90°) roll angles were shifted in such a way that roll undercompensation was significantly (P < 0.01) reduced. However, only three showed a relevant shift of the local function. The dissociation between significant SVV shifts at nearby smaller roll angles for adaptation at ±90° and nearly larger roll angles for adaptation at ±45° is surprising, as our model would predict an effect on both sides of the adaptation position. We hypothesize that the lack of significant shifts at 120° roll after adaptation at ±90° is related to the increased trial-to-trial variability at larger roll angles (Tarnutzer et al. 2009b). SVV variability probably obscures shifts due to adaptation, which are expected to be small for angles larger than the adaptation position. Noteworthy, comparison of the median traces indeed shows a nonsignificant shift at 120° roll-tilt, matching our prediction (see Fig. 4). Lack of significant shifts for roll angles smaller than the adaptation position after adaptation at ±45° is probably due to the pooling of five nonsifting subjects (median shift = 8°) with three shifting subjects. On the group level, this results in pooling of shifts with variable size and even pointing into opposite directions at small roll angles. With only three subjects showing a consistent shift of the function representing local roll overcompensation after adaptation at ±45°, no separate statistical analysis was possible.

Noteworthy, the larger interindividual variability of adjustments matches previous observation (Tarnutzer et al. 2013): while some subjects showed a clear E-effect at small roll angles, others were accurate or even presented with an A-effect. With respect to our hypothesis, it is possible to conjecture that an adapting angle within the range of the E-effect might be less effective in shifting the E-effect itself, as within such a range estimated direction of gravity at the usual (upright) reference position is still preserved from undercompensation.

In summary, static roll over periods as brief as 5 min significantly affected verticality perception in nearby roll positions. A descriptive model implementing both roll undercompensation at larger roll angles and local roll overcompensation near upright successfully fitted the postadapting data by shifting the function representing local overcompensation toward the adaptation position. It could reflect the brain’s strategy to optimize verticality estimates and postural control around recent roll-tilted positions, even though it bears the risk of (small) roll overcompensation (E-effect) at small angles.

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