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How do visual and postural cues combine for self-tilt perception during slow pitch rotations?

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ABSTRACT

Self-orientation perception relies on the integration of multiple sensory inputs which convey spatially-related visual and postural cues. In the present study, an experimental set-up was used to tilt the body and/or the visual scene to investigate how these postural and visual cues are integrated for self-tilt perception (the subjective sensation of being tilted). Participants were required to repeatedly rate a confidence level for self-tilt perception during slow ($0.05°\cdot s^{-1}$) body and/or visual scene pitch tilts up to 19° relative to vertical. Concurrently, subjects also had to perform arm reaching movements toward a body-fixed target at certain specific angles of tilt. While performance of a concurrent motor task did not influence the main perceptual task, self-tilt detection did vary according to the visuo-postural stimuli. Slow forward or backward tilts of the visual scene alone did not induce a marked sensation of self-tilt contrary to actual body tilt. However, combined body and visual scene tilt influenced self-tilt perception more strongly, although this effect was dependent on the direction of visual scene tilt: only a forward visual scene tilt combined with a forward body tilt facilitated self-tilt detection. In such a case, visual scene tilt did not seem to induce vection but rather may have produced a deviation of the perceived orientation of the longitudinal body axis in the forward direction, which may have lowered the self-tilt detection threshold during actual forward body tilt.

1. Introduction

A considerable amount of work regarding spatial orientation has focused on the way visual and postural cues (e.g., vestibular and somatosensory cues) are integrated to produce stable and uniform self-orientation perception (for reviews see Carriot, DiZio, & Nougier, 2008; Harris, Jenkin, Dyde, & Jenkin, 2011; Howard, 1982). For instance, this has already been studied by exposing observers to static disruptions between body and/or visual scene tilts (e.g., DiLorenzo & Rock, 1982; Fouque, Bardy, Stoffregen, & Bootsma, 1999; Mars, Vercher, & Blouin, 2004). A remaining question is what would occur in the case of very slow tilts executed below the threshold for semicircular canal stimulation (Benson, 1990; Goldberg & Fernández, 1977), particularly with regard to updating spatial cues. In the present study, the way such slow tilts of the body and/or a visual scene specifically influence self-tilt perception was investigated. It was also tested whether a concurrent motor task, performed at specific angles during these slow rotations, would facilitate self-tilt detection.

With regard to the influence of visual cues, spatial estimates have been found to be modulated by static or dynamic changes of visual scene orientation, notably for self-orientation perception (for a review see Howard, 1982). On the one hand, consistently rotating a visual background triggers an optic flow that can be perceived as actual self-motion in the opposite direction (i.e., vection; Dichgans & Brandt, 1978; Fischer & Kornmüller, 1930). For instance, rightward rotation of a fully furnished room consistently produces a compelling illusion of leftward self-motion (the 'tumbling illusion'; Allison, Howard, & Zacher, 1999; Howard & Childerson, 1994). On the other hand, static tilt of the visual scene has also been found to influence many spatial orientation tasks such as positioning the body or the head to vertical (Cian, Esquivié, Barraud, & Raphel, 1995; Ebenholtz & Benzschawel, 1977; Sigman, Goodenough, & Flannagan, 1979), aligning a rod along the longitudinal body axis (i.e., apparent median plane; Li, Dallal, & Matin, 2001; Sigman et al., 1979), or verbally estimating body tilt magnitude (Goodenough, Oltman, Sigman, & Cox, 1981; Sigman, Goodenough, & Flannagan, 1978). In roll for instance, the apparent median plane is deviated by a few degrees in the direction of the visual frame (Sigman et al., 1979).

With regard to the influence of postural cues, numerous studies have investigated how body tilt itself can modify self-orientation perception. However, the findings have been rather contradictory (Bauermeister,

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1964; Carriot, Barraud, Nougier, & Cian, 2006; Ceyte, Cian, Nougier, Olivier, & Trousselard, 2007; Ebenholtz, 1970; Fouque et al., 1999; Mast & Jarchow, 1996). For instance, Fouque et al. (1999) found that pitch body tilt induced a substantial bias in the direction of body tilt for estimation of egocentric eye level (i.e., the plane parallel to the transverse plane of the head, called Head Referenced Eye Level; Stoper & Cohen, 1989), while Carriot et al. (2006) did not. This apparent discrepancy may be related to different tilt kinematics, as it is known that the stimulus dynamics leading to a given static tilt can have important consequences on subsequent spatial judgements (Vingerhoets, Medendorp, & Gisbergen, 2008). Several studies also reported that subjects were quite accurate when they had to verbally indicate self-orientation during roll body rotation with acceleration profiles higher than the threshold for semicircular canal stimulation (0.7 to $3°\cdot s^{-2}$; Groen, Howard, & Cheung, 1999; Groen, Jenkin, & Howard, 2002). However, slow body rotations with extremely low acceleration levels produced large misperceptions of body orientation in space (Bourdin et al., 2001; Bringoux, Nougier, Barraud, Marin, & Raphel, 2003; Teasdale et al., 1999; Trousselard, Barraud, Nougier, Raphel, & Cian, 2004). For instance, slow passive pitch body tilts executed at a constant velocity of $0.05°\cdot s^{-1}$ and preceded by an acceleration of $0.005°\cdot s^{-2}$ were not detected below 8° (Bringoux et al., 2003).

With regard to the combined influence of postural and visual cues, the available data mainly concerns judgments performed under static conditions, i.e., when facing a static tilted visual scene and/or long after the body tilt was achieved (e.g., Goodenough et al., 1981; Lopez, Bachofner, Mercier, & Blanke, 2009; Sigman et al., 1978, 1979; Templeton, 1973). In this context, while some studies showed that the subjective visual vertical (SVV) during combined head and visual scene tilts appeared as an additive combination of the estimates recorded for each tilt alone (Guerraz, Poquin, & Ohlmann, 1998), other studies showed that SVV deviations were mainly caused by the visual stimulation itself (DiLorenzo & Rock, 1982; Mars et al., 2004). Most importantly however, even in the case of strong visual dominance, spatial estimates were linked to the relative direction of body and visual scene tilts. Indeed, while SVV errors increased when the visual scene tilt was performed in the same direction as the body/head tilt (Asch & Witkin, 1948; DiLorenzo & Rock, 1982; Mars et al., 2004), DiLorenzo and Rock (1982) showed that tilting the head and a visual scene in the opposite direction did not modify the magnitude of the visual influence observed when the head was not tilted. It could therefore be hypothesized that the multisensory process during combined body and visual scene tilt may depend on the relative direction of tilts.

In the present study, it was tested whether manipulating visual cues relative to the observer's orientation during very slow body tilt could impact self-tilt perception. In addition, it was also investigated whether a motor task could enhance self-tilt detection. Previous experiments had already suggested that the gravitational torque to overcome during a vertical pointing movement may improve arm position sense in space (Bringoux, Blouin, Coyle, Ruget, & Mouchnino, 2012; Gooey, Bradfield, Talbot, Morgan, & Proske, 2000; Worringham & Stelmach, 1985). Supplementary information generated by arm elevation (i.e., efference copy and dynamic proprioceptive cues from muscle spindles and skin stretch receptors; Proske & Gandevia, 2009; Winter, Allen, & Proske, 2005) may not only provide a continuous update of limb position and displacement in space, but may also improve spatial judgments, such as the haptic perception of orientation (Gentaz & Hatwell, 1996; Luyat, Gentaz, Corte, & Guerraz, 2001) or estimation of the Head Referenced Eye Level (HREL; Fouque et al., 1999; Tremblay & Elliott, 2003). For instance, Fouque et al. (1999) revealed that pointing toward a target positioned at HREL considerably reduced errors compared with passive HREL settings made without pointing movement, in particular when the body was no longer vertical. In the present study, body and/or slow visual scene tilts ($0.05°\cdot s^{-1}$) were combined and their influence on self-tilt perception was studied. These combined conditions provided the opportunity to investigate the multisensory integration process underlying self-tilt perception, notably as a function of the orientation between visual and postural (non-visual) cues. It was expected that multisensory integration rules for self-tilt detection might differ relative to the direction of visual scene as shown for the SVV task (Asch & Witkin, 1948; DiLorenzo & Rock, 1982; Mars et al., 2004). Furthermore, it was hypothesized that a concurrent arm pointing task required at some specific angles of the continuous rotation(s) might enhance the feeling of being tilted. Indeed, we expected that the lower gravitational torque to overcome during arm elevation when tilted forward could provide dynamic changes of proprioceptive inputs and a modified sense of effort (Proske, 2006; Proske & Gandevia, 2009), in turn informing that the body was no longer vertical.

2. Methods

2.1. Participants

Fifteen right-handed subjects (9 men and 6 women; mean age ± SD: 23 ± 3 years) were recruited from the students and staff of Aix-Marseille University to participate in this experiment. Subjects reported having normal or corrected-to-normal vision and no neurological or sensorimotor disorders. Stereoscopic vision was checked using the Randot Stereotest®, with all individual scores greater than 70 s of arc. All participants gave written informed consent prior to the study, in accordance with the 1964 Declaration of Helsinki and the written consent of a local institutional review board (IRB) from the Institute of Movement Sciences, which specifically approved this study.

2.2. Apparatus

Subjects were seated in a tilting chair, firmly maintained by a six-point seatbelt (see Fig. 1a). The tilting chair was composed of a bucket seat, whose base and backrest were orientated slightly backward with respect to vertical (12° and 15°, respectively). The Head Mounted Display (HMD) was fixed horizontally onto a headrest attached to the seat which was adjustable in elevation to subject size. The HMD orientation maintained the head naso-occipital axis horizontal when the chair was vertical. This head orientation has been shown to almost cancel out the influence of trunk orientation on spatial estimates (Bourrelly, Vercher, & Bringoux, 2011). Overall, this postural configuration was identical across subjects and trials. The chair could be tilted in the pitch plane by rotation around an axis positioned under the seat. This rotation was performed by lengthening/shortening an electric jack (Phoenix Mecano®, thrust: 3 kN, travel: 0.6 m, precision 0.12 mm) attached to the back of the seat. The angular rotation profile was servo-assisted using an inclinometer fixed to the chair (AccuStar®; resolution: 0.1°; range: ±60°). Chair vibrations due to inclinometer noise were reduced by use of a Butterworth low-pass filter (first order) and two digital filters (average and median). The rotation velocity was set at $0.05°\cdot s^{-1}$ following an acceleration phase at $0.005°\cdot s^{-2}$. During the experiment, earphones provided white noise (0 to 22 kHz; uniform amplitude-probability distribution; constant power spectral density) to mask any auditory cues (e.g., from the rotating chair or the computers). This white noise was used throughout each experimental trial (with or without tilt of the chair) and when the chair was turned back to vertical.

A 3D HMD (CYBERMIND hi-Res900™ 3D, Cybermind Interactive Nederland, The Netherlands; resolution: 800 × 600 pixels; field of view: 31.2° diagonal for each eye) was used to display a stereoscopic visual background based on the image size of the device (111.8 cm at 2 m) and the individual interpupillary distance. This scene was composed of a 3D grid that reinforced horizontal and vertical reference lines positioned at different depth levels (overall scene depth: 3.15 m; vergence angle: 65 min of arc). The front of the scene was positioned at 1.5 m from eye position (137 min of arc). The scene could be tilted in the pitch plane, around an axis of rotation positioned at 2.65 m

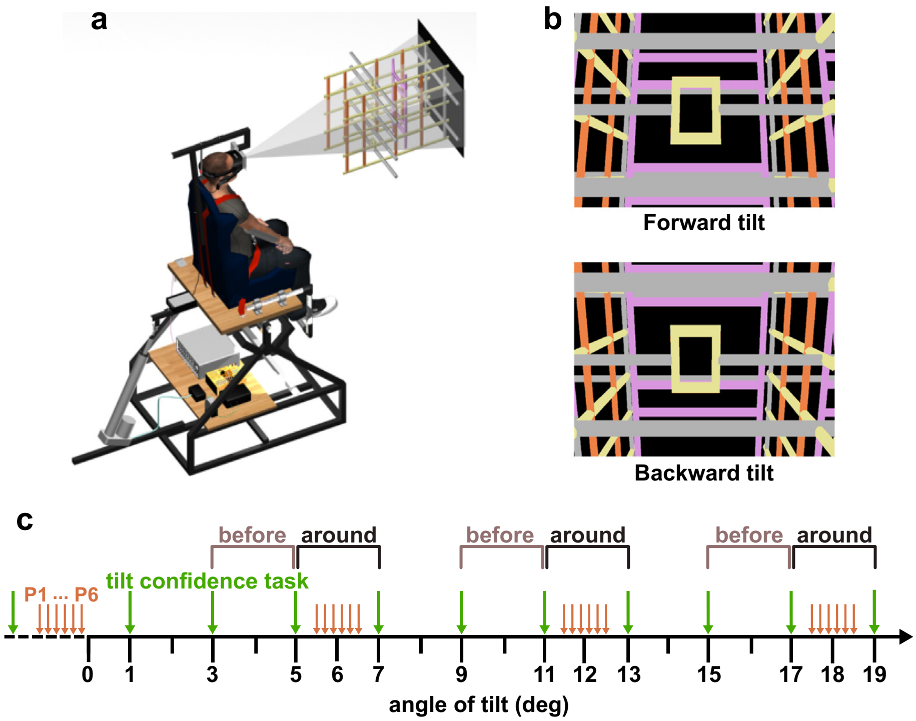

Fig. 1. Experimental setup and procedure. a) Perspective view of the setup. The sketch represents a subject in the initial vertical orientation viewing a structured visual scene displayed in the HMD, as illustrated in front of the subject. b) Screen captures of the visual scene actually viewed by a subject's right eye during a visual scene tilt of 19° forward (upper panel) or backward (lower panel). c) Representation of the sequence of events during rotation of the visual scene and/or the body from 0 to 19°. The perceptual task (indicating the confidence level for self-tilt perception) is depicted by large green arrows while the motor task (6 successive pointing movements toward a target) is depicted by small orange arrows. The link between perceptual and motor tasks was assessed by computing the difference between confidence levels for self-tilt perception before and around pointing movements (see the Data processing section), here represented by gray and black brackets respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

from eye position (78 min of arc) in the middle of the screen in the vertical plane (Fig. 1b).

Importantly, the visual scene was not rotated around the chair's rotation axis. Such a rotation could induce additional illusions due to the presence of a vertical translational optic flow (e.g., target induced motion, Duncker, 1929; and vection, Dichgans & Brandt, 1978), leading to possible conflicting effects on the arm pointing task's outcome.[1] The background was rotated around the center of the screen to minimize the occurrence of such illusions. Vection emergence was also restricted by the slow rotation velocity (Howard & Howard, 1994), the reduced size of the field of view (Allison et al., 1999; Dichgans & Brandt, 1978; Tanahashi, Ujike, & Ukai, 2012), and the absence of scene polarity (e.g., ceiling and floor; Howard & Childerson, 1994) or realism (Riecke, Schulte-Pelkum, Avraamides, von der Heyde, & Bülthoff, 2005). Nonetheless, the presented visual rotation was sufficient to induce errors in judgment relative to the environment or to the body, as simple tilted planes did (Matin & Li, 1992; Poquin, Ohlmann, & Barraud, 1998).

In this visual scene, a pink virtual target (diameter: 1 cm) could be briefly projected (1 s) at the center of the visual background and was always fixed relative to the observer, even during visual and/or body tilts. The target was presented at 0.8 m from eye position (257 min of arc). The HMD device prevented subjects from having visual feedback about the experimental setup and about their current arm location.

A real-time acquisition system (ADwin-Pro®, Jäger, Lorsch, Germany) running at 10 kHz was driven by a customized software (Docometre) to synchronously control visual background and/or chair tilts.

[1] E.g., a pitch forward visual scene tilt might induce: i) a backward self-motion illusion and therefore, potential pointing errors in the forward direction if the target is encoded in an exocentric reference frame; and ii) a backward target motion illusion and therefore, potential pointing errors in the backward direction.

2.3. Procedure

During the experiment, seated subjects, firmly restrained on the rotating chair, were prompted to indicate verbally whether they felt tilted. To that aim, they were instructed to use a subjective scale from 0 to 5 (0: I do not feel tilted at all; 1: I feel tilted with very low confidence; 2: I feel tilted with low confidence, 3: I feel tilted with medium confidence, 4: I feel tilted with high confidence, 5: I feel tilted with the highest confidence: 'I am certain that I am tilted'). These instructions were read by the subjects before the experiment and verbally repeated by the experimenter during the session. It was also clearly specified that the subjects had to report if they felt tilted relative to vertical, without referring to the feeling of being still upright, the tilt amplitude or motion perception. Subjects performed this perceptual task when prompted by an auditory tone at 0° before any stimulation and every 2°, from 1° to 19° of body and/or visual scene tilts (see Fig. 1c).

During the trials, subjects were also required to point toward a target presented at egocentric eye level (i.e., HREL) at specific angles of tilt when prompted by another specific auditory tone (data from this motor task is given in Scotto Di Cesare, Sarlegna, Bourdin, Mestre, & Bringoux, 2014). Specifically, they had to reach a body-fixed visual target, which remained visible for 1 s, as fast and as accurately as possible, using a single-joint shoulder movement (arm outstretched), and then maintain final arm position until target disappearance. A block of 6 pointing movements was performed at 0, 6, 12 and 18° during continuous body and/or visual scene tilts (Fig. 1c).

Once the body and/or the visual scene were tilted by 19°, the visual scene disappeared (black background). If the body was actually tilted, the chair was rotated back to 0° using a trapezoidal velocity profile reaching a constant maximal velocity of $0.8°\cdot s^{-1}$ (i.e., above semicircular canal threshold) with equal acceleration and deceleration phases varying between 2 s and 15 s. The induced acceleration/deceleration values ranged from $0.05°\cdot s^{-2}$ to $0.40°\cdot s^{-2}$ and rotation durations ranged from 27.75 s (with 21.75 s at maximal velocity) to 35.75 s (with 8.75 s at maximal velocity). Such pseudo-random profiles were chosen so that subjects did not infer the angle of tilt that they had previously reached. Between trials (after the chair was turned back to vertical), the HMD was removed and a period of rest in full ambient light for at least 1 min was consistently provided before the next condition was started. This rest period was used to suppress post-rotational effects due to semicircular canal stimulation (Benson, 1990; Goldberg & Fernández, 1977) and to limit possible fatigue. The subsequent body and/or visual scene tilt condition began only when subjects did not feel tilted anymore ('0' score on the confidence levels for self-tilt perception).

During the experiment, the body and/or the visual scene were tilted using forward rotations (body and/or visual scene) and backward rotations (visual scene only) up to ± 19° with the same velocity profile. Overall, 5 experimental conditions were presented: $\mathbf{S_{fwd}}$: forward visual scene tilt (top of the visual scene away from the observer) without body tilt; $\mathbf{S_{bwd}}$: backward visual scene tilt (top toward the observer) without body tilt; $\mathbf{B_{fwd}S}$: forward body tilt with a visual scene remaining static relative to the subject; $\mathbf{B_{fwd}S_{fwd}}$: forward body tilt and forward visual scene tilt; and $\mathbf{B_{fwd}S_{bwd}}$: forward body tilt with backward visual scene tilt. $\mathbf{S_{bwd}}$ and $\mathbf{S_{fwd}}$ were considered visual-only conditions with scene tilt while postural cues conveyed static orientation cues. $\mathbf{B_{fwd}S}$ was conversely considered a postural-only condition inducing body tilt while visual cues conveyed static orientation cues relative to the observer.

All 15 subjects performed 3 repetitions of each of the 5 aforementioned conditions, which were presented in a pseudo-random (a given condition was never repeated twice in a row), counterbalanced order. A training session was provided before data collection actually started, to familiarize subjects with both perceptual task (self-tilt estimates) and motor task (pointing movements). This training session followed exactly the same procedure and instructions as the experimental conditions (see above) but the body and the visual scene were not tilted (both remained vertical). This enabled the subjects to become familiar with the different auditory tones signaling both tasks. The whole experimental session lasted about 2 h.

2.4. Data processing

Firstly, data were inspected by computing for each angle of a given condition, the frequency of confidence levels (percentage) for self-tilt perception (0, 1, 2, 3, 4 or 5), associated with the 3 repetitions performed by the whole group of participants. The effect of condition and tilt magnitude on the mean confidence levels for self-tilt perception was then analyzed using a 5 condition ($\mathbf{S_{fwd}}$, $\mathbf{S_{bwd}}$, $\mathbf{B_{fwd}S}$, $\mathbf{B_{fwd}S_{fwd}}$, $\mathbf{B_{fwd}S_{bwd}}$) × 10 angle of tilt (1 to 19°, 2 ° step) repeated-measures ANOVA. Note that responses at 0° were not included in the analyses as there was no associated dispersion (i.e., no perceived tilt at all). As subjects were required to point toward a target at 0, 6, 12 and 18°; changes in confidence levels for self-tilt perception following the arm pointing movements were also analyzed (see Fig. 1c). The mean difference between responses sampled just before and just after arm pointing movement (± 1° around a pointing movement) was compared with those recorded at previous angles (− 3 to − 1° before a pointing movement). A repeated-measures ANOVA was conducted on these differences for 2 pointing-related episode (around pointing vs. before pointing) × 3 pointing angle (6, 12, 18°) × 5 condition ($\mathbf{S_{fwd}}$, $\mathbf{S_{bwd}}$, $\mathbf{B_{fwd}S}$, $\mathbf{B_{fwd}S_{fwd}}$, $\mathbf{B_{fwd}S_{bwd}}$).

Secondly, self-tilt detection thresholds were determined using a non-linear regression analysis. Specifically, confidence levels for self-tilt perception (0, 1, 2, 3, 4 or 5) were normalized between 0 ('I do not feel tilted at all') and 1 ('I feel tilted with the highest confidence'). A probit model was used to determine the tilt angle corresponding to 50% of confidence in the feeling of being tilted (0.5 value). This model could determine self-tilt detection thresholds only if the subjects felt tilted with the highest confidence at some point. As subjects never felt tilted with the highest confidence during visual scene tilt alone ($\mathbf{S_{fwd}}$ and $\mathbf{S_{bwd}}$), threshold determination for these conditions was not possible. As a consequence, self-tilt detection thresholds were thus actually computed only for $\mathbf{B_{fwd}S}$, $\mathbf{B_{fwd}S_{fwd}}$ and $\mathbf{B_{fwd}S_{bwd}}$ using a probit function defined as follows:

$$Pi = \frac{1}{1 + \left(\frac{At}{T}\right)^{b}}.$$

'*P*' is the probability of confidence in the feeling of being tilted under a given condition '*i*'; '*At*' corresponds to the *Angle of Tilt* during this condition and '*T*' to the tilt *Threshold* for this condition (i.e., angle of tilt for $p = 0.5$); '*b*' is the slope of the tangent at the inflection point of the curve and constitutes an estimation of the discrimination sensitivity relative to the chosen increments. Repeated-measures ANOVAs including $\mathbf{B_{fwd}S}$, $\mathbf{B_{fwd}S_{fwd}}$ and $\mathbf{B_{fwd}S_{bwd}}$ as main levels were conducted on the mean thresholds as well as the 'b' values (to compare the discrimination sensitivity of the probit function).

Overall, post-hoc tests (Newman–Keuls) were performed where necessary and the level of significance was set at .05 for all statistical analyses.

3. Results

To illustrate these findings, Fig. 2 shows the percentage of each confidence level for self-tilt perception as a function of condition and angle of tilt. The level of self-tilt confidence appeared low for visual scene tilt alone, as subjects frequently responded they did not feel tilted at all (i.e., 0 value) whatever the magnitude of the visual scene tilt. Conversely, actual body tilt seemed to induce changes in the percentage of responses over the range of tilt angles. Indeed, the highest confidence level for self-tilt perception appeared as the most common response from 11° up to the largest body tilt angle, regardless of visual scene orientation. Nevertheless, under the condition $\mathbf{B_{fwd}S_{fwd}}$, it can be observed that the percentage of high confidence levels for self-tilt perception increased earlier; while the percentage of low confidence responses decreased earlier accordingly.

3.1. Comparisons between mean confidence levels for self-tilt perception

The ANOVA performed on the mean confidence levels for self-tilt perception revealed an effect of condition ($F_{(4,56)} = 35.2$; $p < .001$) and angle of tilt ($F_{(9,126)} = 112.7$; $p < .001$), as well as an interaction between both factors ($F_{(36,504)} = 19.3$; $p < .001$). Overall, visual scene tilt alone induced a lower confidence level for self-tilt perception ($\mathbf{S_{fwd}}$: 1.1 ± 0.3; $\mathbf{S_{bwd}}$: 1.0 ± 0.3) as compared to conditions with actual body tilt ($\mathbf{B_{fwd}S}$: 2.7 ± 0.5; $\mathbf{B_{fwd}S_{fwd}}$: 3.3 ± 0.5; $\mathbf{B_{fwd}S_{bwd}}$: 2.7 ± 0.5). Also, the mean responses appeared linked to the angle of tilt, as represented in Fig. 3.

Visual scene tilts ($\mathbf{S_{fwd}}$ and $\mathbf{S_{bwd}}$) yielded a slight increase in confidence level for self-tilt perception from 1 to 9° approximately, and the responses reached a plateau from 9° until the maximum range of scene tilts (19°). Conversely, body tilt unsurprisingly induced an increased confidence level for self-tilt perception. Specifically, all body tilt conditions significantly differed from all visual scene tilt conditions when actual tilts were 7° or larger. Interestingly, this increase depended on the orientation of the visual scene. Indeed, the confidence level for self-tilt perception increased earlier when both the visual scene and the body were tilted forward. More precisely, the mean confidence level for self-tilt perception for $\mathbf{B_{fwd}S_{fwd}}$ was higher at 9 and 11° compared to $\mathbf{B_{fwd}S}$ and $\mathbf{B_{fwd}S_{bwd}}$ conditions (e.g., at 9°: 3.2 ± 0.3 vs. 2.2 ± 0.4 and 2.3 ± 0.4, respectively). This difference statistically disappeared from 13° up to the largest body tilt angle, presumably because all

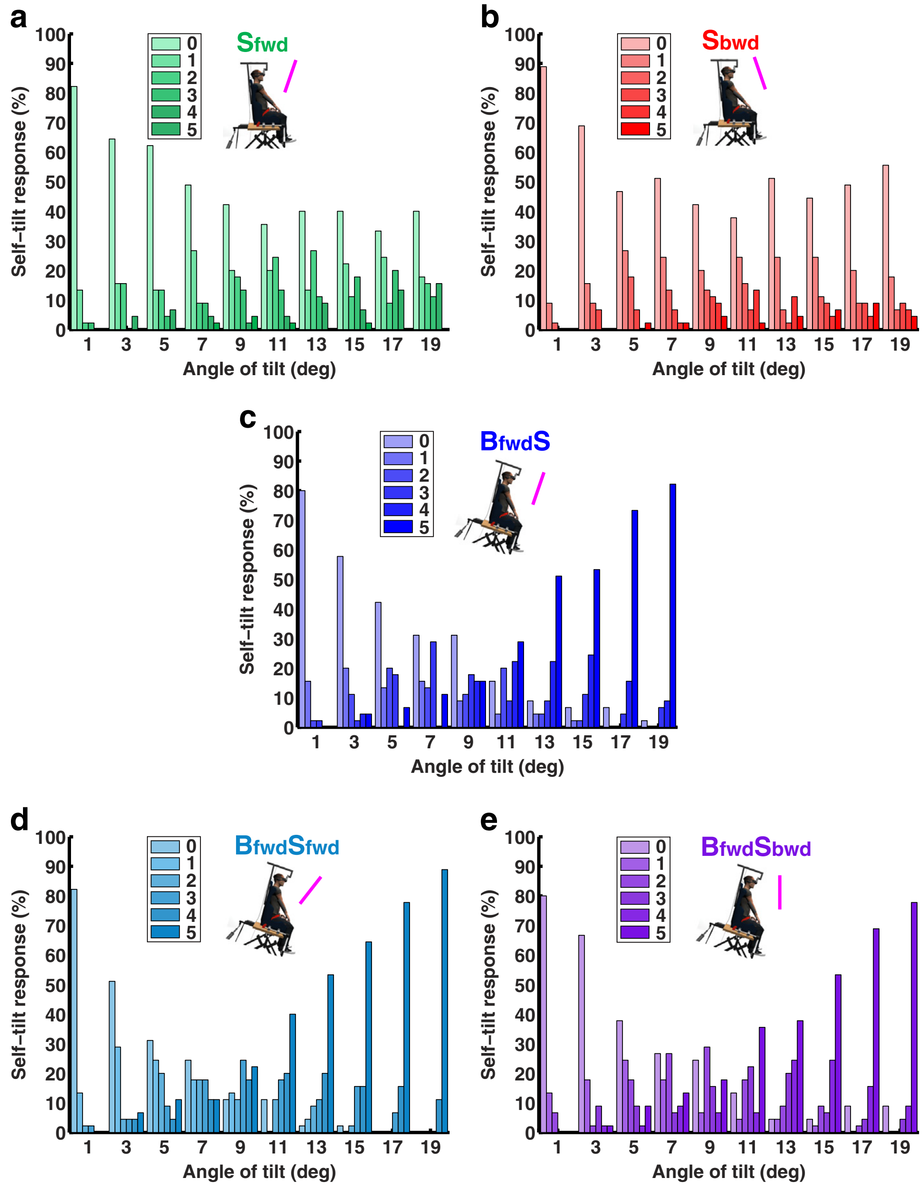

Fig. 2. Percentage of confidence levels for self-tilt perception for all subjects and trial repetitions relative to condition (a: $\mathbf{S_{fwd}}$, b: $\mathbf{S_{bwd}}$, c: $\mathbf{B_{fwd}S}$, d: $\mathbf{B_{fwd}S_{fwd}}$, e: $\mathbf{B_{fwd}S_{bwd}}$) and angle of tilt (1 to 19°, 2 ° step). Percentage of confidence levels for self-tilt perception (0, 1, 2, 3, 4 and 5) for a given angle is represented from left to right, where the value '0' corresponds to the response 'I do not feel tilted at all' and '5' to the response 'I feel tilted with the highest confidence'. Conditions are illustrated on the right side of each figure with pink lines representing scene orientation. (N.B., scene depth distance is not to scale.)

the conditions involving actual body tilt tended to reach the highest tilt confidence response.

3.2. Actual self-tilt perception thresholds

Self-tilt perception thresholds for $\mathbf{B_{fwd}S}$, $\mathbf{B_{fwd}S_{fwd}}$ and $\mathbf{B_{fwd}S_{bwd}}$ conditions were determined using a non-linear regression analysis (probit function). A prior analysis on the 'b' values (see the Data processing section) showed that the sensitivity in threshold determination was consistent between conditions (i.e., no effect of condition: $F_{(2,28)} = 0.4$; $p = 0.69$). The ANOVA performed on the mean self-tilt perception thresholds revealed a main effect of condition ($F_{(2,28)} = 6.5$; $p < .01$). Overall, self-tilt detection appeared relatively late for actual body tilt (above 8°) which furthermore depended on visual stimulus. Indeed, while adding a visual scene (static or tilted backward relative to the observer) to actual body tilt yielded similar detection thresholds (10.0 ± 1.0° and 10.1 ± 1.0°, respectively; $p = .98$); forward visual scene tilt during forward body tilt yielded a lower threshold (8.0 ± 0.8°; $\mathbf{B_{fwd}S}$ vs. $\mathbf{B_{fwd}S_{fwd}}$: $p < .0.1$ and $\mathbf{B_{fwd}S_{bwd}}$ vs. $\mathbf{B_{fwd}S_{fwd}}$: $p < .05$). In other words, only combined forward body and visual scene tilts enhanced the detection of body tilt.

3.3. Influence of arm movement on the confidence level for self-tilt perception

The difference between mean confidence levels for self-tilt perception recorded just before and just after arm pointing movement was compared to the difference between mean confidence responses recorded for the same angular range shortly before the movement was performed (around vs. before). A repeated-measures ANOVA was conducted on these differences with 2 pointing-related episode × 3 pointing angle × 5 condition. The results showed an effect of pointing

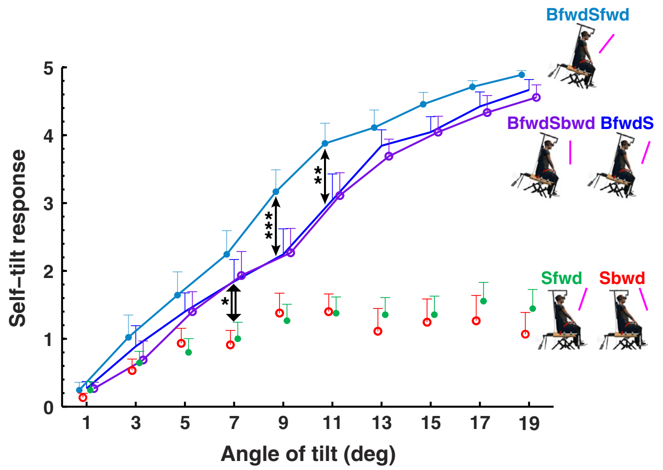

Fig. 3. Mean confidence levels for self-tilt perception as a function of condition ($\mathbf{S_{fwd}}$, $\mathbf{S_{bwd}}$, $\mathbf{B_{fwd}S}$, $\mathbf{B_{fwd}S_{fwd}}$, $\mathbf{B_{fwd}S_{bwd}}$) and angle of tilt (1 to 19°, 2 ° step). Single arrows highlight significant differences between $\mathbf{B_{fwd}S}$ or $\mathbf{B_{fwd}S_{bwd}}$ and $\mathbf{B_{fwd}S_{fwd}}$ conditions. A double arrow shows the lowest angle at which all body tilt conditions statistically diverge from all visual scene tilt conditions. Vertical bars denote positive standard errors. *: $p < .05$; **: $p < .01$; ***: $p < .001$.

angle ($F_{(2,28)} = 6.5$; $p < .01$) and condition ($F_{(4,56)} = 41.9$; $p < .001$), as well as an interaction between both factors ($F_{(8,112)} = 2.2$; $p < .05$). However, no effect of the pointing-related event appeared ($F_{(1,14)} = 4.4$; $p = .06$), neither did interactions with the condition ($F_{(4,56)} = 0.6$; $p = .63$) or pointing angle ($F_{(2,28)} = 0.5$; $p = .64$) or interactions between these 3 factors ($F_{(8,112)} = 0.5$; $p = .81$). Therefore, arm pointing movement did not increase the confidence level for self-tilt perception, as the difference between mean confidence responses around pointing movements was never found to be larger than before pointing movements (Fig. 4). The presence of a non-significant trend ($p = .06$) may suggest that pointing movements could even slow down the body tilt detection process, which is contradictory to the hypothesis of perceptual facilitation induced by arm movement.

4. Discussion

This experiment was designed to investigate whether slow pitch tilts of the body and/or the visual scene could influence self-tilt perception. Forward or backward scene tilts alone did not induce a marked sensation of self-tilt, compared to actual body tilt. Conversely, actual body tilt was detected when large angles of tilt were reached. Combined body and visual scene tilt also modified the self-tilt detection threshold, but this effect was dependent on the direction of visual scene tilt. Indeed, a forward visual scene tilt combined with a forward body tilt lowered the self-tilt detection threshold, whereas a backward visual scene tilt combined with a forward body tilt did not. Finally, in the present experiment, the threshold for self-tilt detection was not reduced by performing successive arm pointing movements at specific angles of tilt during the continuous slow body and/or visual scene rotation. These points will be further discussed in the following sections.

4.1. Slow tilt of the visual scene alone did not yield a marked sensation of self-tilt

When the visual scene alone was tilted, the highest confidence level for self-tilt perception was never reached, hence preventing the possibility of determining a threshold for self-tilt detection. The weak effect of slow visual scene tilts on self-tilt perception strikingly differed from those reported during faster rotations (Groen et al., 1999, 2002; Howard & Childerson, 1994). For instance, the 90 ° rotation of a furnished room in roll at a velocity of $4° \cdot s^{-1}$ biases the perceived static self-orientation up to 60° (Groen et al., 2002). By contrast, it has been shown that static tilts of the visual scene do not impact self-orientation judgments to the same extent (Cian et al., 1995; Sigman et al., 1979). Specifically, less than 1° of error was found when subjects were asked to orient themselves to vertical when facing a 45 ° scene tilt in roll (Cian et al., 1995). The absence of a marked sensation of self-tilt in the present experiment may thus be related to the characteristics of the visual stimulus (e.g., very slow velocity, reduced optic flow) leading to results comparable to those obtained during static visual scene tilts. This weak influence of visual stimuli could be due to the substantial weight attributed in this context to other gravity-related cues (here postural cues), mediated by vestibular and somatosensory inputs. Indeed, although unchanged, postural cues were still present during visual scene tilt alone. With regard to their particular relevance for the perception of verticality/uprightness, it is plausible that these later cues may be reweighted when the body is not tilted, as it has been previously shown that vestibular/somatosensory cues are of prime importance for judging the postural vertical (Bronstein, 1999).

4.2. Slow changes in actual body orientation were only perceived for large tilts

A strong weight attributed to postural cues for feeling upright does not mean that these cues can systematically inform the subjects about actual slow body tilt. Indeed, subjective postural vertical has been

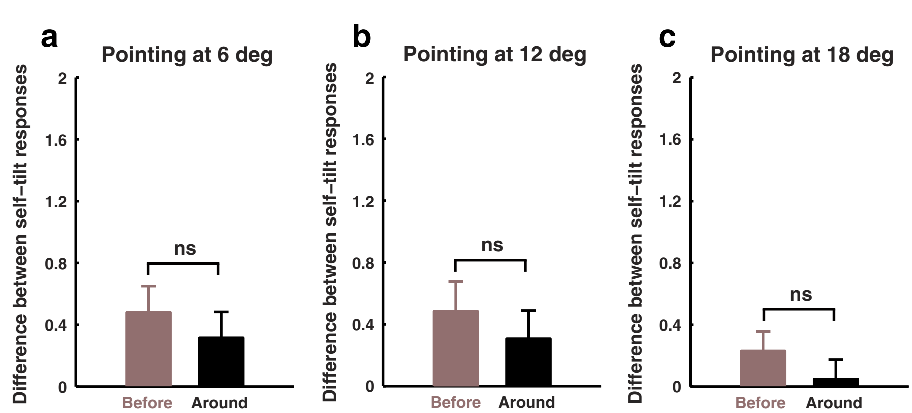

Fig. 4. Influence of arm pointing movements on confidence levels for self-tilt perception. Differences between responses obtained just before and just after arm pointing movements (around: black bars) were compared to the differences between responses obtained on a same angular range shortly before arm pointing movements (before: gray bars). Comparisons are provided for pointing movements at 6° (a), 12° (b) and 18° (c) regardless of condition (mean of all conditions). Vertical bars denote positive standard errors. ns: non-significant.

found to be mainly defined relative to a 'cone of verticality' rather than an accurate gravitational axis (Bronstein, 1999). In the present study, when the visual scene was kept static relative to the observers, slow body tilts performed at $0.05°^{-1}$ from 0 to 19° were not easily detected. Indeed, the threshold for self-tilt detection was only reached at 10°.

This late detection of body tilt reflects the difficulty of correctly perceiving self-orientation relative to the gravitational vertical. This result could be linked to the absence of semicircular canal stimulation, which may impair the ability to update body orientation in space. Overall, several studies have shown that slow body tilts at $0.05° \cdot s^{-1}$ in pitch delayed the detection of self-tilt to higher thresholds up to 12° (Bourdin et al., 2001; Bringoux et al., 2003; Teasdale et al., 1999; Trousselard et al., 2004) suggesting that very slow changes in otolith/somatosensory inputs are insufficient to convey relevant information for updating actual self-orientation. This assumption is also supported by the absence of difference between bilateral labyrinthine-defective subjects and normal subjects for slow self-tilt detection (Bringoux et al., 2002). Otolith signals may thus need to be dynamically integrated to give rise to accurate subjective orientation estimates. We hypothesized here that a constant updating of otolith signals, used to code for head orientation (tonic afferents) and/or head displacement (jerk-dependent phasic afferents; Benson, 1990; Fernández & Goldberg, 1976), would help to detect actual body tilt. Furthermore, since thresholds for the perception of body tilt have been found to rely mainly on somatosensory cues during slow tilts (Bringoux, Marin, Nougier, Barraud, & Raphel, 2000; Trousselard et al., 2004), the lack of salient somatosensory cues relative to gravity may also have played a role in this experiment, as subjects were firmly restrained in a comfortable padded chair, blurring spatial cues for self-tilt detection.

4.3. Combining visual and body tilt yielded context-dependent influences

Interestingly, it was shown that the combination of forward body and forward scene tilt relative to the observer enhanced self-tilt detection, as compared to a forward body tilt associated with a backward or a static visual scene. At first sight, this result may appear surprising, if $\mathbf{B_{fwd}S_{fwd}}$ is considered as a situation where visual scene and body tilts are conflicting (same orientation), and thus may alter self-tilt detection; while $\mathbf{B_{fwd}S_{bwd}}$ may facilitate self-tilt detection (i.e., non-conflicting cues). However, the rotation axis of the body (under the seat) was distinct from the rotation axis of the visual scene (in the middle of the scene) which means that the postural and visual stimuli could be considered as two distinct and specific inputs when combined. Besides, the facilitation of self-tilt detection when a forward visual scene tilt was added to forward body tilt discards the possibility that visual scene tilt induced a sensation of being tilted in a direction opposite to the scene (i.e., vection). Notably, vection occurrence has been extensively studied during *dynamic* rotation of the visual scene (e.g., Allison et al., 1999; Howard & Howard, 1994) and was even suggested for *static* visual scene tilt (Bock, 1997; Cian et al., 1995; Goodenough, Oltman, Sigman, Rosso, & Mertz, 1979; Goodenough, Sigman, Oltman, Rosso, & Mertz, 1979; Sigman et al., 1978). In the present study, the absence of a self-motion illusion in the opposite direction to the visual rotation under the combined conditions was probably related to the characteristics of the displayed scene (see the Methods section).

In contrast, we suggest that the facilitation of self-tilt detection in $\mathbf{B_{fwd}S_{fwd}}$ arises from a deviation of the perceived apparent median plane (i.e., the perceived body longitudinal axis) due to the visual scene tilt. Indeed, many studies have shown that the tilt of a visual scene biases the adjustment of a rod along the longitudinal body, or head axis, in the *same direction* as visual scene orientation (Barnett-Cowan & Harris, 2008; Brosgole & Cristal, 1967; Ebenholtz, 1985a, 1985b; Goodenough et al., 1981; Li et al., 2001; Sigman et al., 1979; Templeton, 1973). In the present study, the forward body and the visual scene tilt would have led the subjects to be more confident in self-tilt perception as they may also have perceived their longitudinal body axis pitched slightly forward. Some authors have already argued that this deviation of the apparent median plane may explain the SVV errors made when the visual scene is tilted, by analogy with the Dietzel–Roelofs effect (Brosgole & Cristal, 1967; Luyat & Ohlmann, 1997). The Dietzel–Roelofs effect has been described as the tendency to deviate estimates of longitudinal body axis toward the center of an eccentric visual scene (Roelofs, 1935). This effect has also been evoked to explain how the tilt of a visual scene may bias the apparent median plane in the *same direction* as a roll tilted frame (Brosgole & Cristal, 1967).

However, the aforementioned influence of visual scene tilt on the apparent median plane was not revealed during combined forward body tilt with backward visual scene tilt, as no difference was found between this condition and that including body tilt with a static visual scene relative to the observer. In this case, based on our previous interpretation, a backward deviation of the apparent median plane might have been expected, which could thereby have delayed forward body tilt detection. Our results do not support this assumption. In contrast, it can be assumed that, in the case of a detrimental influence on self-orientation perception, visual cues may have been ignored in favor of a dominance of postural cues. More precisely, the fact that the visual scene was fixed relative to an exocentric reference frame (i.e., visual scene kept at gravitational vertical) may explain the absence of deviation of the apparent median plane, as the invariant properties of gravity constitute a relevant reference for spatial orientation (Howard, 1982; Mittelstaedt, 1983). The specific dominance of postural cues, as compared to visual cues, has already been found in spatial orientation tasks (Barnett-Cowan & Harris, 2008; Barnett-Cowan, Jenkin, Dyde, Jenkin, & Harris, 2013; Bourrelly, Vercher, & Bringoux, 2014; Bourrelly et al., 2011; Dyde, Jenkin, & Harris, 2006). For instance, Barnett-Cowan and Harris (2008) showed that the egocentric estimate of head longitudinal axis relied on visual cues by only 3% compared to postural cues during combined head and visual static tilt in roll. Our results suggest that the dominance of postural cues is contextually-driven, as visual cues matter when they help enhance self-tilt detection. A similar effect has been found by de Graaf, Bles, and Bos (1998)d, who simulated body tilt using centrifugation. Specifically, these authors found that visual stimulation exerted an influence only for the direction of visual scene rotation which increased the feeling of being tilted, while no reduction of self-tilt sensation appeared in the opposite direction.

4.4. Arm pointing movements did not enhance self-tilt detection

In the present study, it was not found that self-tilt perception was improved by the concurrent performance of arm movements, in contrast to what was expected. Vertical arm displacements could provide additional information about limb/body orientation in space based on dynamic changes in proprioceptive cues and the related sense of effort (Proske, 2006; Proske & Gandevia, 2009). Specifically, the initial gravitational torque to overcome was 33% less when tilted at 18° compared to vertical orientation, a reduction which was not ignored in motor command as the spatio-temporal characteristics of arm movement execution were modified at an early stage when the body was tilted (Scotto Di Cesare et al., 2014). It may be hypothesized that these modifications were not taken into account in conscious detection of body tilt. A potential explanation of this perceptual/motor independence could be that the two tasks involved different reference frames (see Bruno, 2001; Smeets, Brenner, de Grave, & Cuijpers, 2002): namely an egocentric reference frame for pointing vs. an exocentric reference frame for self-tilt perception. More generally, the task requirements and the related reference frames for achieving the task, would have been relevant factors for explaining these results, as suggested by available data in the literature (Bringoux, Tamura, Faldon, Gresty, & Bronstein, 2004; Bringoux et al., 2009; Carriot et al., 2006). Indeed, these authors reported only partial or selective influence of motor involvement, depending on the nature of the spatial task (gravity-related vs. egocentric judgments). Further experiments would be required to investigate whether arm pointing movements could be helpful for self-tilt perception, notably around the range of tilt where the detection occurred (between 8 and 10°), as in the present study arm movements were only performed at 6, 12 and 18°.

5. Conclusion

Overall, this study shows how visual cues modify self-orientation perception during body tilt, depending on contextual factors, such as the direction and dynamics of the stimulation. These findings suggest that visual stimuli impact self-tilt perception during actual body tilt only if its consequences facilitate the detection. Referring mainly to postural cues when perceptual performance is at stake could be a functional strategy to reduce the risk of integrating erroneous cues. Promising lines of further investigation to complement these results may lie in the determination of influences mediated by high-level or cognitive factors, such as the perceptual profile or spatial expertise of subjects.

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