

# Asymmetrical representation of body orientation

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The perceived orientation of objects, gravity, and the body are biased to the left. Whether this leftward bias is attributable to biases in sensing or processing vestibular, visual, and body sense cues has never been assessed directly. The orientation in which characters are most easily recognized—the perceived upright (PU)—can be well predicted from a weighted vector sum of these sensory cues. A simple form of this model assumes that the directions of the contributing inputs are coded accurately and as a consequence participants tilted left- or right-side-down relative to gravity should exhibit mirror symmetric patterns of responses. If a left/right asymmetry were present then varying these sensory cues could be used to assess in which sensory modality or modalities a PU bias may have arisen. Participants completed the Oriented Character Recognition Test (OCHART) while manipulating body posture and visual orientation cues relative to gravity. The response patterns showed systematic differences depending on which side they were tilted. An asymmetry of the PU was found to be best modeled by adding a leftward bias of  $5.6^\circ$  to the perceived orientation of the body relative to its actual orientation relative to the head. The asymmetry in the effect of body orientation is reminiscent of the body-defined left-leaning asymmetry in the perceived direction of light coming from above

and reports that people tend to adopt a right-leaning posture.

## Introduction

A reference orientation direction is fundamental to perception and action. Knowing one's orientation and the orientation of surrounding objects in relation to gravity affects the ability to maintain postural stability (Kluzik, Horak, & Peterka, 2005; Wade & Jones, 1997) as well as the ability to identify (Dyde, Jenkin, & Harris, 2006), predict the behavior of (Barnett-Cowan, Fleming, Singh, & Bühlhoff, 2011) and interact with, surrounding objects (McIntyre, Zago, Berthoz, & Lacquaniti, 2001). Gravity is ideally suited as a reference direction for orientation because it is universally available. However, the senses provide different types of information about the direction of gravity. Thus optimal performance requires integrating orientation cues from multiple senses. Several studies in the perceptual literature suggest that the orientation which best enables the brain to reconstruct the three-dimensional structure of objects, rather than being aligned with gravity, is biased towards the observer's left

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(Jenkin, Dyde, Jenkin, Harris, & Howard, 2003; Jenkin, Jenkin, Dyde, & Harris, 2004; Mamassian & Goutcher, 2001; McManus, Buckman, & Woolley, 2004; Metzger, 1975; Sun & Perona, 1998). Howard, Bergström, & Ohmi (1990) found that obtaining shape from shading is predominantly performed in a headcentric frame of reference, and while trends of a leftward bias relative to the head were found regardless of head tilt they did not reach significance. Results from Jenkin et al. (2003) and Jenkin et al. (2004) also show a small trend for preferred lighting to be to the left relative to the head when oriented upright (Jenkin et al., 2003: see figure 4a; Jenkin et al., 2004: 5.7° to the left, figure 3) and even when upside down (Jenkin et al., 2003, see figure 4b). This latter observation is crucial because it indicates that the bias is in a constant direction relative to the head.

Leftward biases that are constant with change in head orientation can be found in the spatial perception literature as well. Barnett-Cowan and Harris (2008) reported that the perceived direction of the body is significantly biased leftward by 4°–6° when setting a tactile rod or moving the eyes relative to these reference directions and that this bias persists with the body tilted to the left or right by 60°. Similar results were also reported by Schuler, Bockisch, Straumann, & Tarnutzer (2010) who found that the leftward bias when setting a tactile rod to vertical was stronger when upside down relative to gravity. The perceptual upright (PU)—the orientation in which characters appear most upright relative to the observer—has also been shown to be tilted around 4° to the left in upright observers (Dyde et al., 2006) and in microgravity environments (Dyde, Jenkin, Jenkin, Zacher, Harris, 2009).

It seems rather odd that the brain should exhibit such a bias given that there is no reason to suspect that space itself and the average environments in which we find ourselves have such biases. Indeed even if space were biased itself then the bias from the perspective of the observer should reverse by simply turning round. Any such bias must arise in the sensory systems or internal representations involved. If, for example, the eyebrows stuck out further to one side, the vestibular organs were not symmetrically arranged on both sides of the head, or a person habitually tilted their head or body to one side, then a leftward bias could be attributed to how the sensory information about orientation was normally received. Alternatively, a bias may arise during central processing. A general attentional bias towards the right side of space has previously been reported (Spence, Shore, & Klein, 2001) and there is considerable evidence that neurologically intact individuals have a tendency to over-represent the left portion of space (see Bowers & Heilman, 1980; Jewell & McCourt, 2000, for reviews). This phenomenon, known as pseudoneglect, is demon-

strated where individuals bisect a line slightly to the left of the line's true midpoint. Recently, Cattaneo and colleagues (2011) found that in a haptic line bisection paradigm, both sighted and early blind individuals also exhibit a leftward bias, suggesting that the leftward bias is not intrinsic to visual space. Note that a relationship between the leftward bias in pseudoneglect and in spatial tasks is merely speculative as these refer to bias of the left side of space and left tilt respectively. To our knowledge there is no direct evidence suggesting a causal relation.

Here, we set out to determine in which sensory modalities a leftward bias in orientation may arise by measuring the PU in different body orientations while viewing a visual scene rolled by various amounts relative to gravity. This work builds on preliminary results originally presented in poster format (Jenkin et al., 2008). First, we compared the PU with participants oriented left-side-down (LSD), upright and right-side-down (RSD) relative to gravity without visual orientation cues to reveal any body based asymmetry. Next, we compared the effect of rolling the visual background to the left or right with the body upright to reveal any possible bias of visual origin. Finally, as the perceived direction of gravity has been shown to change from an over- to an under-estimation through increasing body tilt angles (Mittelstaedt, 1983; Van Beuzekom & Van Gisbergen, 2000), we also measured the PU in multiple body orientations and show that the PU can be well modeled by the linear vector sum model augmented by the addition of a constant leftward bias of the body.

## Methods

### Participants

Seventeen participants between the ages of 21 and 43 took part in the experiment (10 males, 14 right-handed). All participants were tested with the body upright and when lying left- and right-side-down. Ten of these participants were also tested at oblique body orientations (see below). All participants had normal or corrected-to-normal vision and reported no history of vestibular dysfunction. All participants gave their informed written consent. Experiments conformed to the Ethics Guidelines of York University and the 1964 Declaration of Helsinki.

### Convention

The orientation of all stimuli is defined with respect to the body midline of the participant where 0° refers

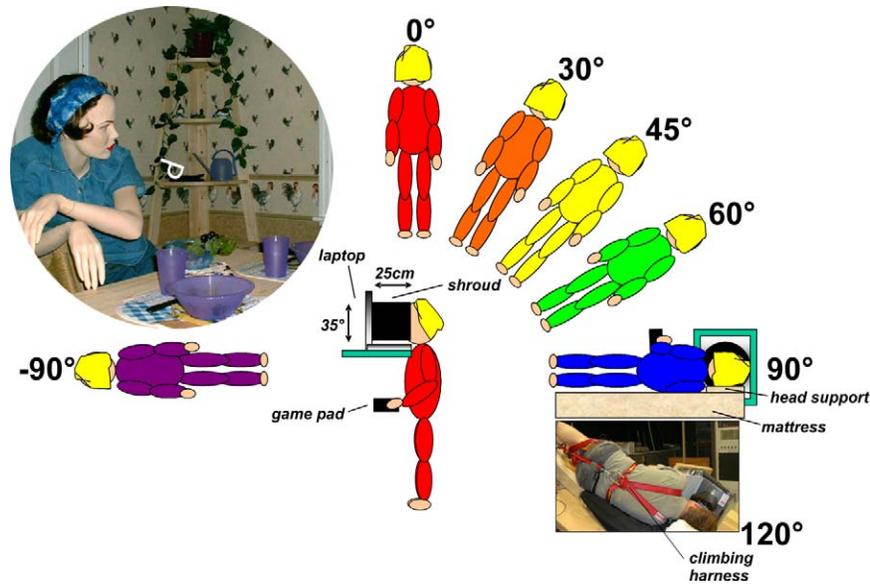


Figure 1. Apparatus. The visual background (upper left) and the body postures used in this experiment. Participants were tested while lying on their side on a foam mattress for all orientations other than upright with their head supported by foam blocks to ensure that their head was aligned with the long axis of the body. A participant is shown wearing the climbing harness for testing at 120°. Participants viewed the display through a shroud to obscure all peripheral vision (central insert). Viewed through the shroud, the screen subtended a 35° diameter circle at a distance of 25 cm.

to the orientation of the longitudinal axis of the body. Positive orientations are clockwise (‘rightwards’) from this reference point, negative orientations are counter-clockwise (‘leftwards’). Thus the gravity defined “up” is at +90° when the participant is lying on their left side. The  $p$  symbol used in the OCHART test (see below) is described as being 0° when the vertical shaft of the symbol is aligned with the body axis with the letter bowl to the right (i.e., the symbol appears as an upright  $p$ ).

## Positioning of the body

Participants stood upright or lay on a foam mattress on their right or left side with their head supported by foam blocks to ensure that their head was comfortably aligned with the body. The bed was oriented at the following tilt angles (in roll relative to gravity): 0° (participant upright), 30°, 45°, 60°, 90°, and 120° right-side-down (RSD), and –90° left-side-down (LSD) (Figure 1). For the 120° body orientation, participants wore a climbing harness while lying on their side, were secured to the top of the bed frame using climbing rope and were then suspended by tilting the bed and frame into the desired orientation (see Figure 1). Participants remained in this partially upside down position for no longer than 35 minutes and were permitted to take breaks upon request.

## Stimulus presentation

Participants observed images presented in their fronto-parallel plane on an Apple iBook laptop computer (Apple, Inc., Cupertino, CA) with a resolution of 48 pixels/cm (21 pixels/°). The screen was masked to a circle subtending 35° when viewed at 25 cm by a black circular shrouding tube that obscured all peripheral vision (Figure 1). The laptop was mounted in an aluminum frame and fixed to the bed to maintain the screen at a fixed orientation relative to the observer (the top of the screen corresponded to the top of the participant’s head) and to hold the shroud. Participants responded using two buttons on a game-pad (Gravis Game Pad Pro, Kensington/Gravis, Redwood Shores, CA).

## Test for perceptual upright (OCHART probe)

The Oriented CHAracter Recognition Test (OCHART) (Dyde et al., 2006) is an indirect measure of the PU. The OCHART has the observer discriminate between the letter  $p$  and the letter  $d$ . As the letter  $p$  when rotated 180° becomes the letter  $d$ , the transitions from  $p$ -to- $d$  and  $d$ -to- $p$  when averaged define the PU. The beauty of this technique is that observers are not asked to make judgments with respect to any frame of reference, but rather only identify the character. Using the method of constant stimuli, the probe character, a

letter *p* ( $3.1^\circ \times 1.9^\circ$ ), was presented rotated around its geometric centre in one of 24 static orientations  $0^\circ$ – $345^\circ$  in  $15^\circ$  increments. The probe character was presented for 500 ms either on a background picture rich in polarized cues that could be presented in one of 18 orientations  $0^\circ$ – $337.5^\circ$  in  $22.5^\circ$  increments (Figure 1), or against a neutral grey background. After 500 ms, stimuli were replaced with a screen of the same mean luminance as the visually polarized image with a central fixation point ( $0.45^\circ$  diameter). Thus for each body orientation there were 456 ( $24 \times 19$ ) character/background combinations which were each presented eight times in a random order resulting in a total of 3,648 ( $456 \times 8$ ) presentations for each body orientation. Testing was divided into two sessions per body orientation (completed in two blocks of 1,824 trials each) which each took approximately 35 minutes to complete. The presentation of stimuli was randomized within each block. No feedback as to participant performance was given.

## Analysis

The percentage of presentations that participants identified the character as a *p* was plotted as a function of the character's orientation for a given background. Two sigmoidal cumulative Gaussian functions (Equation 1) were fitted to the participants' response rate to determine each of the *p*-to-*d* and *d*-to-*p* transitions for each visual background in each body orientation.

$$y = \frac{100}{1 + e^{\frac{x-x_0}{\sigma}}} \% \quad (1)$$

where:  $x_0$  corresponds to the 50% point and  $\sigma$  is the standard deviation. The average of the orientations at which these two transitions occurred was taken as the PU.

## Results

### Body-based bias

A repeated-measures ANOVA was run on the gray background dataset. There were three body orientations (upright, RSD, LSD) and 17 participants. Mauchly's test for sphericity indicated that the assumption of sphericity was violated ( $\chi^2_{(2)} = 11.79$ ,  $p < 0.05$ ). Therefore degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ( $E = 0.647$ ). The results show a significant effect of body orientation on the PU,  $F(1.3, 20.7) = 37.78$ ,  $p < 0.05$ . Post hoc tests revealed that all three body orientations

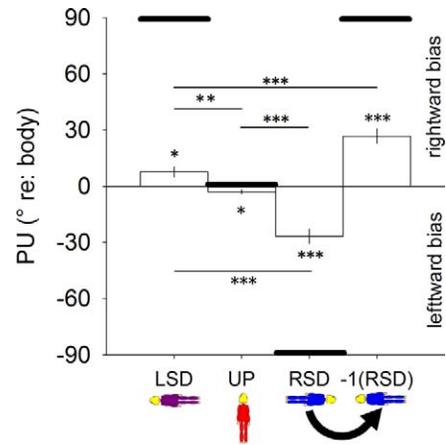


Figure 2. The effect of body orientation on the perceptual upright (PU). The average PU is shown relative to the body measured against a gray background for participants oriented LSD, UP, and RSD relative to gravity. RSD data are shown as inverted ( $-1[\text{RSD}]$ ) to better illustrate the asymmetry of the perceptual upright with body tilt. The direction of gravity relative to the body for each body orientation is indicated by the thick horizontal black lines. \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ .

were significantly different from each other at the  $p < 0.01$  level (see Figure 2). With the body upright, the PU was significantly biased to the left (one-sample *t*-test:  $-3.0^\circ$   $SE$   $1.0^\circ$ ;  $t_{(16)} = 2.9$ ,  $p = 0.010$ ). In order to test the bias between LSD and RSD, we compared LSD results against the negative of the RSD results for the grey background. A repeated-measures ANOVA shows a significant effect of body orientation,  $F(1,16) = 23.88$ ,  $p < 0.05$ . By comparing the LSD PU with the RSD PU, a significant leftward bias of the PU of  $9.5^\circ$  ( $[+7.7^\circ - 26.7^\circ]/2 = -9.5^\circ$ ) is evident.

### Visual scene

In order to assess whether there was a similar bias in the internal representation of the direction of visual cues to upright, we compared the effect of tilting the background left and right. To do so we compared the effect of a scene rotation of given angle (e.g.,  $22.5^\circ$ ; to the right) minus the effect for a scene rotated in the opposite direction (e.g.,  $337.5^\circ$ ;  $22.5^\circ$  to the left). A response bias from responses at  $22.5^\circ$ ,  $45^\circ$ ,  $67.5^\circ$ ,  $90^\circ$ ,  $112.5^\circ$ ,  $135^\circ$ , and  $157.5^\circ$  from upright was computed for each observer as their response to a scene rotated clockwise minus their response to the same display rotated counterclockwise. A repeated-measures ANOVA was run on 17 observers on this display bias. Mauchly's test for sphericity indicated that the assumption of sphericity was violated,  $\chi^2_{(20)} = 204.2$ ,  $p < 0.05$ . Therefore degrees of freedom were corrected

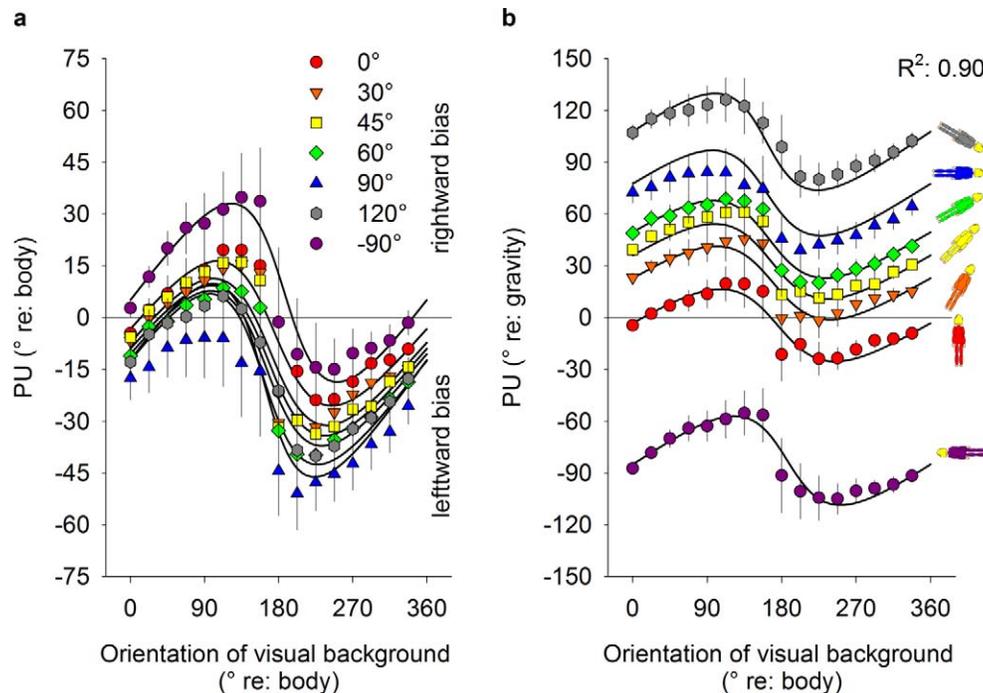


Figure 3. Average and predicted PU as a function of visual background orientation for different body orientations. The data are plotted relative to the body (a) and relative to gravity (b). Negative values are to the left (counterclockwise). Solid curves are the vector model PU predictions ( $R^2$ : 0.90). Error bars represent  $\pm 1$  SEM.

using Greenhouse-Geisser estimates of sphericity ( $E = 0.203$ ). No significant result was found,  $F(1.2, 19.5) = 3.695$ ,  $p = 0.62$ . Importantly, when the scene was upright, no bias of the PU was observed (one-sample  $t$ -test:  $-0.9^\circ$  SE  $1.9^\circ$ ;  $t_{(16)} = 0.48$ ,  $p = 0.635$ ). These results indicate that a bias of the PU does not reside in the interpretation of visual orientation cues.

### The effect of body posture on visual and body biases

In order to see if the leftward bias was present in multiple body tilts, we measured the PU for a range of body and visual combinations. A sample ( $N = 10$ ) of the original participants was tested in four additional body postures ( $30^\circ$ ,  $45^\circ$ ,  $60^\circ$ , and  $120^\circ$ ). The full dataset for these participants was fit using a modified version of the model of Dyde et al. (2006) in which the PU is modeled as the simple linear sum of three vectors corresponding to the visual, body and gravity cues. We augmented the Dyde et al.'s model through the addition of a bias term to the visual and body vectors (see Equation 2).

$$\vec{PU} = \vec{v}_{\theta_v} + \vec{b}_{\theta_b} + \vec{g} \quad (2)$$

where each vector is in the veridical direction relative to the body rotated by a bias term ( $\theta_v$ ,  $\theta_b$ ) in the roll plane

and the relative length of each vector indicates the extent to which the PU is influenced by each factor. We fitted the weighted vector model (Equation 2) to our average PU data shown in Figure 3. The Marquardt-Levenberg optimization algorithm technique was used (Press, 1988) where  $\vec{v}$  (vision) and  $\vec{b}$  (body) are vectors of variable lengths in the orientations of the visual cues and body respectively and  $\vec{g}$  (gravity) is a unity vector in the direction of gravity. The fit was also permitted to add a rotational bias to both  $\vec{v}$  and  $\vec{b}$ .

The data were well predicted by the model ( $R^2 = 0.90$ ). The best fit weights for the magnitude of each vector were  $\vec{v}$ : 2.0 (SE 0.14),  $\vec{b}$ : 4.5 (SE 3.1), relative to  $\vec{g}$  which was fixed to 1.0. A leftward bias of  $-5.6^\circ$  which was significantly different from  $0^\circ$  (SE  $0.7^\circ$ ;  $p < 0.0001$ ) had to be added to the body vector to obtain a best fit as predicted from the results in section 3.2. No significant bias was required to be added to vision ( $0.22^\circ$  SE  $2.0^\circ$ ;  $p = 0.85$ ). Table 1 lists parameter estimates as magnitude ratios relative to gravity as well as percentages. The model fit to the data is drawn through the data plotted as a function of visual tilt for each body orientation with respect to the body (Figure 3a) and gravity (Figure 3b).

It has previously been reported that tilt of the body leads to increased influence of visual cues for estimates of the subjective visual vertical (SVV; Mittelstaedt, 1986) and also increased roll vection (Dichgans & Brandt, 1978). To assess whether body tilt in the

	Cue weight	SE	$p$	Relative cue weight
Vision ( $\vec{v}$ )	2.0	0.14	<0.001	26.7%
Body ( $\vec{b}$ )	4.5	0.31	<0.001	60.0%
Gravity ( $\vec{g}$ )	1.0			13.3%
	Bias	SE	$p$	
$\theta_v$	0.2°	2.0°	0.895	
$\theta_b$	-5.6°	0.7°	<0.001	
$R^2$	0.90			

Table 1. Output of the augmented vector sum model (with biases). Parameter estimates and  $R^2$  of the vector sum model for vision, body and gravity cues as well as bias terms for vision and the body.

present experiment increases the effect of visual cues on the PU, we calculated the difference between the minimum and maximum points for each participant's PU estimates in each body orientation. We call this the "visual effect." We did not find a significant effect of body orientation on the visual effect (Greenhouse Geisser,  $F(2.002, 18.014) = 0.8$ ,  $p = 0.467$ ) and the average visual effect was similar to the maximum visual effect predicted from the model (see Figure 4).

## Discussion

We have identified a persistent leftward bias of the internal representation of the body's orientation relative to the body's true orientation. In order to accurately predict the perceptual upright from the orientations of vision, body and gravity at all body postures it is necessary to add a constant bias of approximately 5.6° to the left of the actual orientation of the body. It is possible that the representation of the body may also be tilted in the pitch plane relative to its true direction but we were unable to measure such a bias with the present protocol. The magnitude of the leftward bias is consistent with previous studies investigating the perceptual upright (Dyde et al., 2006), shape-from-shading (Jenkin et al., 2003; Jenkin et al., 2004; McManus et al., 2004), as well as the perceived directions of gravity and the body (Barnett-Cowan & Harris, 2008) that have all suggested a bias of the PU to the left (relative to the body). This leftward bias of the PU cannot be attributed to sensory information as the vision bias was not significant and the effect of information present in the visual scene on the PU relative to an upright observer was symmetrical (see also Haji-Khamneh & Harris, 2010).

Why should the brain have such a bias in its representation of the body? One possibility is that a leftward bias of the PU arises from asymmetries in brain function. It has been shown that the posterior

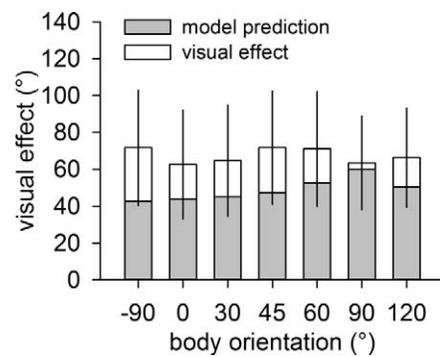


Figure 4. Average visual effect as a function of body orientation compared with model predictions. Error bars represent  $\pm 1$  SEM.

parietal and lateral frontal premotor regions are activated in the right hemisphere more than in the left hemisphere when estimating the midsagittal plane (Vallar et al., 1999). This may underlie the observation that visuo-spatial attention is preferentially directed toward the left (Corbetta, Shulman, Miezen, & Peterson, 1995; Niemeier, Stojanoski, Singh, & Chu, 2008; Posner & Rothbart, 2007). Further, unilateral damage to these brain regions—particularly in the right hemisphere—can result in spatial hemi-neglect (Vallar, 1998). Indeed, it has been shown that this hemispheric asymmetry manifests itself as pseudoneglect, where even normal participants tend to bisect a horizontal line with a leftward bias (see Jewell & McCourt, 2000 for a review). This bias persists when assessed in a supine orientation suggesting that the leftward bias is based predominantly in body coordinates (Nicholls, Smith, Mattingley, & Bradshaw, 2006). As these regions are implicated in contributing to the computation of an egocentric frame of reference (Anderson, Snyder, Bradley, & Xing, 1997), differential activity here between the hemispheres may very well be related to the leftward bias of the perceptual upright that we report.

An alternative hypothesis which could explain our results is that typically people tend to adopt a posture with their heads tilted around 10° to the right during much of everyday life (Greenberg, 1960; Previc, 1991, 1994; Putnam, Noonan, Bellia, & Previc, 1996). Indeed a quick sampling of your family photographs will likely confirm this typical head tilt. Thus, when forced to adopt an accurately upright posture in an experimental setting they perceive their head as tilted in the opposite direction from its "natural" orientation (i.e., to the right). It has been suggested that this natural rightward head tilt results from asymmetries of the body such as leg length where the left leg tends to be slightly longer (Ludwig, 1970; Peters, 1988) as well as an asymmetry of the vestibular system such that people tend to lean towards the side of the weaker (typically right) otolith organ (Curthoys & Halmagyi, 1995; Gresty, Bronstein,

Brandt, & Dieterich, 1992; Previc, 1991). Straightening of the head under laboratory conditions therefore would result in a leftward bias of perceived upright which otherwise would be veridical relative to gravity when adopting a natural, right-tilting head posture. We suggest that this explanation may also contribute to other leftward biases that have been reported in the shape-from-shading literature where it has alternatively been argued that a leftward bias for preferred lighting arises from preferentially arranging lighting sources to the left to facilitate right-handed writing (Metzger, 1975). Explanations based on brain asymmetries and on head tilt are not mutually exclusive as brain asymmetries may of course contribute to the natural right-tilting posture.

The PU was well predicted across multiple physical and visual tilts as arising from a weighted vector sum of the internal representations of the orientation of the body (60%) by vision (27%) and gravity (13%). This corresponds with the letter *p* appearing most like the letter *p* when it is oriented somewhere between the body and gravity. This is easily appreciated by noting the orientation in which you typically hold a book when reading it on your side. These sensory weightings are similar to those previously reported by Dyde and colleagues (2006; body: 54%, vision: 25%, gravity: 21%). Note that the weighted vector sum model of Dyde and colleagues (2006) is a simplification of the weighted vector model of Mittelstaedt (1983). Mittelstaedt's model includes factors to describe adjustments that model torsional eye movements associated with rolled body and visual displays relative to gravity. While we did not model or measure ocular counter-roll, the bias term identified here is constantly to the left and torsional eye movements are leftward when right-tilted but rightward when left-tilted, the constant leftward bias term here can be applied to Mittelstaedt's model as well and may help to reduce errors attributed to modeling ocular torsion.

This relative weighting of multisensory cues for the PU likely explains why other measures of perceived orientation such as the subjective visual vertical (SVV) do not yield similar leftward biases. Dyde et al. (2006) established that the PU and the SVV are distinct, where the SVV is primarily driven by gravity whereas the PU is primarily driven by body. Since the SVV is primarily driven by gravity, and not as much by body (where we show the bias to reside), one would not expect to see an asymmetry using the SVV measure since it is not as sensitive as the PU measure for the contribution of the body. The relative contribution of vision : body : gravity for the SVV is 0.1 : 0.2 : 1.0 but 1.2 : 2.6 : 1.0 for the PU (Dyde et al., 2006) or 2.0 : 4.5 : 1.0 for the PU in the present study. It is thus not surprising that a leftward bias of approximately  $5.6^\circ$  is not typically reported using the SVV measure since the body

contributes only 15% of the SVV as opposed to 60% for the PU as shown here. The PU is therefore four times more sensitive to the body; by extension we would only expect a bias of approximately  $1.4^\circ$  for the SVV ( $5.6/4 = 1.4$ ). Note that it is surprising that leftward biases have not been reported for subjective horizontal (Mittelstaedt, 1983) or vertical (Bisdorff, Wolsley, Anastasopoulos, Bronstein, & Gresty, 1996) body position, and therefore our results also confirm the marked dissociation between perceived posture and spatial perception tasks as previously noted by these authors.

Another distinction between the SVV and PU was also found when analyzing change in the visual effect as a function of body tilt. Mittelstaedt (1986) observed large changes in the influence of the visual field on the SVV when the body was tilted, which he resolved by implementing a gating mechanism to explain the interaction of visual and vestibular information. Lack of significant modulation of the PU visual effect in the present study points to further dissociation between the neural mechanisms, which govern the SVV and PU.

## Conclusions

The OCHART has been used as a means of quantifying whether changes in the relative weightings of sensory cues occurs in microgravity (Dyde et al., 2009; Harris, Jenkin, Jenkin, Zacher, & Dyde, 2011; Jenkin, Dyde, Jenkin, Zacher, & Harris, 2011), between sexes (Barnett-Cowan, Dyde, Thompson, & Harris, 2010b) and in Parkinson's patients with and without medication (Barnett-Cowan, Dyde, Fox, Hutchison, & Harris, 2010a). The ability of the OCHART to identify a robust leftward bias in the perceptual upright could be of practical importance in testing clinical populations with asymmetrical symptoms such as those suffering from stroke, neglect, muscular dystrophy and pusher syndrome.

*Keywords:* body sense, gravity, leftward bias, perceptual upright, multisensory integration

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