



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 ($0.05^\circ \cdot s^{-1}$) 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.

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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 & Benzsawel, 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 $3^\circ \cdot s^{-2}$; 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 $0.05^\circ \cdot s^{-1}$ and preceded by an acceleration of $0.005^\circ \cdot s^{-2}$ 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 (Di Lorenzo & 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; Di Lorenzo & Rock, 1982; Mars et al., 2004), Di Lorenzo 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; Gooley, 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 judgements, 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 ($0.05^\circ \cdot s^{-1}$) 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; Di Lorenzo & 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 \pm 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: $\pm 60^\circ$). 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 $0.05^\circ \cdot s^{-1}$ following an acceleration phase at $0.005^\circ \cdot s^{-2}$. 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

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