RESEARCH ARTICLE

Antihysteresis of perceived longitudinal body axis during continuous quasi-static whole-body rotation in the earth-vertical roll plane

M. Tatalias · C. J. Bockisch · G. Bertolini · D. Straumann · A. Palla

Abstract Estimation of subjective whole-body tilt in stationary roll positions after rapid rotations shows hysteresis. We asked whether this phenomenon is also present during continuous quasi-static whole-body rotation and whether gravitational cues are a major contributing factor. Using a motorized turntable, 8 healthy subjects were rotated continuously about the earth-horizontal naso-occipital axis (earth-vertical roll plane) and the earth-vertical naso-occipital axis (earth-horizontal roll plane). In both planes, three full constant velocity rotations (2°/s) were completed in clockwise and counterclockwise directions (acceleration = 0.05°/s², velocity plateau reached after 40 s). Subjects adjusted a visual line along the perceived longitudinal body axis (pLBA) every 2 s. pLBA deviation from the longitudinal body axis was plotted as a function of whole-body roll position, and a sine function was fitted. At identical whole-body earth-vertical roll plane positions, pLBA differed depending on whether the position was reached by a rotation from upright or by passing through upside down. After the first 360° rotation, pLBA at upright whole-body position deviated significantly in the direction of rotation relative to pLBA prior to rotation initiation. This deviation remained unchanged after subsequent full rotations. In contrast, earth-horizontal roll plane rotations resulted in similar pLBA before and after each rotation cycle. We conclude that the deviation of pLBA in the direction of rotation during quasi-static earth-vertical roll plane rotations reflects static antihysteresis and might be a consequence of the known static hysteresis of ocular counterroll: a visual line that is perceived that earth-vertical is expected to be antihysteretic, if ocular torsion is hysteretic.

Keywords Spatial orientation · Perceived body orientation · Vestibular · Gravity

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Introduction

In every day life, the brain relies on vestibular (otolith organs and semicircular canals), visual, and somatosensory cues to keep track of the body's orientation in space, which is indispensable for accurate spatial orientation and navigation. It is yet unresolved how these sensory signals are integrated into a percept of body in space. In the absence of vision and with minimal somatosensory cues, systematic errors in the perception of earth-verticality and in the sense of self-tilt become apparent. When subjects are tilted from upright in the earth-vertical roll plane and asked to align a luminous line to the perceived earth-vertical, the line deviates from earth-vertical in the direction of body tilt at whole-body roll angles beyond 60° (A-effect) (Aubert 1861). At smaller roll angles, a line deviation in the opposite direction of body tilt may occur (E-effect) (Mueller 1916; see also Howard 1982, 1986, for review). Interestingly, in the same whole-body roll position, estimation of self-roll is more accurate than estimation of earth-verticality (Mast and Jarchow 1996; Mittelstaedt

1983). If, for example, subjects are asked to verbally report their estimated roll tilt positions, systematic errors are much smaller than if they are asked to estimate earth-verticality (Kaptein and Van Gisbergen 2004; Van Beuzekom and Van Gisbergen 2000; Vingerhoets et al. 2008). This suggests that sensory signals of head and body position relative to gravity are processed differently between estimating self-tilt and estimating earth-verticality.

In a recent attempt to better characterize the perception of whole-body orientation Kaptein and Van Gisbergen (2004), measured self-estimation of body tilt in healthy human subjects who were rotated to various whole-body roll positions over the full range of 360°. These authors found that verbally reported body tilt estimations (using an imaginary clock scale) differed depending on whether identical positions were reached by a "direct" rotation from upright or by an "indirect" rotation in the other direction passing through the upside-down position. Specifically, errors of body roll could be interpreted as underestimations of the previous roll rotation. These errors were most obvious after returning to upright after a full 360° roll rotation: subjects always estimated their final body position as if they were rotated less than 360°. Thus, estimation of body tilt at a given static whole-body position was not unequivocally determined by the whole-body roll position itself but also depended on the direction of the previous whole-body roll rotation. Since Kaptein and Van Gisbergen (2004) used relatively fast velocities (30°/s) to reach static whole-body roll positions, it remains unclear whether the observed effect depended on the history of previous whole-body roll positions or on the velocity of whole-body roll rotation. Conceivably, both factors in combination could play a role.

Recently, we investigated torsional eye position during constant low-velocity quasi-static whole-body roll rotations in healthy human subjects (2°/s) (Palla et al. 2006). After a 360° rotation from the initial upright whole-body position, the eyes did not completely rotate back to their initial torsional position, but settled at a torsional offset position in the direction of the previous counterroll. As in the case of body tilt estimation, there was no unambiguous torsional position of the eyes at a specific whole-body roll position, but rather ocular torsion depended on the direction of body roll rotation performed to reach the current position, reflecting hysteresis.[1] Since, in these experiments, the whole-body roll rotation was performed quasi-statically, i.e., very slowly, it was concluded that the torsional offset of the eyes in the direction of the previous counterroll depended only on the history of previous whole-body roll positions and not on roll velocity or other time-critical

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[1] The term "hysteresis" describes a property of systems whose states depend on their immediate history.

factors. Therefore, the effect was considered to result from a static hysteresis mechanism.

In the current study, we set out to clarify whether observed errors in the estimation of whole-body roll tilt were still present when the estimation depended solely on the history of previous whole-body roll positions. Dynamic influences were excluded by applying very slow, i.e., quasi-static, continuous whole-body roll rotations. Completing three full 360° turntable rotations allowed characterizing the critical parameters of initial and steady state behavior of self-roll estimation. Finally, to delineate the contribution of gravitational cues on perceptive misalignments, we repeated the same experiments with subjects lying in supine position and being rotated about the earth-vertical naso-occipital axis, thereby excluding changes in the gravity vector relative to the head.

Methods

Definitions

Coordinate system

For better visualization of hysteresis effects, we applied an absolute definition of the angle α between the perceived longitudinal body axis (pLBA) and the true longitudinal body axis (LBA). The head-fixed coordinate system is, therefore, independent of the direction of the whole-body roll rotation. If pLBA coincides with the true longitudinal body axis, the angle is zero ($\alpha = 0$). As shown in Fig. 1, the angle becomes positive ($\alpha > 0$) for pLBA tilts toward the right ear (=clockwise from the subject's viewpoint) and negative ($\alpha < 0$) for pLBA tilts toward the left ear (=counterclockwise from the subject's viewpoint).
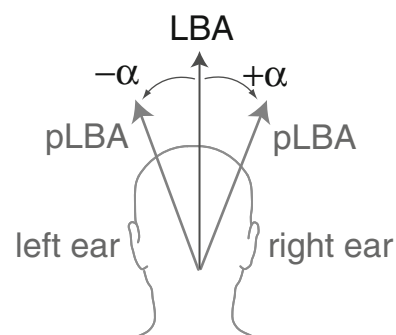

Fig. 1 Definition of the angle α between the perceived longitudinal body axis (*pLBA*) and the true longitudinal body axis (*LBA*). The head-fixed coordinate system is independent of the direction of the whole-body roll rotation: α is positive for pLBA tilts toward the *right ear* (=clockwise from the subject's viewpoint) and negative for pLBA tilts toward the *left ear* (=counterclockwise from the subject's viewpoint)

"Lead" and "lag"

The terms "lead" and "lag" of pLBA are used in a descriptive sense and not in the context of linear operations. "Lead" of pLBA describes a deviation of pLBA from the actual longitudinal body axis in the direction of the whole-body roll rotation. Figure 2 depicts four examples of pLBA settings at identical whole-body roll positions of 120° left ear down. In the left panels (Fig. 2a–c), this body position is reached by counterclockwise (CCW) and in the right panels (Fig. 2b–d) by clockwise (CW) rotations. A positive angle α corresponds to a "lag" of pLBA after a CCW body rotation (Fig. 2a) and to a "lead" of pLBA after a CW body rotation (Fig. 2b). Conversely, a negative angle α corresponds to a "lead" of pLBA after a CCW body rotation (Fig. 2c) and to a "lag" of pLBA after a CW body rotation (Fig. 2d). A "lag" of pLBA during both CW and CCW rotations leads to different angles α at the identical whole-body position (compare Fig. 2a–d). This phenomenon, so-called hysteresis, is a property of systems whose states depend on their immediate history.
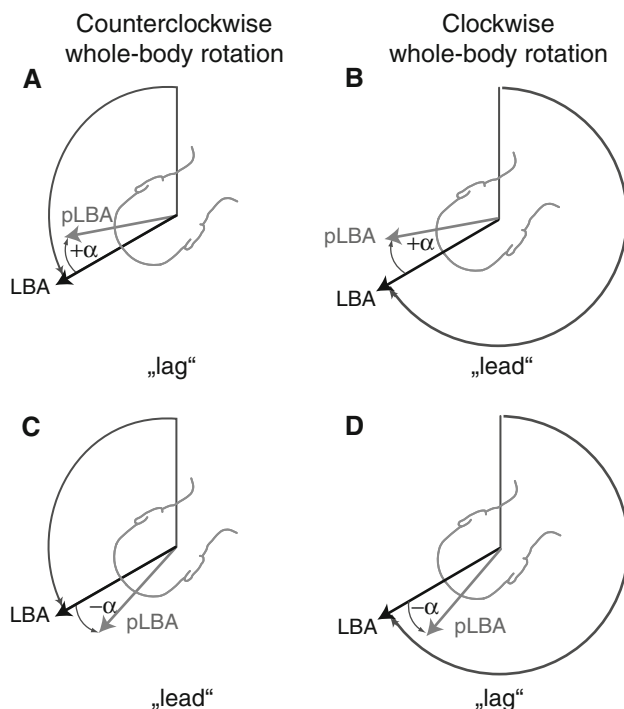
The opposite phenomenon with different angles α at the identical whole-body position (compare Fig. 2b, c), so-called antihysteresis, develops from a "lead" of pLBA during both CW and CCW. To our knowledge, in the field of neurophysiology, the term "antihysteresis" was first used by Collins (1975) to describe the fact that the tension of eye muscles is leading their length during stretching and relaxing. Here, as for the terms "lag" and "lead," we use the term "antihysteresis" in a purely descriptive sense.

Subjects

Eight healthy human subjects (5 women, 3 men; 25–46 years old) participated in this study. Two participants were familiar with the experimental protocol, and six were naïve. Informed consent of all subjects was obtained after full explanation of the experimental procedure.

Experimental set up

Subjects were seated upright on a turntable with three servo-controlled motor-driven axes (prototype built by Acutronic, Jona, Switzerland). An individually molded thermoplastic mask (Sinmed BV, Reeuwijk, the Netherlands) restrained the head. Subjects were positioned so that the intersection of the interaural and naso-occipital axes was at the intersection of the three axes of the turntable. For rotations along the earth-horizontal naso-occipital axis (earth-vertical roll plane rotations), a chair-fixed laser projected a line with an arrowhead (length: 500 mm; width: 3 mm) onto the center of a sphere (1.5 m in front of the subject) in otherwise complete darkness. For rotations along the earth-vertical naso-occipital axis (earth-horizontal roll plane rotations), the chair-fixed laser projected a luminous line with an arrowhead (length: 220 mm; width: 3 mm) onto the center of a screen located 0.65 m away from the subject. For both earth-horizontal and earth-vertical roll plane rotations, the center of the luminous line was straight ahead from the subject's eyes. Chair position and line orientation signals were digitized at 200 Hz per channel with 16-bit resolution and stored on a computer hard disk for off-line processing.

Estimation of body position in space during quasi-static roll rotations was assessed by letting subjects repeatedly set a luminous line in otherwise complete darkness along the pLBA. Other authors have used verbal reports by the subjects (Kaptein and Van Gisbergen 2004; Van Beuzekom and Van Gisbergen 2000; Vingerhoets et al. 2008). In our study, we opted to apply the visual method because we expected direction-specific effects of quasi-static whole-body rotation to be small. Using verbal reports was not an option, as Van Beuzekom and Van Gisbergen (2000) had noted remarkably large random errors with this method,

Fig. 2 Examples of perceived longitudinal body axis (*pLBA*) deviations with the subject in rear view. The angle α in these examples corresponds to a "*lag*" of pLBA, equivalent to an underestimation of the true longitudinal body axis (*LBA*) when reached by a CCW whole-body roll rotation (**a**) and equivalent to an overestimation of LBA when reached by a CW whole-body roll rotation (**d**). Conversely, α corresponds to a "*lead*" of pLBA, equivalent to an underestimation of LBA when reached by a CW whole-body roll rotation (**b**) and to an overestimation of LBA when reached by a CCW whole-body roll rotation (**c**)

particularly for small whole-body tilts. It needs to be stressed, however, that the visual method is different from the verbal method, because the orientation of the projected luminous line on the retina can influence torsional eye position and the perception of body orientation in space (Curthoys 1996; Mezey et al. 2004; Pavlou et al. 2003; Wade and Curthoys 1997). We also considered letting subjects manually align a bar with pLBA in total darkness. Yet this somatosensory method is less accurate than the visual method and shows already in upright position a large intra-individual variability for setting the bar earth-vertical (Bauermeister 1964; Kerkhoff 1999; Lejeune et al. 2009).

Experiments

Starting either from the upright position or from the supine position, subjects were rotated in the earth-vertical roll or earth-horizontal roll plane CW (negative direction of turntable rotation) or CCW (positive direction of turntable rotation), respectively, at a constant angular velocity of 2°/s. CW and CCW were defined from the subject's viewpoint. The velocity plateau of the turntable was reached with an acceleration of $0.05°/s^2$, which is below the detection threshold of the semicircular canals (Diamond et al. 1982; Shimazu and Precht 1965). On the turntable, a total of three consecutive 360° rotations and an additional 40° rotation were performed in both directions (i.e., a total of 1,120° CW and CCW rotation). Subjects were instructed to rapidly (duration ≤ 2 s) adjust the orientation of the luminous line, with its arrowhead pointing in the direction of the subject's head, along their pLBA, while the turntable was rotated at constant angular velocity. Visual line adjustments were made by turning a knob placed on a remote control box in front of the subjects. A button near the knob was used to confirm completion of each adjustment. Then, the orientation of the luminous line was pseudorandomly offset either CW or CCW (random offset range: 0–360°; time interval for offsetting the line until its new appearance: 2 s).

Data analysis

Chair and visual line signals were processed with interactive programs written in MATLAB (MathWorks, Natick, MA). Angle α, i.e., the angle between the pLBA and the true longitudinal body axis (LBA), was plotted as a function of CW and CCW whole-body position in the earth-vertical or earth-horizontal roll planes, respectively.

pLBA settings were first investigated for normal distribution with Kolmogorov–Smirnov statistics. To describe the influence of consecutive whole-body roll cycles, ANOVA for repeated measures and post hoc Holm–Sidak test for multiple comparisons were performed on angle α

for whole-body positions within + 15° from upright (i.e., [0° 15°], [360° 375°], [720° 735°], [1,080° 1,095°]) turntable positions. Statistics were computed with SPSS software (SPSS, Chicago, IL). Angle α as a function of turntable position was fitted by the following sine function to each rotation cycle separately:

$$y = A \times \sin(\omega t + \varphi) + c$$

where A is the amplitude, ω the frequency, φ the phase, and c the offset. The variables A, φ, and c were optimized by iteratively finding the best curve using non-linear least square fitting (Matlab function: lsqcurvefit.m). Directional effects of body rotation were investigated by determining at identical whole-body roll positions the differences between angles α during CW and CCW rotations. Data from each rotation cycle were fitted by the sine function as described earlier. To compute the 95% confidence interval of the curves (for purposes of investigating the effect of rotational direction), bootstrapping was used: 1,000 random samples with replacement from the original data set were fitted to the sine functions. The Wilcoxon rank-sum test was used to investigate differences of the angle α between CW and CWW whole-body rotations at identical turntable positions.

Results

First, we explored whether the direction and magnitude of perceived longitudinal body axis (pLBA) estimates were influenced by the initial orientation of the luminous line, which was pseudorandomly offset every ≤4 s in either clockwise (CW) or counterclockwise (CCW) rotations before subjects adjusted the line (see "Methods"). In no subject, we found a correlation between initial and final line orientations, as determined by linear regression for both rotation directions ($R^2 < 0.001$; $P > 0.1$).

In a next step, we investigated the relation between the angle α, i.e., the angle between pLBA and the true longitudinal body axis (LBA), and the whole-body roll position. Figure 3 depicts data from a typical subject (M.B.; upper two panels) and from all eight subjects (lower two panels). Note again that angle α is defined in a head-fixed coordinate system with α > 0 for pLBA tilts toward the right ear (see "Methods"). Starting from the position with the body upright, the turntable performed three complete quasi-static (2°/s) continuous whole-body rotations about the earth-horizontal naso-occipital axis (earth-vertical roll plane rotations). The three consecutive rotations were applied CW and CCW in a pseudorandom order. For both CW and CCW turntable rotations, a periodic pattern of angle α with an initial gradual increase and consecutive gradual decrease during each hemicycle was observed over all
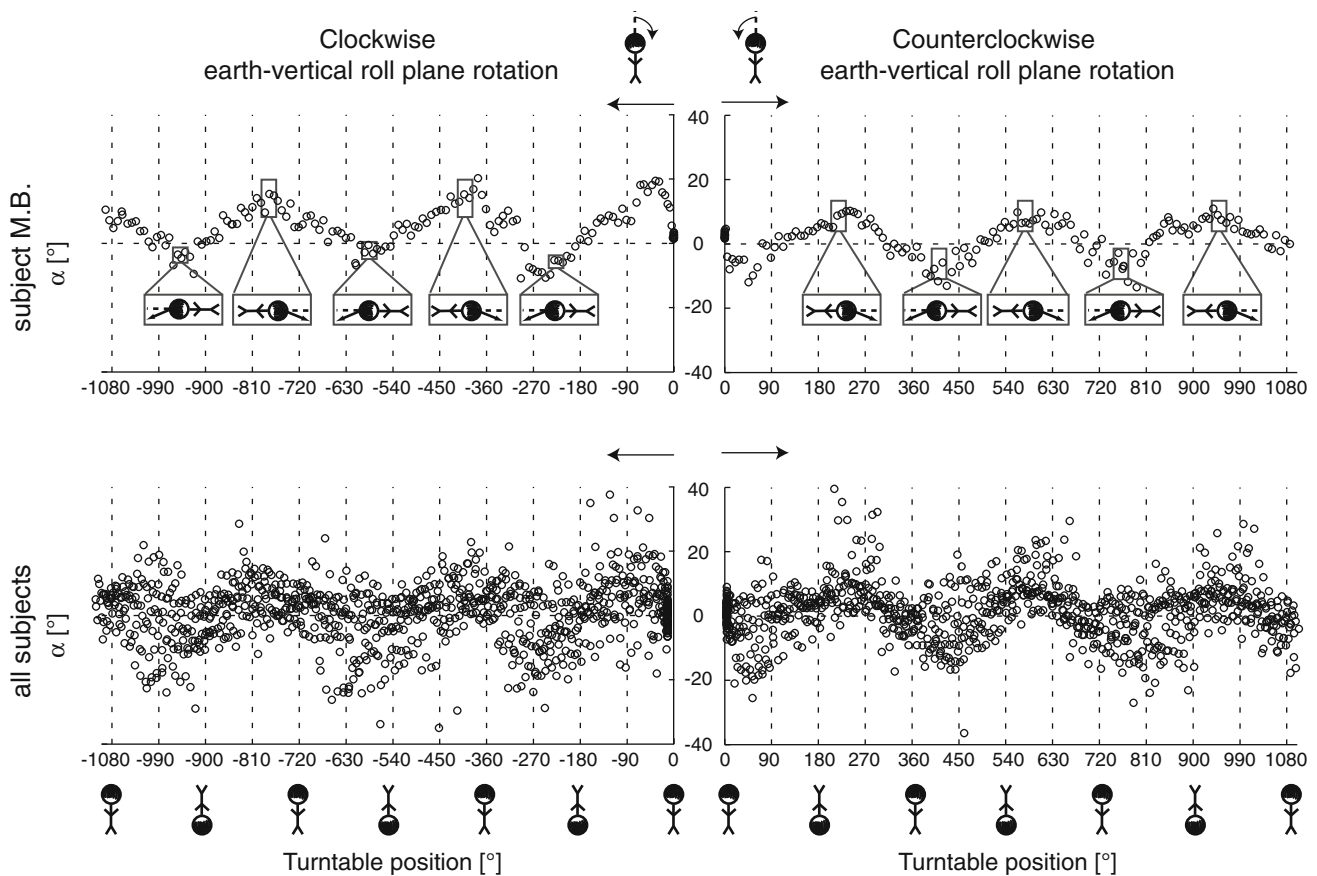
Fig. 3 Typical examples of adjustments of a *luminous line* along the perceived body longitudinal axis (*pLBA*) plotted as a function of whole-body position in a subject (*upper two panels*) and in all eight subjects (*lower two panels*). Positive α values, i.e., the angle between pLBA and the true longitudinal body axis (*LBA*), during CW turntable rotations correspond to CW pLBA deviations from actual whole-body roll positions and negative α values for CCW turntable rotations correspond to CCW pLBA deviations from actual whole-body roll positions (see Fig. 1 for definition)

three rotations. On average, peak values of angle α scattered around ±40°.

We then compared the angle α between CW and CWW whole-body rotations at identical turntable positions. Figure 4 illustrates box plots from all eight subjects during CW and CWW rotations. Since visual line adjustments occurred within a certain time interval (≤4 s) during constant velocity roll rotations and not at a defined whole-body tilt position, average α was computed from data points recorded within positional intervals of 15° (i.e., responses occurring within [0° 15°], [15° 30°], etc). By this procedure, two estimates of the angle α within the positional intervals were averaged for each subject. Figure 4 demonstrates that, at the beginning of the second and third body rotation, angle α was tilted in the direction of turntable rotation; in other words, pLBA was "leading" the true longitudinal body axis (LBA).

Figure 5 quantifies the effect of consecutive whole-body rotations on angle α in all eight subjects. In every subject, pLBA settings around upright (interval: + 15°) were selected and corresponding angles α were averaged for the

upright position before rotation and upright positions after the first, second, and third CW and CCW rotation cycles (open circles). Data points during CCW rotations were multiplied by (−1) to allow pooling. Therefore, positive values of angle α in this plot indicate a "lead" of pLBA for both CW and CCW rotations. Clearly, after the first full rotation, pLBA was "leading" in all subjects. This "lead" persisted after the two consecutive rotation cycles (average angle α ± 1SD: prior to rotation: $-0.4° \pm 2.2°$; after 1 cycle: $3.5° \pm 4.4°$; after 2 cycle: $4.3° \pm 4.1°$; after 3 cycle: $3.5° \pm 4.5°$). The impact of each rotation cycle on angle α in upright whole-body position was statistically analyzed by ANOVA for repeated measures with cycle as factor. Data points before the beginning of rotation were assigned to the zero cycle. A significant main effect of rotation cycle was found ($F(4) = 6.18$; $P < 0.01$). Post hoc Holm–Sidak test for multiple comparisons revealed that α was not significantly different after the first, second, and third roll rotation cycles ($P > 0.5$), but differed significantly from α prior to the initiation of whole-body roll (pairwise comparisons between prior and after first rotation cycle:

Fig. 4 *Box plots* of averages of angle α within intervals of 15° of turntable roll displacements plotted as a function of whole-body positions. Note the "*lead*" of perceived body longitudinal axis (*pLBA*) at upright whole-body positions emerging after the first rotation cycle
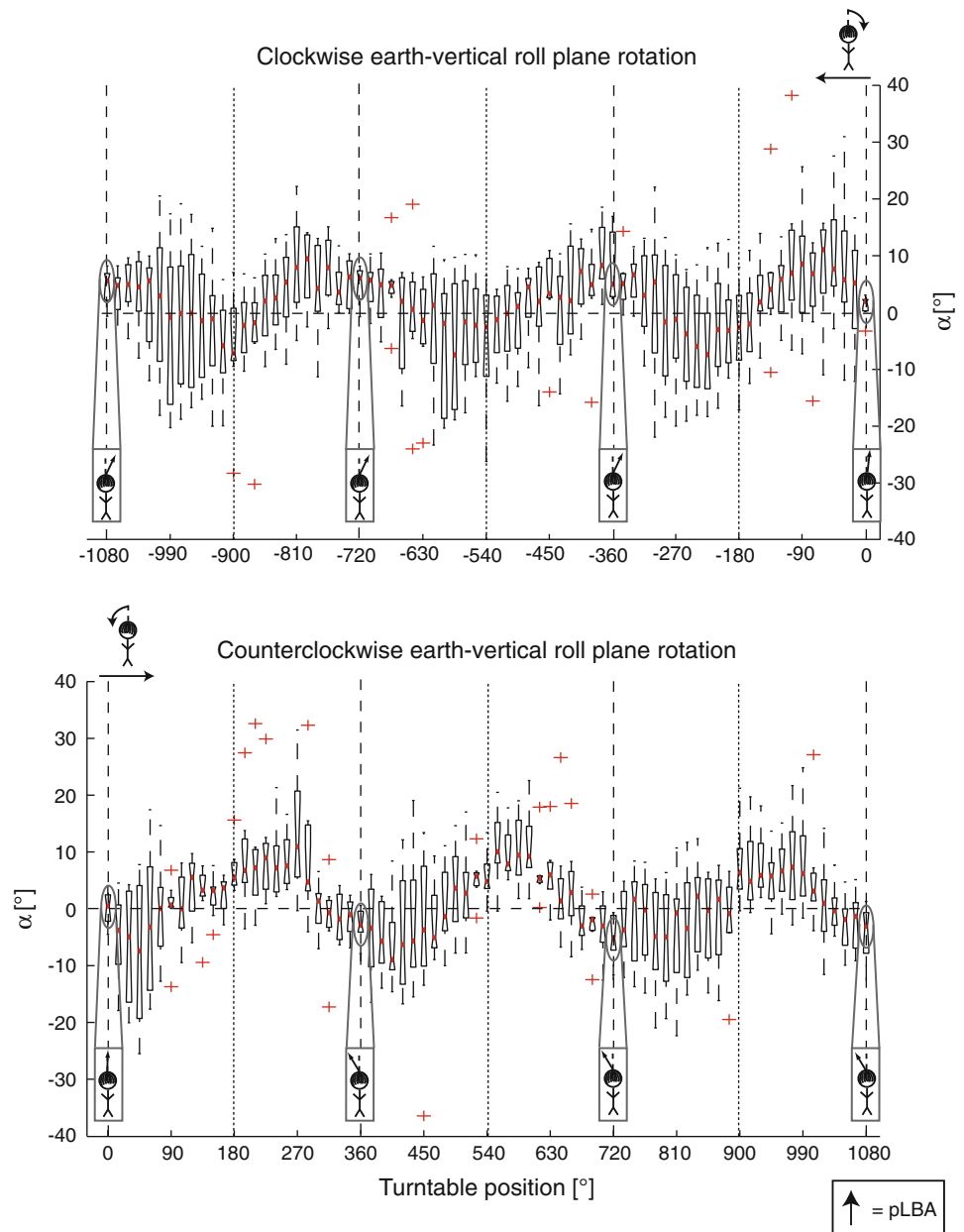
Thus, when the first 360° roll rotation was completed, pLBA in upright position deviated in the direction of turntable rotation. This "lead" of pLBA was unchanged after the consecutive rotation cycles.

Next, the influence of rotation direction on pLBA was investigated. Figure 6 provides enlarged views of the box plots during the first CW and CCW rotations (taken from Fig. 4). In general, at identical whole-body roll positions, angle α differed between the two directions of rotation. A Wilcoxon rank-sum test on the angle α between CW and CWW whole-body rotations at identical turntable positions revealed significant differences in the majority of tilt positions.

To further quantify the effect of rotation direction on pLBA, we subtracted the data of CCW cycles from the data of CW cycles. A first harmonic sinusoidal function was fitted to these differences of angle α for each of the three whole-body roll cycles separately. As shown in Fig. 7, the minimum of all three curves was around the head-down position (cycle 1: 184°; cycle 2: 167°; cycle 3: 168°), which indicates the symmetry of the phase lead. For better comparison, sinusoidal fits of all three rotation cycles are plotted in the lowest subpanel of Fig. 7. Tables 1, 2 shows gains and phases of sine fits.
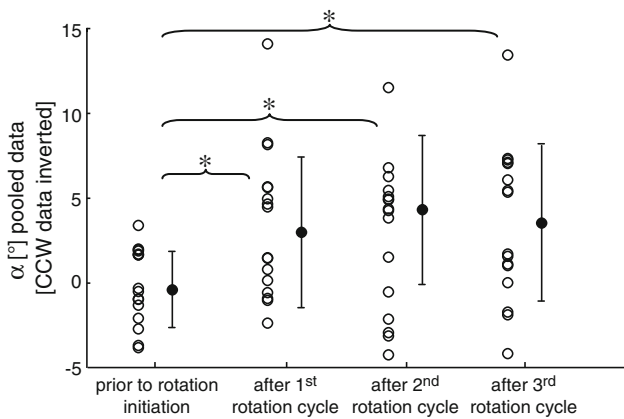
Fig. 5 Values of α in upright whole-body positions after the first, second, and third whole-body roll rotations in all 8 subjects. Data points of CW and CCW rotations are pooled. To allow pooling, data points of CCW rotations are inverted (i.e., multiplied by −1). On the right of each population of data points, average values ± 1SD (symbols with *error bars*) are plotted. Note the significant differences of α after the first, second, and third rotation cycles compared with prior to rotation initiation (*$P < 0.04$). Positive values of angle α in this plot correspond to a "*lead*" of perceived body longitudinal axis

The modulation of angle α CW/CCW differences is consistent with a "lead" of pLBA as a function of whole-body roll position, as schematically explained in Fig. 8. While a "lag" produces a maximum around the upside-down (180°) position, a "lead" results in a minimum at this position. Note that Fig. 8 depicts a general picture arising from the data, but is not meant to suggest that the phases of the sinusoidal functions fitted to pLBA CW/CCW differences are significantly different from zero. In fact, the apparent phase differences did not reach significance in our population of 8 subjects (see Tables 1, 2 for values of gains and phases of sine fits during the three rotation cycles (A) as well as gains and phases of sinusoidal functions fitted to CW/CCW differences (B)).

The contribution of gravitational cues on pLBA was examined by repeating the same experiments but with subjects continuously rotated with the same velocity about the earth-vertical naso-occipital axis (earth-horizontal roll plane). Figure 9 shows the results of all subjects. No periodic pattern was observed, and pLBA adjustments were more accurate (angle α < 10°) than during rotations along the earth-vertical roll plane. Interestingly, α was, in general, positive over all cycles, i.e., tilted in CW direction from the whole-body longitudinal axis independent of the turntable rotation.

Discussion

We investigated the perceived direction of longitudinal body axis (pLBA) in space in eight healthy human subjects.
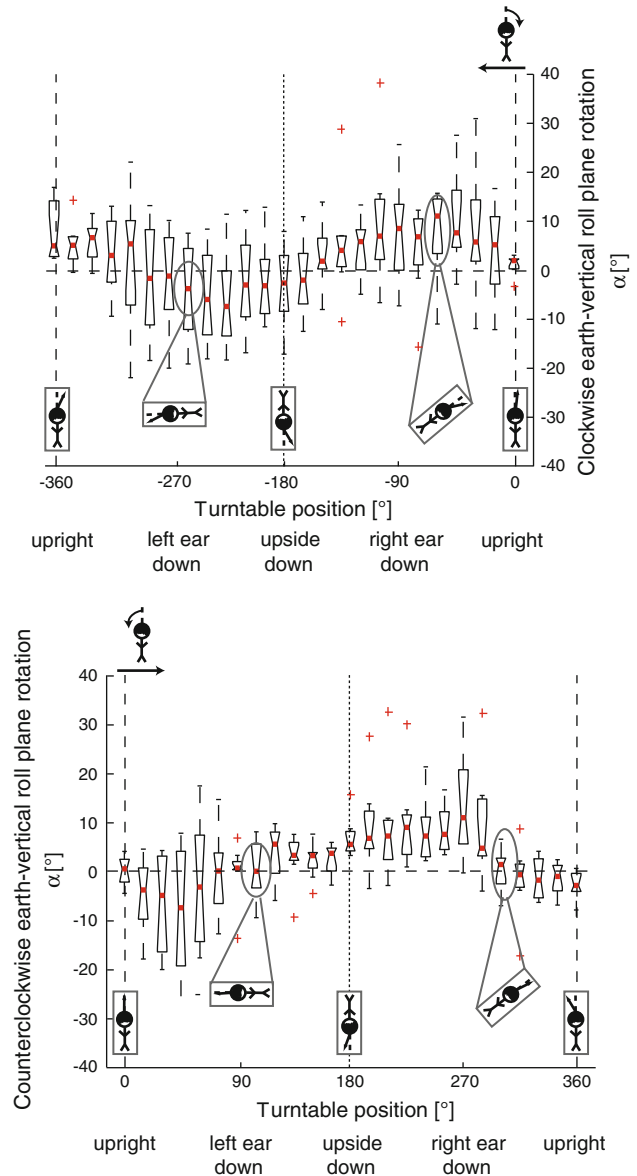

Fig. 6 *Box plots* of averages of angle α within intervals of 15° of turntable roll displacements plotted as a function of whole-body positions during the first CW and CCW rotation cycle (enlarged view taken from Fig. 4). Note that at identical whole-body roll positions, angle α differs between CW and CCW rotation directions

Constant low-velocity quasi-static whole-body rotations (2°/s, 0.05°/s²) were applied about the earth-horizontal naso-occipital axis, i.e., in the earth-vertical roll plane, and about the earth-vertical naso-occipital axis, i.e., in the earth-horizontal roll plane. We found that in the majority of whole-body earth-vertical roll plane positions, the angle α between pLBA and the true longitudinal body axis (LBA) differed depending on whether a body position was reached by passing through upside down or by "direct" rotation from upright. The pattern of pLBA deviation from LBA during both CW and CCW rotations was consistent with a
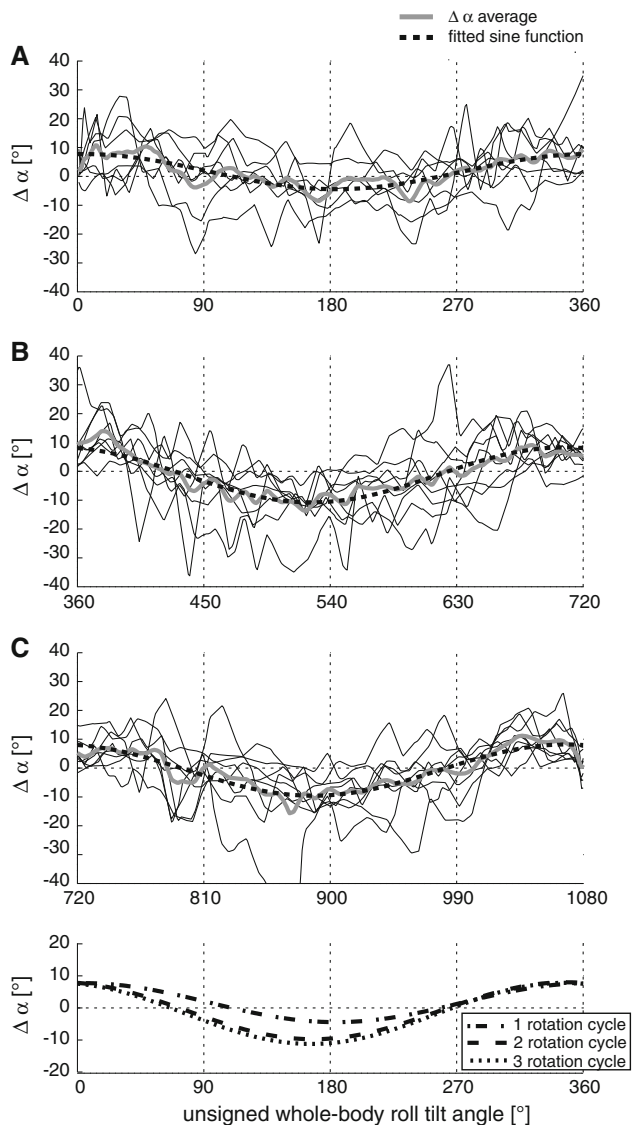
Fig. 7 Differences of angle α at identical whole-body roll tilt angles between CW and CCW rotations plotted as a function of whole-body position (Δ α). For example, Δ α at 270° is obtained by subtraction of α at a 270° whole-body roll tilt position reached by a CCW rotation from α at a 270° whole-body roll tilt position reached by a CW rotation. Separate analysis of first (**a**), second (**b**), and third (**c**) rotation cycles. *Black lines* responses of individual subjects; thick *gray line* average of Δ α responses over all 8 subjects; *dashed black line* sine function fitted to Δ α responses. For comparison, sine function fitted to Δ α responses of first, second, and third rotation cycles (*black lines*) are also shown in (**d**). The sine modulation of Δ α demonstrates a "*lead*" of perceived body longitudinal axis (*pLBA*) modulation during CW and CCW rotations; if pLBA responses would have been similar for CW and CCW roll rotations, Δ α would have scattered around *zero horizontal axes*

"lead" of pLBA as a function of whole-body roll position. After the first full earth-vertical roll plane rotation cycle, this pLBA differed significantly from pLBA in upright position before the beginning of rotation but, however, was unchanged after the consecutive rotation cycles, i.e., the

Table 1 Values of sinusoidal functions fitted to angle α during each rotation cycle

Rotation	Cycle 1	Cycle 2	Cycle 3	P-values
Phases				
CW	0.5 ± 0.9	2.1 ± 4.9	0.3 ± 2.1	0.5
CCW	−0.5 ± 0.8	−1.1 ± 3.5	−1.1 ± 1.7	0.7
Gains				
CW	7.1 ± 6.6	5.5 ± 6.0	5.9 ± 5.9	0.7
CCW	6.2 ± 6.7	8.4 ± 4.2	6.1 ± 7.6	0.8
Offsets				
CW	2.4 ± 5.9	0.7 ± 5.3	1.6 ± 5.8	0.6
CCW	1.1 ± 3.8	1.8 ± 3.5	2.3 ± 3.8	0.6

Values represent average ± 1SD. *P*-values are obtained by one-way factor within subjects' analysis of variance (ANOVA). *CW* clockwise rotation, *CCW* counterclockwise rotation

Table 2 Gains and phases of sinusoidal functions fitted to CW/CCW differences of angle α during each rotation cycle

	Cycle 1	Cycle 2	Cycle 3
Gain	6.1 [CI(−1, 6)]	9.5 [CI(−3, 22)]	−8.8 [CI(−25, 8)]
Phase	1.5 [CI(−10, 13)]	8.0 [CI(−1, 17)]	−1.3 [CI(−9, 7)]

Values represent best fitting parameters from sinusoidal functions fitted to angle α over all subjects; 95% confidence intervals are obtained by bootstrap method

"lead" of pLBA developed during the first cycle of whole-body roll. During rotations about the earth-horizontal roll plane, pLBA was similar at identical whole-body roll positions, i.e., independent on whether the positions were reached by a CW or CCW rotation and independent of the rotation cycle.

The "lead" of pLBA at upright whole-body position emerging after the first earth-vertical roll plane rotation cannot be explained by dynamic factors because the acceleration level used in our study ($0.05°/s^2$) was below the threshold of the semicircular canals (SCC), and the subsequent velocity plateau was low (2°/s), i.e., quasi-static. It rather implies static antihysteresis (see "Methods" for "Definition") of the perceptual error and is the opposite of the static hysteresis, i.e., the non-dynamic lagging effect found for ocular counterroll (Palla et al. 2006). An obvious mechanism for the antihysteretic behavior of pLBA is suggested by the inverse relation between pLBA and ocular counterroll: if ocular counterroll is "lagging," a luminous line perceived as earth-vertical will be "leading" whole-body roll rotation as a consequence of ocular optics (see Fig. 10 for explanation).

As depicted in Fig. 11, static hysteresis of ocular torsion during quasi-static whole-body rotations recorded in an earlier study (Palla et al. 2006) mirrors the static antihysteresis effect of pLBA at upright whole-body positions

Fig. 8 Schematic explanation of Fig. 7. Two *sinusoidal curves* representing angle α responses are plotted for CW or CCW roll rotations. Sinusoides are either shifted by a phase *lag* (**a**) or by a phase *lead* (**b**), which results in curves representing the difference between settings during CW and CCW rotations (**c**, **d**). The modulation of α CW/CCW differences in Fig. 7 resembles subpanel **d**
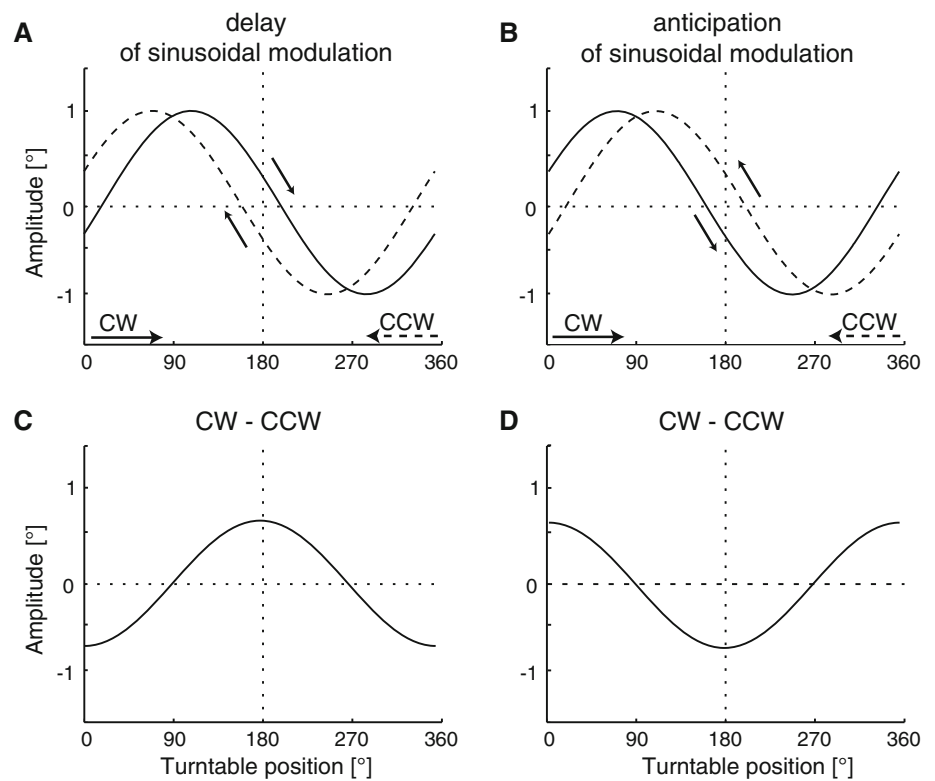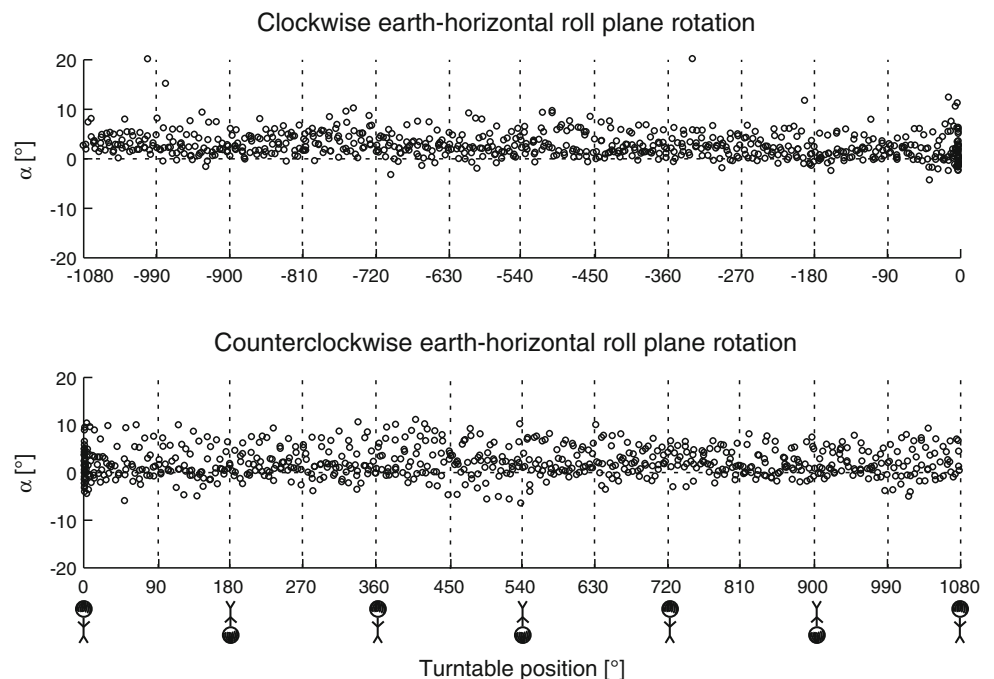
Fig. 9 α plotted as a function of whole-body position in all eight subjects for CW and CCW *turntable* rotations along the earth-horizontal roll plane (*supine position*). Note the lack of periodic modulation observed for roll plane rotations and the generally positive deviations of α

after the first, second, and third full rotation cycles. We think that this reverse relation between torsional eye position and pLBA could be causal. As previously reported, ocular torsion induces changes in visual line settings and thus influences the perceived visual line orientation (Curthoys 1996; Mezey et al. 2004; Pavlou et al. 2003; Wade and Curthoys 1997). Wade and Curthoys (1997), showed a close relationship between the magnitude of a visual line deviation from the gravitational horizontal and the magnitude of ocular torsion during yaw axis rotations. The visual line deviation closely followed ocular torsion up to about 6°, which is approximately the maximal torsional position the eyes can reach statically. Moreover, during earth-vertical eccentric yaw axis rotations, Pavlou et al.
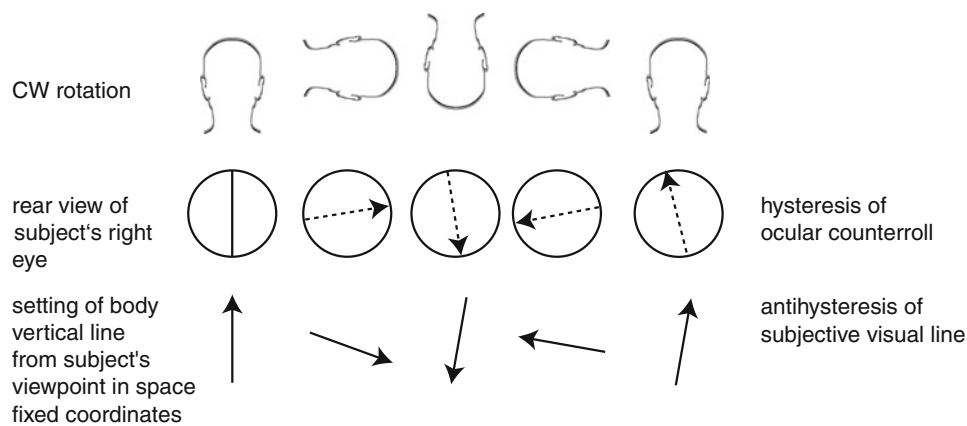
Fig. 10 Schematic explanation of perceived body longitudinal (*pLBA*) if ocular counterroll influences the setting of the *luminous line*. After a 360° quasi-static whole-body roll rotation, the eyes do not completely *rotate back* to the initial torsional position, but settled at a torsional offset position in the direction of the previous counterroll explained by static hysteresis. If ocular counterroll determines the setting of the luminous line, pLBA appears to "*lead*" quasi-static whole-body roll rotation, i.e., reflecting static antihysteresis properties
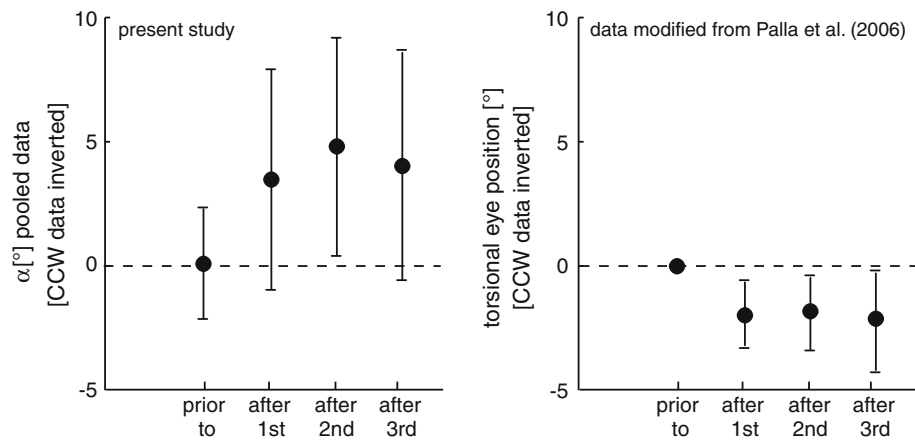

Fig. 11 Comparison of angle α and ocular torsion in response to quasi-static whole-body roll rotation. *Left panel* α values (average ± 1SD) in upright whole-body positions after the first, second, and third whole-body roll rotations for CW and CCW rotation directions. Note that for comparison with ocular torsion (in contrast to Fig. 5), an offset, i.e., angle α prior to rotation initiation, is subtracted from all angles α. *Right panel* pooled data (average ± 1SD) of ocular torsion for right and left eye as well as for CW and CCW directions (detailed data in Palla et al. 2006, Fig. 3). As for angle α, ocular torsion at upright whole-body position during CCW rotations was inverted to allow pooling. Negative torsional values correspond to a "*lag*" of ocular torsion, while positive values correspond to a "*lead*", respectively

(2003) demonstrated that the mean deviation of a visual line from earth-vertical was 76% of the torsional eye position change. Therefore, at whole-body roll positions from upright, setting a luminous line to the longitudinal body axis may be influenced by ocular counterroll.

In our experiments, static antihysteresis of pLBA was not only evident in upright whole-body roll positions but also over the course of whole-body roll cycles. pLBA deviations from LBA at identical whole-body roll positions differed depending on the rotation direction with the largest CW/CCW divergence around upside-down positions. Such modulation of pLBA CW/CCW difference is consistent with a symmetric "lead" of pLBA during CW and CCW

rotations in the earth-vertical roll plane (see Fig. 8). The fact that the phases of the sinusoidal functions fitted to pLBA CW/CCW differences did not significantly differ from zero could be due to the relatively small number of tested subjects. Alternatively, it might suggest that pLBA antihysteresis was confounded by other factors dominating body tilt estimations during non-upright whole-body positions, such as vestibular and proprioceptive cues (Anastasopoulos et al. 1997; Bisdorff et al. 1996; Bronstein 1999) as well as higher cortical mechanisms that integrate visual, vestibular, and proprioceptive inputs (Angelaki and Cullen 2008; Brandt 1997; Brandt and Dieterich 1999). In particular, proprioceptive sensory signals (e.g., truncal

somatosensors, skin pressure sensors, muscle and joint proprioceptors, and kidney and vessel-wall graviceptors) seem to critically contribute to the percept of body orientation in non-upright whole-body positions (Mittelstaedt 1995, 1998). Based on the recent observation of an improved sense of body tilt during active versus passive body tilts, i.e., in the presence of increased proprioceptive cues but unchanged effects on visual line settings to the direction of gravity, Van Beuzekom et al. (2001) proposed a model in which the selective improvement of self-tilt estimation depended mainly on the presence of non-vestibular cues. We emphasize, however, that neither proprioceptive nor vestibular cues are able to explain the "lead" modulation in our data, since, when using verbal reports to perceive body orientation in space, i.e., by only relying on vestibular and proprioceptive cues, estimations of body tilt "lag" the actual whole-body positions (for review see Van Beuzekom and Van Gisbergen 2000). At this point, we must also stress the caveat that we can only hypothesize an inverse relation between pLBA and ocular counterroll since ocular torsion was not measured in the present study. Moreover, this hypothesis is based on findings from Palla et al. (2006), in which subjects had to fix a laser dot and not to a luminous line. As already stated earlier, the orientation of a luminous line can influence torsional eye position and therefore possibly could have an additional impact on the perception of body orientation in space.

To determine the contribution of gravitational cues on pLBA, we repeated the same experiment with the turntable rotating along the earth-horizontal roll plane (supine position). pLBA responses lacked the periodic modulation found during earth-vertical roll plane rotations. This confirms that gravitational cues, indeed, are indirectly (via static ocular counterroll hysteresis) responsible for the antihysteresis property of pLBA. An unexpected finding was that the visual line setting to the body longitudinal in supine position predominantly deviated clockwise from the whole-body longitudinal axis orientation during both CW and CCW turntable rotations (see Fig. 9). In a recent study from Ceyte et al. (2007) on the role of gravity-based information of perceived body longitudinal, healthy subjects adjusted a visual line on average toward the right of their veridical body longitudinal when lying in supine. Although the authors did not find a significant difference in longitudinal body axis estimation between supine and upright whole-body positions, their results support our finding. We can only speculate about the origin of this observed effect. Could it reflect a perceptual shift of the subjective body longitudinal, i.e., a rightward shift of one's own (egocentric) frame of reference when otolithic cues are minimized? Other authors have shown that the subjective position of the body midline is influenced by gravitational changes (see Carriot et al. 2008 for review).

On the other hand, we cannot exclude that the observed CW bias is the result of the experimental paradigms itself, because all of our subjects adjusted the knob, which controlled the visual line, with their right hand. In their report, Ceyte et al. (2007) did not specify by which hand their healthy subjects operated the joystick that modified the orientation of a luminous rod. Future studies should clarify the origin of this issue.

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