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Abstract: Body position relative to gravity is continuously updated to prevent falls. Therefore, the brain integrates input from the otoliths, truncal graviceptors, proprioception and vision. Without visual cues estimated direction of gravity mainly depends on otolith input and becomes more variable with increasing roll-tilt. Contrary, the discrimination threshold for object orientation shows little modulation with varying roll orientation of the visual stimulus. Providing earth-stationary visual cues, this retinal input may be sufficient to perform self-adjustment tasks successfully, with resulting variability being independent of whole-body roll orientation. We compared conditions with informative (earth-fixed) and non-informative (body-fixed) visual cues. If the brain uses exclusively retinal input (if earth-stationary) to solve the task, trial-to-trial variability will be independent from the subject's roll orientation. Alternatively, central integration of both retinal (earth-fixed) and extra-retinal inputs will lead to increasing variability when roll-tilted. Subjects, seated on a motorized chair, were instructed to (1) align themselves parallel to an earth-fixed line oriented earth-vertical or roll-tilted 75° clockwise; (2) move a body-fixed line (aligned with the body-longitudinal axis or roll-tilted 75° counter-clockwise to it) by adjusting their body position until the line was perceived earth-vertical. At 75° right-ear-down position, variability increased significantly ($p < 0.05$) compared to upright in both paradigms, suggesting that, despite the earth-stationary retinal cues, extra-retinal input is integrated. Self-adjustments in the roll-tilted position were significantly ($p < 0.01$) more precise for earth-fixed cues than for body-fixed cues, underlining the importance of earth-stable visual cues when estimates of gravity become more variable with increasing whole-body roll.

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Visually guided adjustments of body posture in the roll plane

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Abstract Body position relative to gravity is continuously updated to prevent falls. Therefore, the brain integrates input from the otoliths, truncal graviceptors, proprioception and vision. Without visual cues estimated direction of gravity mainly depends on otolith input and becomes more variable with increasing roll-tilt. Contrary, the discrimination threshold for object orientation shows little modulation with varying roll orientation of the visual stimulus. Providing earth-stationary visual cues, this retinal input may be sufficient to perform self-adjustment tasks successfully, with resulting variability being independent of whole-body roll orientation. We compared conditions with informative (earth-fixed) and non-informative (body-fixed) visual cues. If the brain uses exclusively retinal input (if earth-stationary) to solve the task, trial-to-trial variability will be independent from the subject's roll orientation. Alternatively, central integration of both retinal (earth-fixed) and extra-retinal inputs will lead to increasing variability when roll-tilted. Subjects, seated on a motorized chair, were instructed to (1) align themselves parallel to an earth-fixed line oriented

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Keywords Vestibular · Multisensory integration · Perception · Postural vertical · Visual vertical

Introduction

Sensory input from various sources [including vestibular and extra-vestibular (truncal) graviceptive signals, trunk and neck proprioception as well as vision] is weighted by the brain in a task-specific fashion to compute head-relative-to-trunk position and body orientation in space (Angelaki et al. 2009; Barra et al. 2010). Amongst these sensors, the otolith organs are thought to be of major importance, as they are the only sensors that directly measure the gravito-inertial force vector (Schoene 1964). Graviception was studied extensively by subjective visual vertical (SVV) and subjective haptic vertical (SHV) adjustments in the past, demonstrating a modulation of trial-to-trial variability as a function of whole-body roll-tilt (Tarnutzer et al. 2009a; Schuler et al. 2010). This phenomenon was explained by the properties of the otolith afferents (Fernandez et al. 1972; Fernandez and Goldberg 1976) and by central processing that is not

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optimally tuned for head roll angles distinct from upright (Tarnutzer et al. 2009a). In contrast, the signal-to-noise ratios of visual and proprioceptive inputs are thought not to show such roll-angle-dependent modulation (De Vrijer et al. 2009).

We use external, space-fixed references preferentially along the direction of gravity and along the horizon to align our body with gravity. To better understand the mechanisms and sensory cues of self-positioning, we studied self-positioning relative to gravity, but also relative to space-fixed objects in body roll-tilted positions. This study was fueled by the observation that sensory input may change its accuracy and precision when roll-tilted, facilitating or compromising self-positioning. For example, the noise of otolith input increases with head roll, making estimates of direction of gravity more variable. Specifically, we asked how well self-positioning to orientations distinct from upright can be achieved and whether visual orientation cues improve performance. One of our basic assumptions was that the relative contribution of the individual sensors depends on their reliability or “usefulness”. For example, an earth-fixed visual cue may serve as a landmark for self-adjustments. This leads us to the hypothesis that self-adjustments in the roll plane parallel to an earth-fixed visual cue (see Fig. 1a for illustration) could theoretically be achieved by relying solely on vision. For this task, the subject aligns the body-longitudinal axis with the perceived line orientation (paradigm 1). Whether such a “purely visual strategy” is in fact being used, however, has not yet been determined. The hypothesis of the “purely visual strategy” predicts that, for

self-adjustments along an earth-fixed visual cue, the trial-to-trial variability remains unaffected by the body roll position as the signal-to-noise ratio of the retina’s ability to determine stimulus position modulates little with the torsional orientation of a visual cue. In a recent study, however, we proposed that for both the SVV and the SHV, sensed direction of gravity influences a task that—in theory—could be done solely by retinal input (Tarnutzer et al. 2012). We call this strategy, which includes otolith input independently of the task, the “all sensors’ integration strategy”. If this strategy is also used for visually guided whole-body self-adjustments along an earth-fixed object in the roll plane, an increase in trial-to-trial variability for desired roll-tilted positions is predicted for paradigms that may theoretically be solved based on retinal input only.

The obvious control condition for self-adjustments along an earth-fixed visual cue consists of line adjustments along perceived direction of gravity (the SVV), while the subject remains in a given (upright or roll-tilted) position (Fig. 1c). In both paradigms, the angle between the body-longitudinal axis (BLA) and the visual cue roll orientation is variable. In this SVV control paradigm (=paradigm 3), however, no adjustments of the postural position are required. Therefore, a second control condition that includes self-adjustments is advantageous: A visual cue has a fixed torsional orientation relative to the body-longitudinal axis, that is, is body-fixed and the angle between the BLA and the visual cue is constant. The subject is required to align the visual cue with the earth-vertical. Obviously, this can only be achieved by changing the whole-body roll orientation (Fig. 1b). In this control paradigm

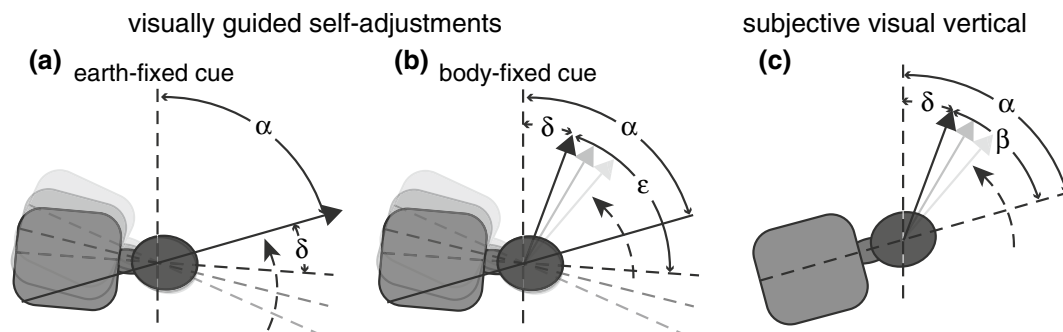


Fig. 1 Schematic illustrations of the visually guided self-adjustments when providing an earth-fixed (a) or a body-fixed (b) cue and for the SVV paradigm (c). Angle α refers to whole-body roll in the SVV paradigm (75° RED in this example) and to the desired whole-body roll orientation in the self-adjustment paradigms (75° RED in this example). The solid gray arrows and the black arrow indicate the subject performing the adjustment task with the black arrow representing the final line roll orientation. Whereas the line is rotated by the subject in the SVV task (d) and for self-adjustments with a body-fixed cue (b), it remains stationary for self-adjustments in presence of an earth-fixed cue (a). Angle β refers to the compensatory rotation of the visual line away from the body-longitudinal

axis in the SVV paradigm. In this example, β is smaller than α , resulting in roll under-compensation as referred to by angle δ . ϵ refers to the constant angle between the line and the body-longitudinal axis for self-adjustments with a body-fixed cue. For perfect self-adjustments with a body-fixed cue $\epsilon = \alpha$. Whenever roll under-compensation occurs in this paradigm, actual whole-body roll orientation is given by $\delta + \epsilon$. For visually guided self-adjustments with earth-fixed cues (a), the subject is requested to move its body-longitudinal axis parallel to the line orientation (black arrow), that is, to minimize angle δ . In this example (a), adjusted roll orientation exceeds the desired roll angle, resulting in a final roll angle relative to earth-vertical of $\delta + \alpha$

(=paradigm 2) with the BLA—visual cue angle remaining constant, the subject has to rely on extra-retinal inputs, as the retinal cue does not provide a reference. In analogy to the SVV and SHV, we predict that for self-adjustments with a body-fixed visual cue, trial-to-trial variability increases with increasing whole-body roll orientation, determined by the torsional angle between the visual line and the body-longitudinal axis. If extra-retinal inputs are integrated (“all sensors’ integration strategy”) for self-adjustments independent of whether the visual cue is body-fixed or earth-fixed, one could still hypothesize, that space-fixed visual cues could serve as a reference for self-adjustments, and therefore decrease the trial-to-trial variability compared to conditions with non-informative, body-fixed visual cues.

Materials and methods

Subjects

Twelve healthy human subjects (three women and nine men, aged 26–63 years, mean \pm 1 SD: 33.5 ± 10.6 years) participated in paradigm 1 (self-adjustments providing earth-stationary visual cues) and paradigm 2 (self-adjustments providing body-fixed visual cues). For comparison, we collected classic SVV adjustments (paradigm 3, line adjustments while being in a stationary roll position and providing no visual orientation cues) in nine healthy human subjects (4 women and five men, aged 26–42, mean \pm 1 SD: 33 ± 4.8 years). Two of these nine subjects had also participated in experiments 1 and 2. Informed consent of all subjects was obtained after full explanation of the experimental procedure. The protocol was approved by a local ethics committee and was in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki for research involving human subjects.

Definitions of frequently used terms

Adjustment errors refer to the deviations of actual SVV or self-positioning in the roll plane relative to the desired (either upright or 75° roll-tilted) position. The trial-to-trial variability reflects the degree of variability between single adjustments in individual subjects and is equal to one standard deviation. The visual cue (or the luminous line) was either space-fixed (i.e., did not change orientation relative to gravity during chair roll movements) or body-fixed (i.e., the line orientation in the roll plane relative to gravity changed by the same angle as the chair roll position).

Experimental setting

Subjects were placed on a motorized chair (Acutronic, Jona, Switzerland) in such a way that the roll axis of the chair

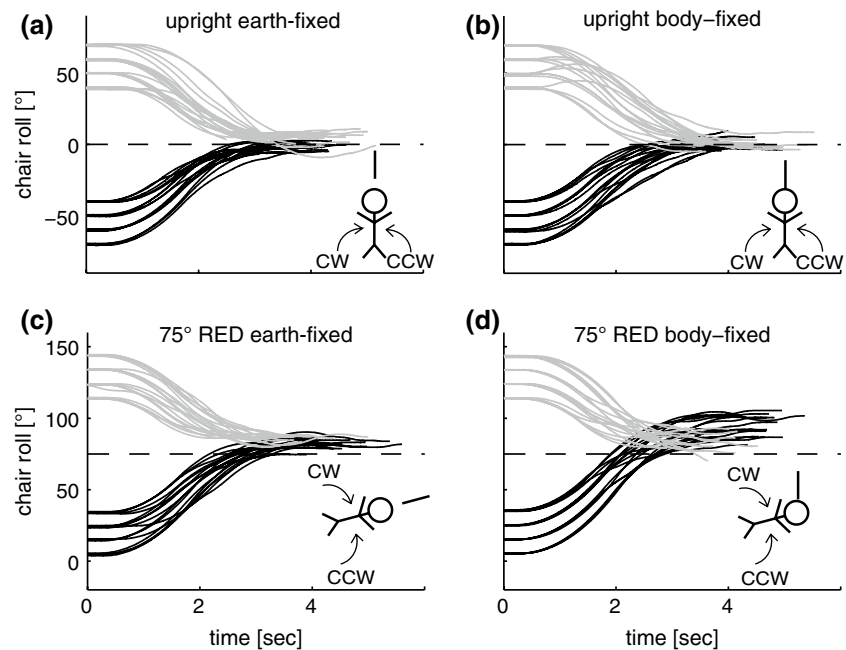
intersected the center of the inter-aural line. They were secured with a 4-point safety belt. The subject’s head was restrained viewing straight ahead with a thermoplastic mask (Sinmed BV, Reeuwijk, The Netherlands) that tightly covered the head. Vacuum pillows placed on both sides of the chest and hips minimized body movements. Subjects with myopia wore their glasses on top of the mask. All paradigms were performed in darkness except for the visual cue presented. For paradigms 1 and 2, the chair roll position was self-guided. The direction of chair roll [clockwise (CW) or counter-clockwise (CCW)] was defined as seen by the subjects. They were instructed to keep their hands on a joystick (paradigms 1 and 2) or a box with a turning knob (paradigm 3) placed in front all the time to avoid any additional sensation of body motion or position. A luminous line was projected from a body-fixed laser onto the center of a sphere in front of the subject. This line was used as visual cue in all paradigms. The inner surface of the sphere was 1.5 m from the subject’s eyes. At this distance, the line (length: 500 mm; width: 3 mm) subtended 9.5° of the binocular visual field.

Experimental paradigms

Paradigms 1 and 2: Subjects were instructed to move the chair as quickly and as precisely as possible along the shortest path of roll rotation by use of a joystick controlling chair velocity. A time limit of 6 s was defined. The acceleration/deceleration was set to $\pm 30^\circ/\text{s}^2$ for these subject-guided chair roll movements. Before data collection, subjects practiced chair adjustments until they could be performed reliably within the time limit. The percentage of trials rejected as for being not completed within the time limit was below 10 % in all subjects. The different paradigms, both for the earth-fixed and the body-fixed condition, are shown in Fig. 1. In paradigm 1, the orientation of the line was either earth-vertical (Fig. 2a) or tilted 75° CW relative to earth-vertical (Fig. 2c). In paradigm 2, the line was set either parallel to the body-longitudinal axis (Fig. 2b) or was rolled CCW relative to the body-longitudinal axis by 75° (Fig. 2d). Obviously, in the body-fixed condition, the visual cue was not stable in space and therefore provided no space-fixed reference for the subject.

Subjects were instructed to rotate the chair in such a way that the body-longitudinal axis was perceived parallel to the line (paradigm 1) or that the line was perceived earth-vertical (paradigm 2). In both paradigms, the desired whole-body roll orientations (0° and 75° right-ear down or RED) were well defined for a perfect completion of the task. However, only in paradigm 1 could the visual line serve as a reference during chair rotation, as the angle between the body-longitudinal axis and the luminous line was changing. In paradigm 2, the angle between the visual line and the sensed body-longitudinal axis remained stable, and the

Fig. 2 Single trial chair roll positions (in *black*: CW chair rotations; in *gray*: CCW chair rotations) are plotted against time for a single subject, showing the interval from the laser (and the subject-guided chair control) being turned on to the confirmatory button press by the subject. The *dashed line* refers to the desired chair roll orientation. Symbolic illustrations of trial types are shown in the *lower right corner of each panel*, indicating desired whole-body roll orientation, direction of chair rotation (*solid curved arrows*) and condition (earth-fixed paradigm: line apart from body; body-fixed paradigm: line attached to body)



visual line was non-informative and was used to indicate the estimated direction of gravity. The chair starting position in the roll plane was predefined (offsets of 40°, 50°, 60°, or 70° CW or CCW relative to the desired chair position), but the trial order was random. Subjects either had to perform a CW or CCW chair roll movement to match the desired chair and line orientations. The task started approximately 5 s after the chair had reached the starting position. Previously, we have shown that after a brief delay of less than 10 s after the end of such chair repositioning rotations torsional nystagmus as an indicator for possible semicircular canal (SCC), input has ceased almost completely (Tarnutzer et al. 2009b). After each trial, the chair starting position for the next trial was set, using a chair roll acceleration/deceleration of $\pm 10^\circ/\text{s}^2$. A few (usually 5 or less) practice trials to become familiar with the interface to control chair roll orientation were completed at the beginning. For both paradigms 1 and 2, 20 trials with either CW or CCW chair rotations were applied, resulting in a total of 160 trials (split up into 4 blocks) for the four different conditions, recorded in a single session. Subjects were informed verbally on the subsequent paradigm (paradigm 1 or 2) they had to perform after the chair reached its starting position. A short break with the lights turned on was given at the end of each block. The break terminated visual adaptation to the dark and allowed the subjects to relax and remove the mask.

Whereas in paradigms 1 and 2, subjects controlled the chair roll orientation by use of a joystick, in *paradigm 3*, subjects were asked to adjust the orientation of the line to perceived earth-vertical while being in a stationary whole-body upright or 75° RED roll orientation. Again, the time

limit was set to 6 s. Whenever completion of the task was not confirmed within this time limit, the trial was repeated at the end of the block. The presentation of the line started 10 s after the chair came to a full stop and was offset CW or CCW randomly between 28 and 72° relative to earth-vertical. For each roll orientation, 24 trials were obtained, resulting in a total of 48 trials in a single session. After each trial, chair roll orientation was changed automatically using the same acceleration/deceleration values as in paradigms 1 and 2.

Data analysis

Selected and confirmed chair roll positions (experiments 1 and 2) and roll line orientations (experiment 3) were determined. Adjustment outliers were defined in all three paradigms as data points more than two standard deviations (SD) away from the mean and were discarded. In addition to the final chair position, we also analyzed the dynamics of self-adjustments. We therefore identified maximal overshoot (i.e., the amount of additional roll relative to the final roll orientation) and calculated the individual average overshoot. To evaluate for a potential correlation between the amount of overshoot and the error or the variability of adjustments, a regression analysis was performed. Whenever both variables considered for correlation analysis were dependent variables, that is, measured with error, principal component analysis (PCA) providing major axis regression was chosen. This procedure is equivalent to orthogonal linear regression or total least squares, which minimizes the perpendicular distances from the data points to the fitted model

(Van Huffel and Vandewalle 1991). As a measure of the goodness of fit, we provide the FE1 value, which represents the fraction of variability explained by the first component of the PCA. To estimate the sampling distribution of the slope of the fit obtained by PCA, we used bootstrapping to construct 1,000 resamples and calculated the 95 % confidence interval (CI). The correlation between the dependent variables was considered significant whenever the 95 % CI did not include zero. If not stated otherwise, statistical analysis was done using analysis of variance (ANOVA, Minitab, Minitab Inc., State College, USA) including Tukey's correction for multiple comparisons. However, some parts of the statistical analysis were based upon paired *t* tests. Whenever multiple *t* tests (number of tests = *m*) were performed, Holm's correction was used (Holm 1979).

Results

Single trial chair roll rotations (paradigms 1 and 2) are plotted against time in Fig. 2 for an individual subject. For trials with a desired upright chair orientation, adjustments showed only minor position errors in both the earth-fixed (Fig. 2a) and body-fixed (Fig. 2b) conditions, and trial-to-trial variability was small. In the earth-fixed condition at desired 75° RED orientation (Fig. 2c), adjusted whole-body positions were shifted to slightly larger roll angles than actually required, and variability was similar compared to that in upright position. In the body-fixed condition, both deviations and trial-to-trial variability were markedly larger at desired 75° RED orientation (Fig. 2d) compared to upright. This suggests that besides the impact of gravity on adjustment performance also the reference frame of the visual orientation cue (earth-fixed vs. body-fixed) influences whole-body roll self-adjustments.

Errors and variability of self-adjustments and SVV adjustments

In experiments 1 and 2, subjects confirmed chair adjustments on average 4.4 s (± 0.4 s) after trials started. Statistical analysis (3-way ANOVA; factors: task, whole-body roll orientation, direction of chair rotation) of individual average chair adjustment errors (paradigms 1 and 2) showed a significant main effect for the task ($F(1,22) = 8.17, p = 0.005$) and for the whole-body roll orientation ($F(1,22) = 22.70, p < 0.001$). No main effect was observed for the direction of chair rotation ($F(1,22) = 0.26, p = 0.613$), and we therefore pooled trials with CW and CCW chair rotations for further analysis.

Resulting mean deviations in chair roll position relative to the desired chair orientation are presented in Fig. 3. For desired upright chair positions, average deviations were

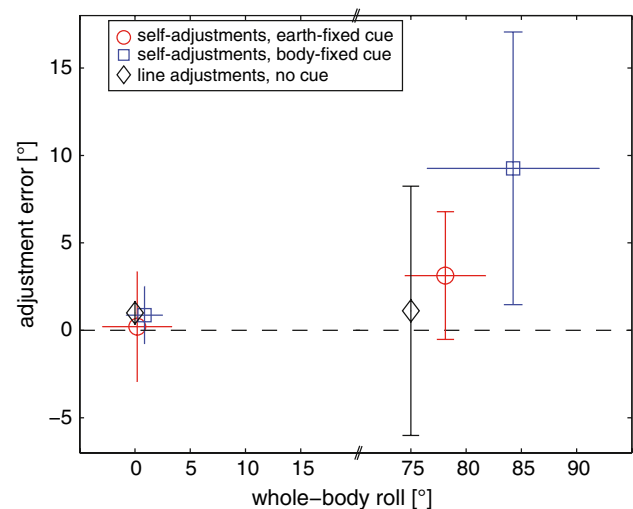


Fig. 3 Average adjustment errors for both the earth-fixed (*open circle*) and the body-fixed (*open square*) paradigm are plotted against average whole-body roll positions. SDs are provided for both the individual whole-body roll positions (*horizontal error bars*) and the errors in self-positioning relative to the desired whole-body roll-tilt position (*vertical error bars*), which was by definition set to zero (indicated by the *dashed line*) in all paradigms shown. Note that CW and CCW chair rotations were pooled

small both for the earth-fixed ($0.2^\circ \pm 3.2^\circ; \pm 1$ SD) and the body-fixed ($0.9^\circ \pm 1.6^\circ$) paradigm. In trial types with a desired chair roll orientation tilted RED by 75°, deviations were CW (i.e., chair roll angles measured were larger than 75°) and were increased compared to trials with desired upright orientation. This was true for both the earth-fixed ($3.2 \pm 3.7^\circ$) and the body-fixed paradigm ($9.3 \pm 7.8^\circ$). These deviations were significantly different from zero in both the earth-fixed (*t* test, $p < 0.05$) and the body-fixed ($p < 0.01$) paradigms. For comparison, classic SVV adjustments while remaining at a given whole-body roll orientation (paradigm 3) are also provided in Fig. 3. SVV adjustment errors (trials with CW and CCW arrow rotation pooled) in both upright and 75° RED roll orientation were minor and nonsignificant ($p > 0.05$) only.

Trial-to-trial variability of adjusted chair roll angles within a trial type and within a subject is shown in Fig. 4 for all three paradigms. Statistical analysis of variability of adjustments in paradigms 1 and 2 (3-way ANOVA) showed a significant main effect for whole-body roll orientation ($F(1,22) = 72.86, p < 0.001$), while the task ($F(1,22) = 2.45, p = 0.121$) and the direction of chair rotation (and therefore the starting roll orientation) ($F(1,22) < 0.01, p = 0.961$) did not yield a significant main effect. Therefore, trials with CW and CCW chair rotation were pooled for further analysis of trial-to-trial variability. The same was true for SVV adjustments, again showing no direction-dependent (CW vs. CCW line rotations) main effect.

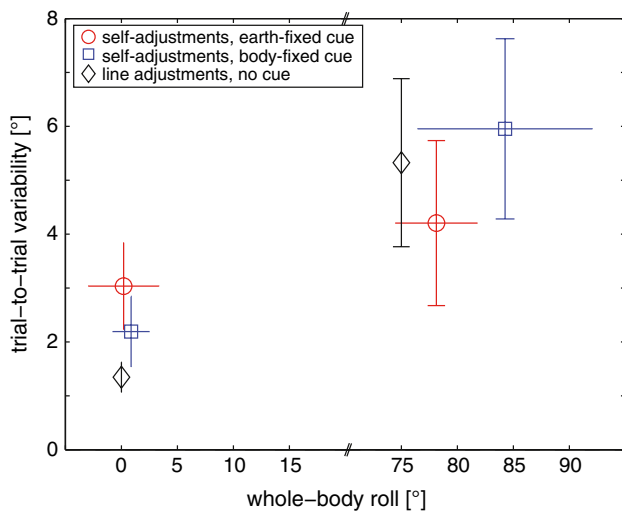


Fig. 4 Average trial-to-trial variability for both the earth-fixed (*open circle*) and the body-fixed (*open square*) paradigm are plotted against average whole-body roll positions. SDs are provided for both the individual whole-body roll positions (*horizontal error bars*) and the errors in self-positioning relative to the desired whole-body roll-tilt position (*vertical error bars*), which was by definition set to zero (indicated by the *dashed line*). Note that CW and CCW chair rotations are pooled since no significant differences in trial-to-trial variability were found

A significant interaction was noted between the task and the whole-body roll orientation for adjustment variability in paradigms 1 and 2 ($F(1,22) = 20.13$, $p < 0.001$). To determine, which conditions (defined by the whole-body roll orientation and the task) were significantly different in their trial-to-trial variability, pairwise comparisons using Tukey's correction for multiple tests were applied. For desired upright chair orientations, no significant differences in trial-to-trial variability were found between the earth-fixed and the body-fixed condition ($3.0 \pm 0.8^\circ$ vs. $2.2 \pm 0.7^\circ$, $p > 0.05$). Trial-to-trial variability in upright position was significantly smaller than in desired 75° RED orientation in both the earth-fixed ($3.0 \pm 0.8^\circ$ vs. $4.2 \pm 1.5^\circ$, $p < 0.05$) and the body-fixed paradigm ($2.2 \pm 0.7^\circ$ vs. $6.0 \pm 1.7^\circ$, $p < 0.001$). Comparing only trials with desired 75° RED roll position revealed that trial-to-trial variability was significantly lower for the earth-fixed condition than for the body-fixed paradigm ($4.2 \pm 1.5^\circ$ vs. $6.0 \pm 1.7^\circ$, $p < 0.001$). These findings indicate that, when roll-tilted, variability rose faster in the body-fixed task compared to the earth-fixed task. For comparison, trial-to-trial variability in upright position was considerably lower for the SVV, whereas it ranged in-between the two conditions related to chair self-adjustments when roll-tilted 75° RED.

Dynamics of self-adjustments

Setting chair acceleration/deceleration to $\pm 30^\circ/\text{s}^2$, peak average chair velocities of $30.2^\circ/\text{s}$ ($\pm 5.7^\circ/\text{s}$; ± 1 SD) during

self-adjustments were observed (see online supplemental material figure 1, showing mean chair velocity traces plotted against time). Statistical analysis (3-way ANOVA; factors: direction of chair rotation, whole-body roll orientation, reference frame of the visual cue) showed a main effect for the direction of chair rotation on peak chair velocities ($F(1,22) = 32.39$, $p < 0.001$). The reference frame of the cue and the whole-body roll orientation, however, did not show a main effect. Between the three factors, a significant interaction was found ($F(1,22) = 4.18$, $p = 0.044$). Pairwise comparisons showed significantly ($p < 0.001$) higher chair peak velocities in the body-fixed paradigm at desired 75° RED position for trials starting near upright (requiring CW rotations; $35.0 \pm 4.9^\circ/\text{s}$) than for trials starting near upside-down orientation (requiring CCW rotations; $24.0 \pm 7.0^\circ/\text{s}$). This could be related to the subjects' tendency to position the chair to roll angles larger than actually required. For the earth-fixed (upright and 75° RED position) and the body-fixed (upright only) paradigm, no significant interactions were found ($p > 0.05$). We computed a fast Fourier transform on the individual average self-generated movements (Harris 1998) to estimate the amount of semicircular canal (SCC) stimulation. We found that an average 90 % of the power was below 0.27 Hz (± 0.04 Hz; ± 1 SD). Since the SCC act as high-pass filters (Minor et al. 1999; Bertolini and Ramat 2010), these subject-guided chair maneuvers provide relatively poor SCC stimulations.

Different strategies may be used when moving the chair to the desired roll orientation, for example, one may slow down or stop before reaching the desired orientation or one may initially overshoot and then move the chair slowly back into the opposite direction. For all trial types and both CW and CCW active chair rotations, the amount of overshoot was determined (see Fig. 5).

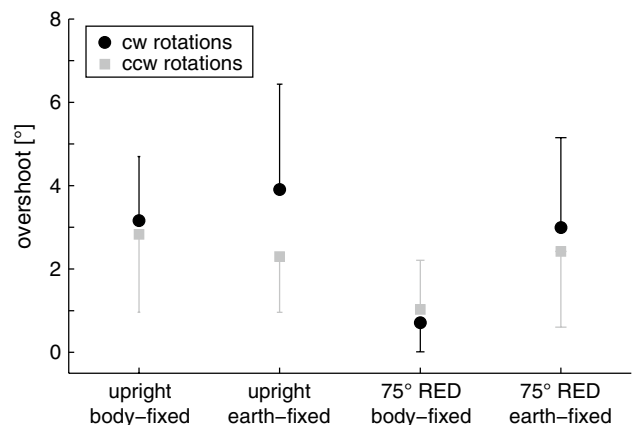


Fig. 5 Overall mean overshooting of chair adjustments (± 1 SD) relative to the final chair roll orientation (as confirmed by button press) for all paradigms and both CW (*black circles*) and CCW (*gray squares*) chair rotations

PCA revealed a moderate, but significant inverse correlation between the amount of maximal overshoot and the size of adjustment errors ($FE1 = 0.61$; slope = -0.35 , 95 % CI = -0.48 to -0.25). However, no significant correlation between maximal overshoot and the trial-to-trial variability ($FE1 = 0.51$; slope = 0.93 , 95 % CI = -0.80 to 1.40) of adjustments was noted. Furthermore, maximal overshoot correlated with peak chair velocity, that is, higher peak chair velocity was associated with more overshooting ($FE1 = 0.67$; slope = 0.33 , 95 % CI = 0.26 – 0.44).

Discussion

The novelty of the experimental conditions used here was that self-adjustments in the roll plane were visually guided. This allowed a precise definition of the desired whole-body roll orientation, whereas without visual orientation cues, only the principle (horizontal and vertical) positions can be tested reliably.

For visually guided self-adjustments extra-retinal cues are integrated independently of the frame of reference

The variability of self-adjustments reflects the overall effectiveness of the sensory systems involved and their integration within the central nervous system [see (Angelaki and Cullen 2008) for a comprehensive review]. The processing of various sensory cues is performed in a manner consistent with a weighted linear combination of the perceptual estimates from the individual cues (Angelaki et al. 2009). When an earth-fixed visual cue is provided, self-adjustments along this cue could theoretically be completed by relying solely on visual input. Alternatively, the brain may integrate both retinal and extra-retinal cues even when retinal input may be sufficient to solve the task. In fact, we found significantly higher variability for desired 75° RED whole-body roll compared to desired upright position in the earth-fixed paradigm, supporting the “all sensors’ integrated hypothesis”. This phenomenon was recently also reported for visual line adjustments along the body-longitudinal axis in whole-body roll-tilted positions (Tarnutzer et al. 2012). Such a behavior is compatible with the previously observed whole-body roll-angle-dependent increase in SVV variability, which most likely reflects head roll-dependent variability of otolith signals (Tarnutzer et al. 2009a). Similarly, for visual alignments (Cai et al. 1997), estimated target location (Dassonville et al. 1995) and spatial memory (Baker et al. 2003), extra-retinal input was reported to be taken into consideration for tasks that theoretically may be solved based on retinal input solely. This, however, does not completely exclude a retinal origin of such a roll-angle-dependent modulation (see below). Furthermore, apart from vestibular input,

other extra-retinal sensory signals (e.g., from skin pressure sensors or truncal graviceptors) are likely integrated to solve the paradigms applied in our experiments. However, whether these sensors modulate in terms of variability in the roll plane or not is not known.

Two considerations concerning the retinal projections of the visual line should be discussed: (1) With the line either along the desired whole-body roll-tilted position (paradigm 1) or rolled 75° CCW relative to the body-longitudinal axis (paradigm 2), its torsional orientation relative to the retinal vertical will differ: While the line will be approximately parallel to the retinal vertical in the earth-fixed paradigm, it will deviate CCW relative to the retinal vertical by approximately 75° in the body-fixed paradigm. (2) Head roll leads to compensatory eye torsion in the opposite direction, termed “ocular counterroll” or OCR (Diamond et al. 1982; Collewijn et al. 1985). Thereby, the visual line will not be projected with exactly the same angle on the retina in upright and 75° RED roll orientation. This is true for all three paradigms applied here. Since visual orientation discrimination thresholds depend on the object roll orientation [the “oblique effect” (Appelle 1972)], the increase in turntable adjustment variability could still have a visual origin. However, the gain (eye-roll divided by head roll) of OCR is only about 0.1 (Diamond et al. 1982; Collewijn et al. 1985). So, when roll-tilted 75° RED, a body-fixed visual cue that is offset CCW relative to the body-longitudinal axis by 75° will be projected approximately at 67.5° (75°–7.5°) CCW relative to the retinal vertical. At the same roll-tilt angle, an earth-fixed visual cue that is roll-tilted 75° CW relative to earth-vertical is projected about 7.5° CW relative to the retinal vertical because of OCR. The question is, whether the OCR-related shifts in line roll orientation relative to the retinal vertical and the known retinal anisotropy are sufficient to explain the whole-body roll-angle-dependent modulation of variability in paradigm 1. We do not think that this is the case. First, orientation discrimination thresholds increase from approximately 0.5° (when presenting the visual stimulus along the retinal vertical) to 1.5–2.0° when the visual stimulus is roll-tilted 30° (Orban et al. 1984), while we observed greater variability for the earth-fixed paradigm (~3° in upright position and ~4° in 75° RED). Second, the oblique effect decreases or even disappears when the head is roll-tilted, (Luyat et al. 2001; McIntyre et al. 2001).

Torsional eye position becomes more variable with increasing head roll, and this increase in OCR noise is correlated with the variability of SVV adjustments (Tarnutzer et al. 2009b). However, trial-to-trial variability of alignment tasks increases independently from the presence/absence of retinal input when the subject is roll-tilted (Tarnutzer et al. 2012), so increased variability in our tasks cannot be explained solely on the basis of variability of torsional eye position. At the same time, the oblique effect diminishes

when the head is roll-tilted (Luyat et al. 2001; McIntyre et al. 2001), mostly due to increased discrimination thresholds along the principal axes. Therefore, the accuracy by which the roll orientation of a visual stimulus on the retina can be sensed becomes independent from its retinal roll orientation (in relation to the retinal cardinal axes).

Torsional eye position is not only driven by vestibular (otolith) input, but can also be modulated by visual stimuli. While rotating visual stimuli may induce torsional eye movements (Mezey et al. 2004), the gain of these movements is small (<0.02) and can be discounted as contributing much to our results.

The frame of reference of visual cues affects the variability of self-adjustments

While otolith signals make a significant contribution for computing an internal estimate of the direction of gravity (Tarnutzer et al. 2009a), other sensory signals may become more important in roll-tilted positions where otolith variability increases. The usefulness of a visual cue might affect the variability of self-adjustments, resulting in less trial-to-trial variability when both proprioception and “useful” (i.e., earth-stationary) visual cues contribute to the estimate of earth-vertical. We found body-fixed cues, which are potentially misleading as they suggest stationary conditions when the subject was in fact moving, resulted in more variable self-positioning than earth-station cues. However, this was true only for roll-tilted whole-body orientations when the otolith signal is more variable than in upright position.

Differences in the task complexity may also have influenced the variability. The body-fixed task requires estimates of both the orientation of the visual line relative to the subject’s head and the subject’s head orientation relative to gravity. The earth-fixed paradigm, on the other hand, may be solved successfully based on an estimate of the visual line orientation relative to the subject’s head only. Potentially, the variability from distinct estimates may be additive, which would explain the larger trial-to-trial variability for the body-fixed task found. However, we previously found that an estimate of head orientation relative to gravity is also integrated when solving visual alignment tasks in egocentric frames of reference (Tarnutzer et al. 2012). This would increase the level of variability in the earth-fixed task and makes different levels in task complexity between the body-fixed and the earth-fixed task a less likely explanation for the observed difference in trial-to-trial variability.

Visually guided self-adjustments in the roll plane show an A-effect

Alignments to vertical were more accurate than to roll-tilted positions in all tasks and matches observations from

the classic SPV paradigm obtained in complete darkness (Bisdorff et al. 1996; Anastasopoulos et al. 1997). Whereas perceived horizontal self-adjustments in complete darkness also suggest high accuracy (Mittelstaedt 1983; Mast and Jarchow 1996), our subjects moved the chair to larger roll angles than actually required whenever the desired chair roll angle was 75° RED. These deviations may originate from the same, likely vision-dependent, mechanism that causes the A-effect in the SVV (Aubert 1861; Howard 1982). The similarities between SVV errors and visually guided self-adjustments in the roll plane are illustrated in Fig. 1. Accurate adjustments of the SVV (Fig. 1c) require that the subject compensates for body roll by rotating the line away from the body-longitudinal axis by an angle β equal to the estimated body roll. For a desired whole-body roll angle α of 75° RED, however, systematic roll under-estimation (with $\beta < \alpha$) and therefore roll under-compensation (“A-effect”), resulting in an error δ , has been reported when assessing the SVV (Aubert 1861; Van Beuzekom and Van Gisbergen 2000; Kaptein and Van Gisbergen 2004). For the body-fixed paradigm used here, the constant angle ε between the visual line and the body-longitudinal axis is added to the error δ , which results in a whole-body roll orientation larger than desired. This mechanism would explain why self-adjusted whole-body roll is larger than actually required.

If indeed, the brain is unaware of OCR (Wade and Curthoys 1997), changes in torsional eye position might have also contributed to the errors when roll-tilted. OCR will then cause the retinal projection of the earth-fixed line to fall on an orientation CW relative to the retinal vertical when tilted RED. Self-alignments parallel to the line will therefore cause the subject to roll-tilt too far to the right side. This would be consistent with our data, showing overall slight CW adjustment errors relative to the visual line in the earth-fixed paradigm. In the body-fixed paradigm, OCR would lead to an under-estimation of the angle between the line and the body when roll-tilted. This would predict that subjects move the chair to a smaller roll angle than required to set the line along earth-vertical. However, in our data set, we observed the opposite, speaking against a major contribution of OCR to adjustment errors in the body-fixed paradigm.

Limitations

Difficulties handling the joystick used to rotate the chair and possible discomfort of subjects due to far right-ear down roll-tilted positions might have influenced the variability of adjustments. We studied 12 subjects and found considerable inter-individual variability of adjusted chair roll angles and large trial-to-trial variability within subjects as indicated by the error bars in Figs. 2 and 3. This may have masked more

subtle differences between the two paradigms. There could be a roll-angle-dependent discomfort of subjects making it harder to focus on the task at large roll angles and therefore negatively influencing the variability of chair adjustments.

We frequently observed overshooting during self-adjustments in the range of 1–4°, followed by compensatory movements in the opposite direction. Most likely, overshooting is a result of the acceleration/deceleration of the chair being limited and the subjects not fully compensating for this limit. Since subjects had the time to make corrective movements, however, we do not think this difficulty greatly affected the final errors.

The role of the vestibular organs in self-positioning is still debated. Anastasopoulos et al. (1997) have reported that acute unilateral vestibular loss strongly shifts perceived visual vertical toward the side of the lesion, whereas the subjective postural vertical (SPV) remained veridical, suggesting different weighting of the participating sensory systems for determining the SPV and the SVV. These authors concluded that the SPV is derived from somatosensory input mainly, so that even mild to moderate acute vestibular imbalance does not bias it (Bisdorff et al. 1996; Anastasopoulos et al. 1997, 1999). However, vestibular input does contribute to the percept of body posture along with extra-vestibular truncal graviceptors (Mittelstaedt 1998), and it was shown that otolith input decreases the variability of the SPV (Bisdorff et al. 1996). Taken together, these studies indicate that for self-positioning in space, otolith input is likely integrated, but may play a less prominent role than for the visual vertical. Whether the roll-angle-dependent modulation of variability observed in earth-fixed and body-fixed paradigms is only related to the characteristics of the otolith organs or not remains therefore an open issue. Potentially, other extra-retinal sensors (as the truncal graviceptors or skin pressure sensors) may show a similar roll-angle-dependent modulation of their signal-to-noise ratio and therefore could also contribute to the increase in trial-to-trial variability when roll-tilted.

Dynamic paradigms assessing self-orientation in space may stimulate both rotational (semicircular canals or SCC) and translational (otolithic) vestibular sensors. This raises the question to which extent the self-adjustments were affected by SCC stimulation. Considering that the subject-guided chair repositioning movements yielded frequencies below 0.27 Hz (90 % cutoff) and that the SCC are high-pass filters, we hypothesize that SCC stimulation is minor.

Conclusions

Combining visual orientation cues with self-adjustments in the roll plane allowed accurate and precise movements to

predefined roll-tilted positions. This constitutes a valuable extension of the classic postural vertical or horizontal paradigm without visual cues. We showed that in many aspects, visually guided self-adjustments resemble static SVV adjustments. Specifically, we observed increasing variability in self-adjustments to desired roll-tilted positions both when providing an earth-fixed or a body-fixed visual orientation cue as it has previously been described for the SVV. This suggests that also for self-adjustment tasks, which may theoretically be completed solely based on matching the visual cue orientation with the retinal vertical and the body-longitudinal axis, extra-retinal cues—likely including otolith input—are centrally integrated. For a desired 75° RED roll-tilted position, self-adjustments were significantly more precise in the presence of an earth-fixed visual cue compared to a body-fixed cue. This underlines the importance of earth-stable visual input whenever internal estimates of gravity become more variable.

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