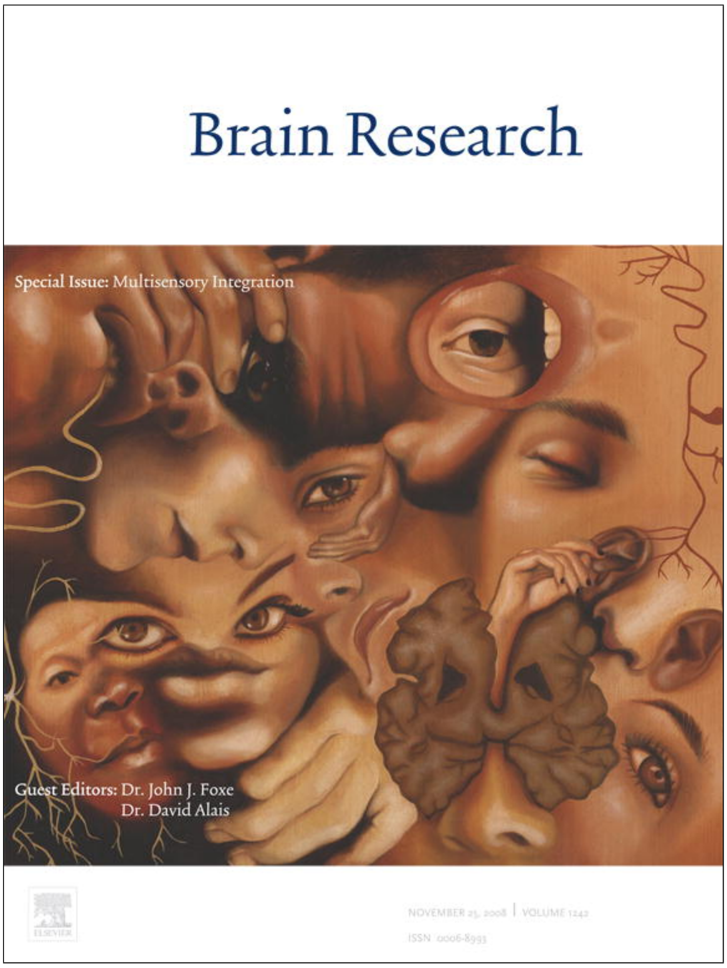

Brain Research
Special Issue: Multisensory Integration
Guest Editors: Dr. John J. Foxe
Dr. David Alais
NOVEMBER 25, 2008 | VOLUME 1242
ISSN 0006-8993

BRAIN RESEARCH 1242 (2008) 231–243

available at www.sciencedirect.com

ScienceDirect

www.elsevier.com/locate/brainres

ELSEVIER

BRAIN RESEARCH

Research Report

Perceived self-orientation in allocentric and egocentric space: Effects of visual and physical tilt on saccadic and tactile measures

*Michael Barnett-Cowan**, *Laurence R. Harris*

Multisensory Integration Laboratory, Centre for Vision Research, Department of Psychology, York University, 4700 Keele Street, Toronto, Ontario, Canada M3J 1P3

ARTICLE INFO

Article history:
Accepted 12 July 2008
Available online 29 July 2008

Keywords:
Allocentric
Egocentric
Gravity
Internal representation
Multisensory integration
Orientation
Reference frame
Saccades
Subjective saccadic vertical
Subjective tactile vertical
Subjective visual vertical
Tactile
Tilt
Vertical
Vestibular
Vision

ABSTRACT

Do physical tilt and tilt of the visual environment affect perception of allocentric and egocentric space? We addressed this question using two perceptual-motor tasks: alignment of a tactile rod (ROD) and saccadic eye movements (EM). Nine participants indicated the vertical axis of their heads (egocentric task), as well as the direction of gravity (allocentric task). Head orientation (±60° and 0°) and visual environment orientation (±120°, ±60° and 0°) were independently manipulated in the fronto-planar roll plane. ROD and EM estimates of both allocentric and egocentric reference directions varied with head and room orientation. Physical tilt dominated allocentric estimates in the dark where overestimates of physical tilt were noted up to 11° using both measures. Allocentric ROD and EM estimates were significantly correlated across all head orientations ($r=.70$, $p<.01$) but only when upright for egocentric estimates ($r=.38$, $p<.01$). The relative contributions of the visual environment, gravity's direction and long-body axis to the estimation of allocentric and egocentric directions were determined by vector modeling. This modeling found that vision determined about 14% of the allocentric ROD and EM estimates, that the long-axis body reference played no discernible role, and that the largest factor was gravity, the effective direction of which was non-veridical. For egocentric estimates, vision contributed about 3% with the largest factor being the body reference. We conclude that perception of allocentric and egocentric space is likely influenced by multiple senses that define common egocentric and allocentric frames of reference accessible for saccadic and tactile estimates of perceived self-orientation.

1. Introduction

The perceived orientation of the head with respect to gravity (perceived self-orientation) is influenced by vestibular, visual, and proprioceptive cues. Under normal circumstances when the head is upright with respect to the direction of gravity's force and with respect to the orientation of a polarized visual environment, perceived self-orientation within an allocentric

* *Corresponding author*. Fax: +1 416 736 5857.
E-mail address: mikebc@yorku.ca (M. Barnett-Cowan).

Abbreviations: EM, eye movement(s); ROD, tactile rod; SVV, subjective visual vertical; STV, subjective tactile vertical; SSV, subjective saccadic vertical

0006-8993/$ – see front matter
doi:10.1016/j.brainres.2008.07.075

(Earth-centric) field of reference is reinforced by such sensory cues. Perceptual stability is compromised, however, when orientation information from the senses is discordant. Given that physical tilt and tilt of the visual environment affect the perception of an allocentric field of reference, is the perceived orientation of an egocentric (head-centric) field of reference also affected by physical tilt and tilt of the visual environment? If allocentric and egocentric fields of reference are both affected by physical tilt and tilt of the visual environment this could indicate a common internal representation of allocentric and egocentric space accessible to multiple perceptual-motor actions.

Whether there is a common internal representation of gravity accessible to both perception and action systems has been addressed in spatial perception research using various methodologies (Merfeld et al., 1999; Van Beuzekom and Van Gisbergen, 2000; McIntyre et al., 2001; Angelaki et al., 2004; Barnett-Cowan et al., 2005; Zago et al., 2005; Zupan, 2005). Perception of self-orientation relative to gravity has traditionally been measured using the subjective visual vertical (SVV) in which a visible line is adjusted to align with the perceived direction of gravity (see Howard (1982) for a review). Judgments of the SVV are affected by physical tilt as well as frontoplanar roll of the visual environment relative to gravity. When participants are physically tilted by less than approximately 60° they set a luminous line so that it is tilted in the opposite direction to their roll-tilt (Van Beuzekom and Van Gisbergen, 2000). Such an error is indicative of an overestimation of physical tilt and is often referred to as an E-effect—from "entgegengesetzt", German for opposite (Müller, 1916). At tilts beyond about 60° participants make errors in setting a line in the same direction as their roll-tilt. Such errors are indicative of an underestimate of physical tilt, and are often referred to as an A-effect—in recognition of its discovery by Hermann Rudolph Aubert (Aubert, 1861). Static tilt of the visual environment also leads to errors in estimating gravity's direction (Asch and Witkin, 1948; Witkin and Asch, 1948; Mittelstaedt, 1988; Zoccolotti et al., 1992; Howard and Childerson, 1994; Luyat, 1997; Guerraz et al., 1998; Groen et al., 2002; Dyde et al., 2006). These errors increase when a subject is also physically tilted (Parker et al., 1983; Yardley, 1990; Zoccolotti et al., 1992; Poquin et al., 1995; Guerraz et al., 1998; Groen et al., 2002).

A potential confound of using the SVV is ocular counterroll (de Graaf et al., 1992; Wade and Curthoys, 1997). Other measurements have been obtained by aligning an unseen tactile rod with the perceived orientation of gravity (the subjective tactile vertical, STV) or by asking an observer to indicate this orientation by moving their eyes with respect to gravity (the subjective saccadic vertical, SSV). In contrast with the SVV, the SSV and STV tend to produce exaggerated E-effects at small tilt angles (e.g. $<60°$) (SSV: Pettorossi et al. (1998); Wood et al. (1998); Van Beuzekom and Van Gisbergen (2000); Jaggi-Schwarz and Hess (2003), STV: Bauermeister et al. (1964); Guerraz et al. (2000); Bortolami et al. (2006)). Thus, when the SVV is set in the same direction as physical tilt indicating an underestimate of tilt, both the SSV and the STV are set in the opposite direction to physical tilt indicating a simultaneous overestimate of tilt. This has also been confirmed in tactile and visual oblique effects (Luyat and Gentaz, 2002). Furthermore, it has been shown that verbal reports of perceived physical tilt reflect an underestimate of tilt at tilts of less than 60° and overestimate of tilt for larger tilts while the opposite is reported when testing the STV in the same experiment (Bortolami et al., 2006). This paradox suggests that multiple reference frames are used for the various tasks, a hypothesis recently put forward with respect to oblique effects (Gentaz et al., 2008).

To measure egocentric perception using the SSV subjects are asked to move their eyes up and down relative to their own heads. There are conflicting reports as to whether the trajectory of eye movements during head tilt indicates either generally accurate egocentric estimates (Pettorossi et al., 1998) or not (Wood et al., 1998). Whether visual orientation cues influence perceived head orientation remains unknown.

The objectives of this study were to measure the effect of physical and visual tilt on saccadic and tactile measures for both allocentric and egocentric space. In this study, physical and visual tilt are both manipulated and saccadic and tactile estimates of gravity (allocentric space) and the longitudinal axis of the head (egocentric space) are fit with a simple vector sum model to determine whether these methods are equally affected by gravity, body reference, and visual orientation cues. Finally, correlations between saccadic and tactile measures are performed to look for evidence of a common internal representation of allocentric and egocentric space accessible to multiple perceptual-motor actions.

2. Results

2.1. Egocentric judgments (dark)

Fig. 1A shows 2D-Cartesian eye-movement plots in Fick coordinates with the plots tilted to align with gravity for participant JS with linear regression fits to selected eye-movement end points (see Experimental procedures), shown relative to the longitudinal axis of the head for each head orientation. Note the leftward bias relative to the actual longitudinal axis of the head for each head orientation. The mean eye-movement (EM) trajectory and the mean tactile rod (ROD) estimates (i.e. population averages) are plotted as a function of head orientation in Fig. 2A. A significant effect of head orientation was found for EM estimates of the longitudinal axis of the head ($F_{(2,16)}=5.081$, $p=.020$), however, only EM estimates of the longitudinal axis of the head with the head at 60° to the left were significantly different than with the head upright ($t_{(1,8)}=-2.611$, $p=.031$). No effects of head orientation were observed for ROD estimates of the longitudinal axis of the head. A significant leftward bias (negative in our convention) was found for ROD (mean $=-8.2°$, $t_{(1,8)}=-3.623$, $p=.005$) but not EM (mean $=-2.8°$, $t_{(1,8)}=-1.787$, $p=.112$) estimates of the longitudinal axis of the head. ROD and EM estimates in the dark were not correlated with each other for the longitudinal axis of the head ($r=-.096$, $p=.634$).

2.2. Allocentric judgments (dark)

Fig. 1B shows eye-movement plots with the plots tilted to align with gravity for participant JS shown relative to gravity for each head orientation where saccadic overestimates of gravity

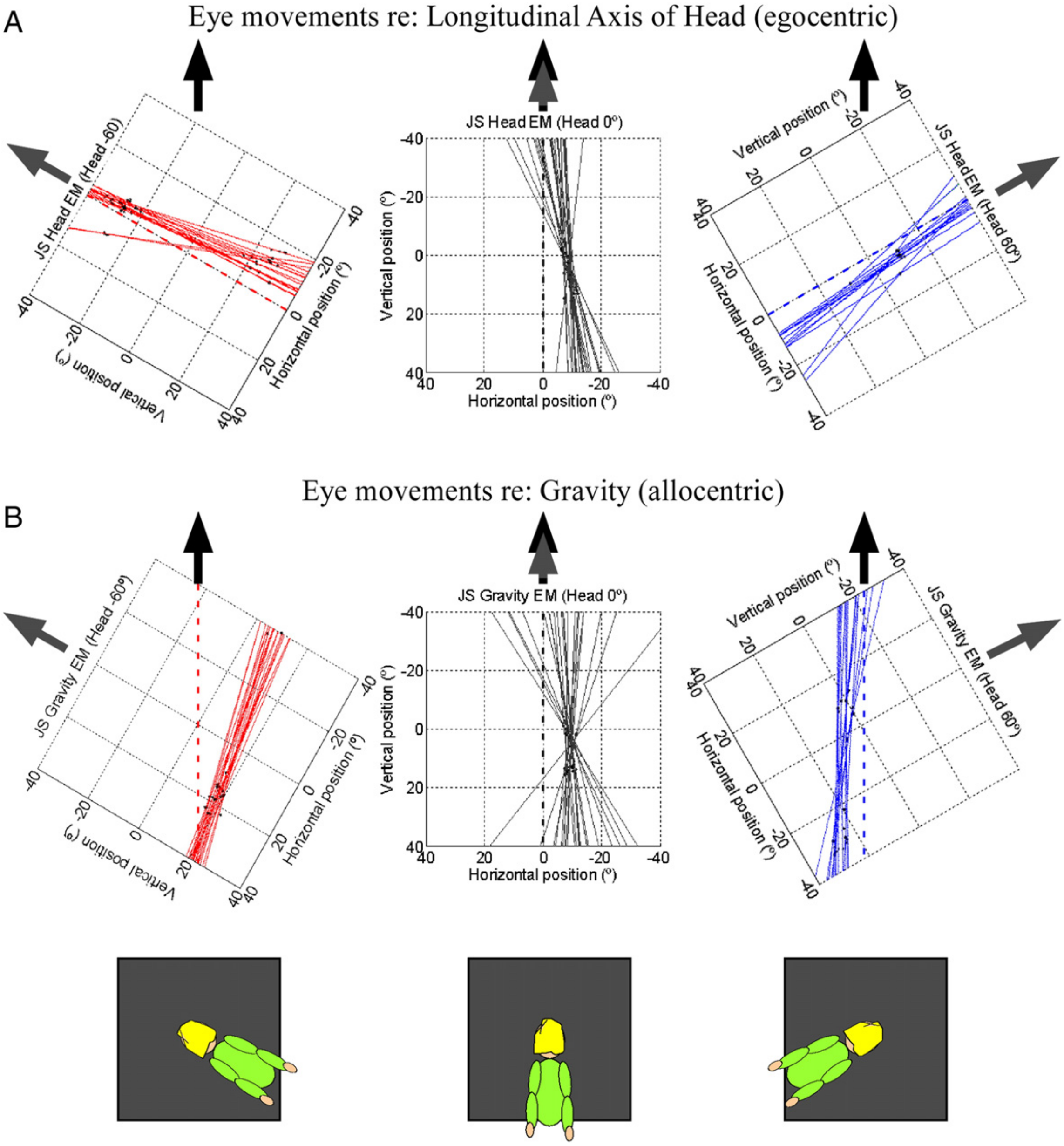


Fig. 1 – Sample egocentric and allocentric judgments: effects of body tilt. (A) Regression fits through the eye-movement end point positional data for participant JS asked to move their eyes along the longitudinal axis of the head in the dark (egocentric task) (red: head −60°, black: head 0°, blue: head 60°). Data are presented relative to the participant's point of view, where grey arrows indicate the orientation of the top of the head (i.e., relative to the orientation of the yellow-haired figure at the bottom of the figure) and black arrows indicate the orientation of gravity. Positive values in Fick coordinates are equal to downward and leftward eye movements. (B) Eye movement end points with regression fits from the same participant asked to move their eyes relative to gravity in the dark (allocentric task). Again, data are presented relative to the participant's point of view and rotated to align with gravity with the vertical axis of this page.

(i.e. E-effect) are particularly noticeable for physical tilt to the left. The mean EM and ROD estimates are plotted as a function of head orientation in Fig. 2B. A significant effect of head orientation was found for both EM and ROD estimates of gravity ($F_{(2,16)}=8.735$, $p=.003$; $F_{(2,16)}=24.371$, $p<.001$, respectively). EM estimates of gravity with the head tilt at 60° to the left (mean = 11.3°) were significantly different from when the head was upright (mean = −4.5°, $p<.05$) but EM estimates with the head tilt at 60° to the right (mean = −1.8°) were not different from when the head was upright ($p>.05$). ROD estimates of gravity with the head tilt at 60° to the left (mean = 11.8°) and to the right (mean = −10.6°) were significantly different from when the head was upright (mean = −2.5°, both: $p<.01$). There was a significant leftward bias for EM (mean = −4.5°, $t_{(1,8)}=-3.500$, $p=.008$) but not ROD (mean = −2.5°, $t_{(1,8)}=-1.139$, $p=.288$) estimates of gravity. A strong correlation was

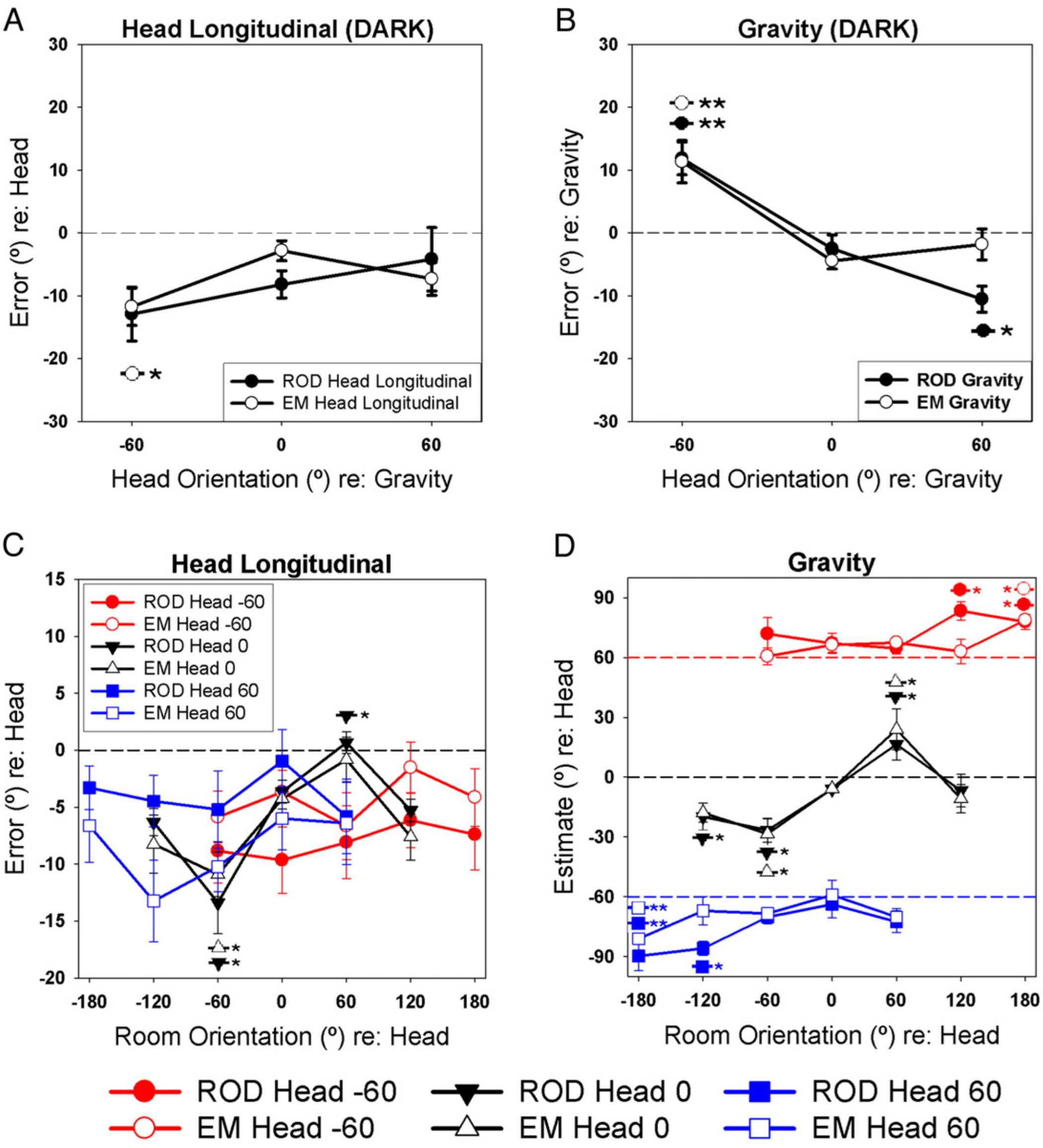


Fig. 2 – Egocentric and allocentric judgments: effects of vision and body tilt. Average ROD estimates (filled circles) and average EM estimates (open circles) are plotted as a function of body orientation with inter-subject standard error bars. Data shown in A and C are errors relative to the longitudinal axis of head and in B relative to gravity. For D, absolute settings relative to the longitudinal axis of the head are shown. Top panel (A and B) average data collected in the dark and plotted as a function of head tilt, bottom panel (C and D) collected with the lights on in the Tumbling Room (see Fig. 6) plotted as a function of room orientation relative to the head (red: head −60°, black: head 0°, blue: head 60°). Positive values are equal to clockwise errors or settings relative to the participant's viewpoint. Significant differences from when the head was upright are indicated by asterisks (* = $p<.05$, ** = $p<.01$).

observed between ROD and EM estimates in the dark for gravity ($r=.606$, $p=.001$).

2.3. *Egocentric judgments: Effects of vision*

Fig. 3A shows eye-movement plots for participant YM shown relative to the longitudinal axis of the head for each room orientation with the head upright where saccadic estimates of the longitudinal axis of the head can be seen as biased in the direction of visual tilt. Fig. 2C shows the mean EM and ROD estimates relative to the longitudinal axis of the head for each head orientation as a function of room orientation. Significant main effects of room orientation were found for the EM and ROD estimates ($F_{(4,32)}=5.181$, $p=.002$; $F_{(4,32)}=7.025$, $p<.001$, respectively). No main effects were found for head orientation for either EM or ROD estimates. A significant interaction between room and head orientation was found for ROD ($F_{(8,64)}=58.020$, $p=.021$) but not EM estimates. A significant leftward bias when the head and room were upright relative to gravity was found for EM (mean=−4.258°, $t_{(1,8)}=-4.704$, $p=.002$) and ROD (mean=−3.644°, $t_{(1,8)}=-3.623$, $p=.007$) estimates of the longitudinal axis of the head. A significant correlation between ROD and EM estimates across all visual tilt angles for the longitudinal axis of the head was

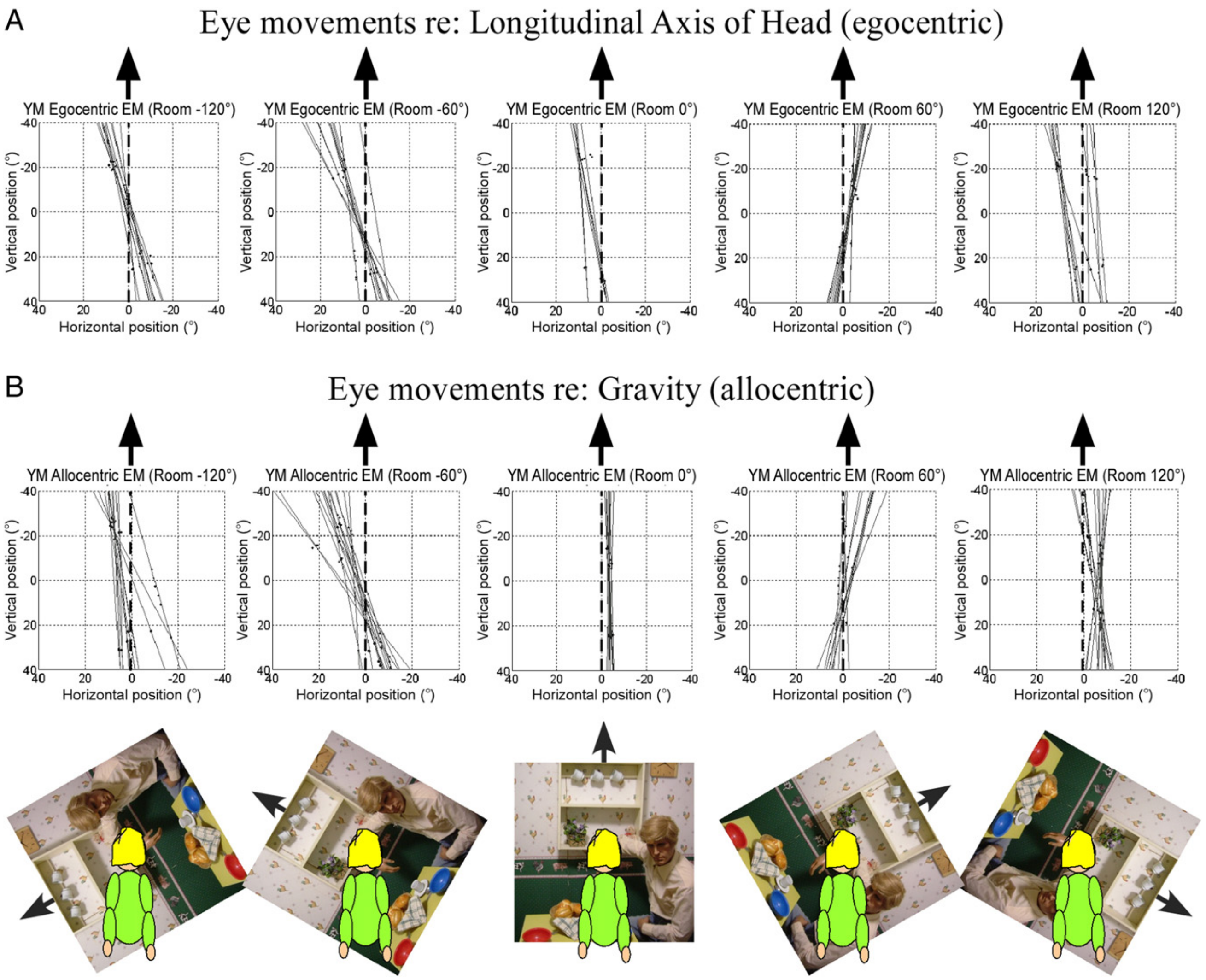


Fig. 3 – Sample egocentric and allocentric judgments: effects of vision. (A) Eye movements for participant YM made along the perceived longitudinal axis of the head and (B) aligned with gravity in the Tumbling Room rotated from −120° to +120°. Conventions as for Fig. 1. Grey arrows in lower panel with upright figure indicate the orientation of the top of the room.

only found with the head upright(r=.375, p<.001). These are displayed in Fig. 4.

2.4. *Allocentric judgments: Effects of vision*

Fig. 3B shows eye-movement plots for participant YM shown relative to gravity for each room orientation with the head upright where saccadic estimates of gravity can be seen as biased in the direction of visual tilt. Fig. 2D shows the mean EM and ROD estimates plotted as a function of room orientation for each head orientation. Note that the effect of visual tilt is more pronounced here for gravity than for the longitudinal axis of the head shown in Fig. 2C. Significant main effects of room orientation ($F_{(4,32)}=5.534$, $p=.002$; $F_{(4,32)}=9.322$, $p<.001$, EM and ROD respectively) and head orientation ($F_{(2,16)}=25.873$, $p<.001$; $F_{(2,16)}=20.578$, $p=.013$, EM and ROD respectively) were found. The interaction between head and room orientation was not significant. A significant leftward bias was found when the head and room were upright relative to gravity for EM (mean=−5.826°, $t_{(1,8)}=-3.101$, $p=.015$) and ROD (mean=−5.956°, $t_{(1,8)}=-4.456$, $p=.002$) estimates of gravity. Significant correlations were observed between ROD and EM estimates across all visual tilt angles for gravity in all head orientations (−60°: $r=.269$, $p<.05$; 0°: $r=.852$, $p<.01$; 60°: $r=.511$, $p<.01$). These are displayed in Fig. 4.

3. Discussion

This is the first study to report that a rotated visually polarized environment significantly biases judgment of orientation in both allocentric and egocentric reference frames as measured using both saccadic and tactile measures. The effect of visual tilt was more pronounced for the perceived direction of gravity than the longitudinal axis of the head and saccadic and tactile measures were highly correlated for gravity and the longitudinal axis of the head, albeit only when upright for the latter. There was a small but consistent leftward bias for

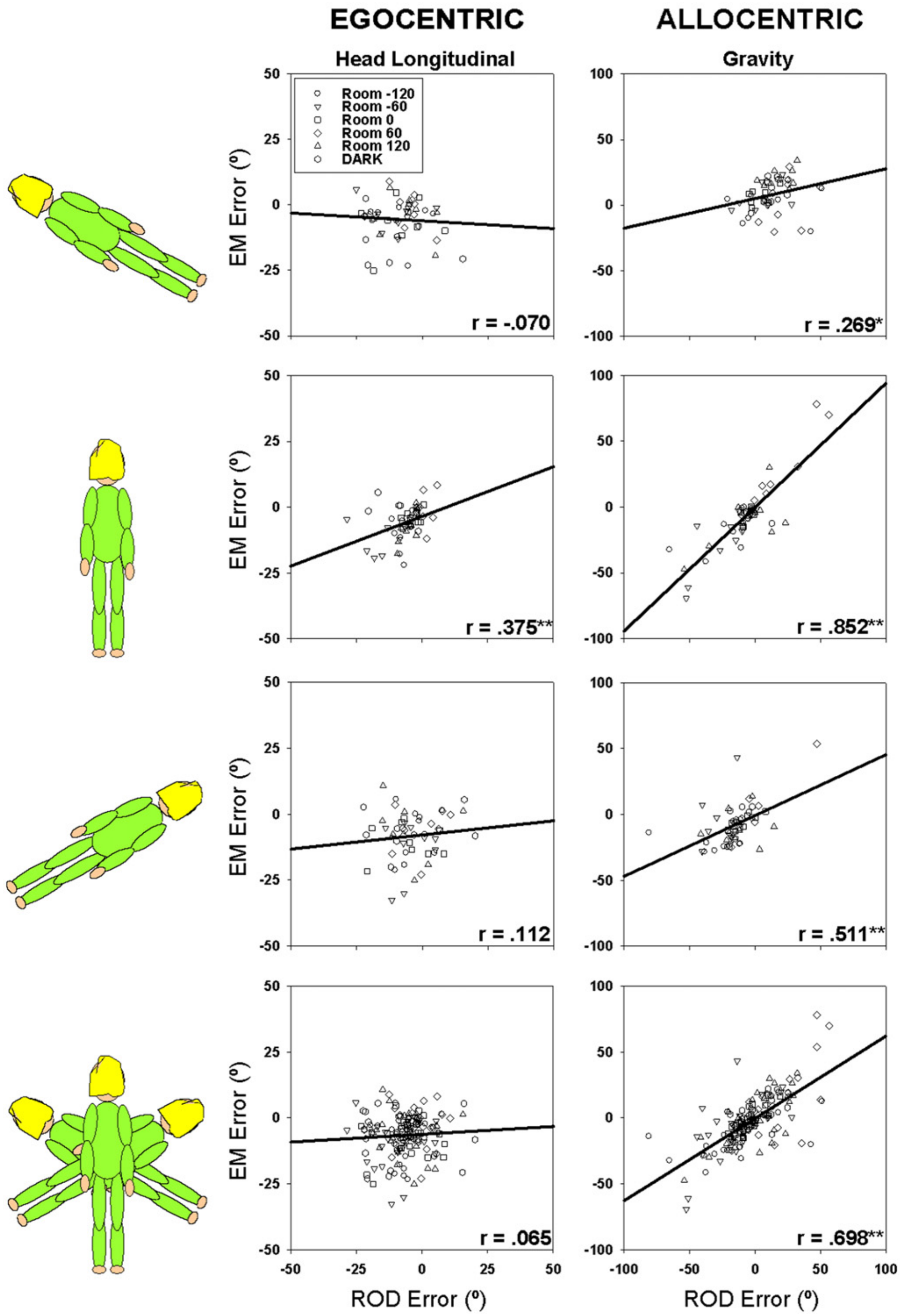


Fig. 4 – Correlations of saccadic vs. tactile measures. Separate correlations are shown for each body orientation (top three rows), and across all body orientations combined (bottom row). EM errors are plotted as a function of ROD errors relative to the head for estimates of the longitudinal axis of the head (egocentric: left column) and relative to gravity for estimates of gravity (allocentric: right column). Data are pooled from both dark and Tumbling Room data.

estimates of gravity (allocentric) and the longitudinal axis of the head (egocentric) for most conditions. We also confirm previous studies showing that physical tilt of 60° in the dark produces overestimates of head tilt as indicated using both saccadic and tactile measures. We now discuss these findings in greater detail below.

3.1. *The effect of physical tilt*

Errors in estimating the direction of gravity have been repeatedly demonstrated as a consequence of physically tilting an observer but the errors found depend on the measurement system used. We found that participants consistently overestimate physical tilt using the STV when tilted by 60°. Our results are comparable with other studies (Bauermeister et al., 1964; Guerraz et al., 2000; Bortolami et al., 2006). With respect to the SSV, participants tend to overestimate physical tilt when tilted by less than 60° (Wood et al., 1998; Van Beuzekom and Van Gisbergen, 2000; Jaggi-Schwarz and Hess, 2003), and underestimate physical tilt at tilts greater than 60° (Pettorossi et al., 1998; Van Beuzekom and Van Gisbergen, 2000; Jaggi-Schwarz and Hess, 2003), where peak overestimates of physical tilt occur when tilted ~±30° and peak underestimates of physical tilt at ~±135° (Van Beuzekom and Van Gisbergen, 2000). We found a large and significant overestimate of physical tilt when tilted to the left by 60°, whereas other reports would have suggested near-zero error estimates of the direction of gravity at this tilt angle (Van Beuzekom and Van Gisbergen, 2000; Jaggi-Schwarz and Hess, 2003). One possible explanation of this is that in our study, participants remained in each orientation for up to 30 min during testing. It has been shown that after prolonged head tilt the magnitude of underestimating physical tilt measured using the SVV decreases (Wade, 1970; Stockwell and Guedry, 1970; Guedry, 1974; Schöne and Lechner-Steinleitner, 1978; Bronstein, 1999). However, it has also been shown that STV estimates are stable over time (Luyat, 1997). Future experiments are required to test this explanation by varying duration of tilt exposure across a larger array of body-tilt positions while measuring both the STV and SSV.

We did not find an effect of physical tilt on egocentric tactile judgments and we are not aware of any other study that has investigated this. We did, however, find an effect of physical tilt on saccadic judgments of the longitudinal axis of the head where errors were made in the direction of physical tilt. However, this was only the case for physical tilts of 60° to the left. Egocentric errors made in the same direction as physical tilt have also been reported for tilts up to 45° (Wood et al., 1998).

What might these over- and underestimate errors, and such an asymmetry be attributable to? We suggest that the internal representation of allocentric space as well as the internal representation of the head are not particularly robust: physical tilt biases estimates of allocentric directions and it may also bias estimates of egocentric directions. However, further investigation of the latter point across multiple visual and body-tilt angles is required. Further investigation across multiple body-tilt angles is also required to explain asymmetries found in response to physical tilt alone for saccadic estimates.

In the following section we discuss how visual tilt also affects judgments of allocentric and egocentric space.

3.2. *The effect of visual tilt*

We confirm previous studies that have shown that a rotated visually polarized environment biases estimates of allocentrically referenced directions. Here we extend these studies to show that eye movements are also biased. The effects of visual tilt as measured using the SVV are well known (Asch and Witkin, 1948; Witkin and Asch, 1948; Mittelstaedt, 1988; Zoccolotti et al., 1992; Howard and Childerson, 1994; Guerraz et al., 1998; Dyde et al., 2006) and similar effects have been found using the STV (Howard and Childerson, 1994). More importantly, however, we are the first to report that a rotated visually polarized environment significantly biases estimates of *egocentrically* referenced directions. That is to say, observers within a visually tilted environment are likely to misperceive the orientation of their own heads! This result suggests that the internal representation of the head is not completely robust in the presence of conflicting visual orientation cues, albeit the effects reported here are 3% in magnitude and a previous study has reported a robust internal representation of the head when making judgments in the dark (Pettorossi et al., 1998).

The perceived direction of gravity is influenced by the visual environment, the true direction of gravity, and the body reference. Previous studies have attempted to model the relative contributions of these cues in estimates of the subjective visual vertical (Mittelstaedt, 1983, 1986; Van Beuzekom and Van Gisbergen, 2000; Kaptein and Van Gisbergen, 2004; Dyde et al., 2006). Inspired by the work of Mittelstaedt (1983) and similar to Dyde et al. (2006) we modelled the effects of visual cues, the body and gravity on saccadic and tactile estimates of gravity and the longitudinal axis of the head. Our simple weighted vector model is similar to that of Mittelstaedt (1983) and Dyde et al. (2006) where the weights of the contributions of vision, the body and gravity are assessed. We applied this model to saccadic and tactile estimates of gravity. To allow for overestimates of the perceived direction of gravity (i.e. E-effect) that were observed using saccadic and tactile measures, our model has an added "head tilt gain parameter" in addition to the simple three vector model used by Dyde et al. (2006). Note that the head tilt gain parameter is not applied for modelling the longitudinal axis of the head. Eq. (1) models estimates of gravity and Eq. (2) models estimates of the longitudinal axis of the head and the output of these models are shown in Fig. 5.

$$\overrightarrow{\mathrm{STV}} \text{ and } \overrightarrow{\mathrm{SSV}} = \vec{v} + \vec{b} + \vec{g}_1 + \text{bias} \tag{1}$$

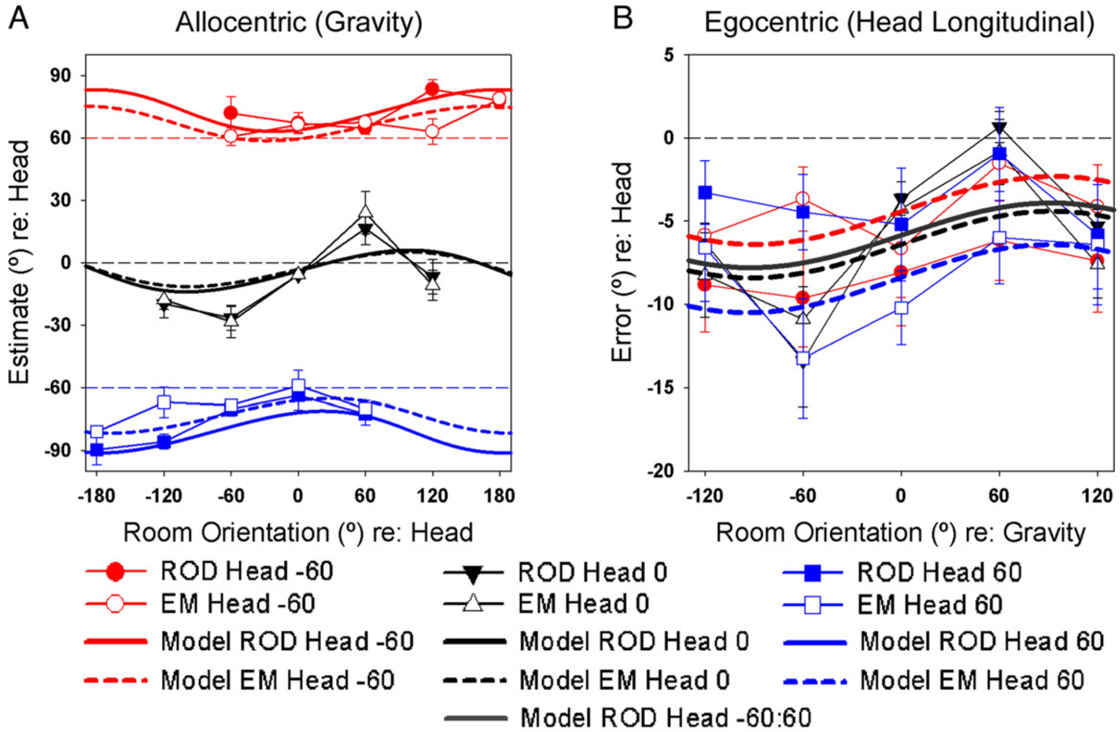
where $\vec{v}$ and $\vec{b}$ are vectors of variable lengths in the orientations of the visual cues and long-body axis respectively and $\vec{g}_1$ is a vector in the direction of gravity displaced by the tilt of the head multiplied by the "head tilt gain". Since we are only assessing the direction of the STV and SSV rather than their magnitude, we arbitrarily set $\vec{g}_1$ to unity. The bias is a displacement of all the vectors involved in a constant direction, independent of all manipulations.

$$\overrightarrow{\mathrm{STV}} \text{ and } \overrightarrow{\mathrm{SSV}} = \vec{v} + \vec{b} + \vec{g} + \text{bias} \tag{2}$$

Eq. (2) is defined as in Eq. (1), with the noted exclusion of the "head tilt gain" and where $\vec{b}$ is set to unity.

The modified three vector model described by Eq. (1) quantifies the extent to which the STV and SSV are influenced by each sensory input. The best fit weights of each vector (obtained by comparing the output of the model with the data), the head tilt gain, and the bias are listed in the tables of Figs. 5C and D for allocentric and egocentric estimates, respectively. The output of the model using these weights is plotted through the data in Figs. 5A and B for allocentric and egocentric estimates, respectively.

For allocentric estimates gravity was the dominant cue (STV: 85%, SSV: 87%) and was six to seven times more



C

	STV			SSV		
	ROD	ROD %	StdErr	EM	EM %	StdErr
vision (v)	0.17	14.9%	0.06	0.15	12.7%	0.08
body (b)	0.00	0.0%	0.59	0.00	0.0%	0.94
gravity (g)	1.00	85.1%	0.00	1.00	87.3%	0.00
bias	-3.99°		2.25	-3.24°		2.95
head tilt gain	x1.3		0.58	x1.1		0.96
R^2	0.99			0.97		

D

	ROD	ROD %	StdErr	EM	EM %	StdErr
vision (v)	0.03	3.3%	0.02	0.04	3.4%	0.02
body (b)	1.00	96.7%	0.00	1.00	92.7%	0.00
gravity (g)	0.00	0.0%	0.02	0.04	3.9%	0.02
bias	-5.86°		0.86	-6.41°		0.66
R^2	0.21			0.51		

Fig. 5 – (A) Output of the weighted vector sum model (see text) for estimates of gravity (allocentric) is plotted through the data plotted as a function of room orientation shown relative to the longitudinal axis of the head. (B) Output for estimates of the longitudinal axis of the head (egocentric) is plotted through the data plotted as a function of room orientation shown relative to gravity. Solid lines are the predictions for ROD data, dashed lines are the predictions for EM data. The model fits for ROD estimates of the longitudinal axis of the head overlap and are plotted as a single grey line. Parameter estimates and statistics for the best fits to the ROD and EM data are tabulated for gravity (C) and the longitudinal axis of the head (D).

influential than vision (STV: 15%, SSV: 13%) with no discernable effect of the body. The model also required a leftward bias for both measures of approximately 3.5°.

For egocentric estimates the orientation of the body was the dominant cue (ROD: 97%, EM: 93%), vision contributed a small amount (ROD: 3%, EM: 3%) with gravity only contributing to EM estimates (4%). The model was unable to fit the small interaction effect between head and room orientation. Egocentric estimates also required a leftward bias for both measures of approximately 6°.

What could be the explanation for such a consistent leftward bias? We suggest that the significant leftward biases found here could be related to the brain's apparent assumption that light comes from above and slightly to the left as measured in shape perception experiments (Howard et al., 1990; Mamassian and Goutcher, 2001; Jenkin, 2003; Adams et al., 2004).

It has been suggested that correlations between different measures of estimating gravity are indicative of a shared common signal representing the orientation of gravity relative to the head that is accessible to different perceptual measures (Van Beuzekom and Van Gisbergen, 2000). Van Beuzekom and Van Gisbergen (2000) report that the SSV and the SVV are correlated suggesting that the visual and saccadic systems have access to the same neural signal or frame of reference. We found highly significant correlations between the SSV and the STV across all body orientations. We also found significant correlations between these measures for saccadic and tactile estimates of egocentric space but only when oriented upright. These correlations suggest that saccadic and tactile estimates are derived from similar egocentric and allocentric reference frames which in turn are influenced by visual, somatosensory, and vestibular orientation information.

Not all estimates of self-orientation may be derived from such multisensory reference frames. Numerous studies have shown that participants are capable of accurately indicating when their bodies are aligned with the vertical or horizontal (Mittelstaedt, 1988; Bisdorff et al., 1996; Mast and Jarchow, 1996; Anastasopoulos et al., 1997) and that body-tilt estimates of are not correlated with the SVV (Mittelstaedt, 1988; Mast and Jarchow, 1996) suggesting that these two tasks do not share a common neural signal or frame of reference.

However, Van Beuzekom and Van Gisbergen (2000) demonstrated that across a large range of body-tilt angles, participants underestimate body-tilt and that body-tilt estimates are correlated with SVV estimates. Further, that we did not find an effect of body reference for allocentric estimates of gravity should be interpreted cautiously as we only tested participants at ±60° yielding E-effects. We anticipate that in the presence of A-effects, our model would account for an effect of the body reference frame on allocentric estimates of gravity.

In apparent contradiction to this, Bronstein et al. (2003) report of two patients with lesions in the lateral pontomedullary region who reported intact tactile estimates of gravity, while the reported visually perceived vertical was tilted relative to gravity. They and others (Sharpe, 2003) concluded that these lesions might have influenced the perceived direction of gravity indirectly by means of ocular torsional effects rather than by disrupting a central internal representation of verticality. These results thus suggest that the egocentric and allocentric reference frames used for estimating self-orientation might be based on the integration of visual, body, and eye orientation information rather than direct vestibular inputs. In support of this hypothesis, there is ample evidence for multisensory signals and eye movements influencing common frames of reference for motor control has been found in the posterior parietal cortex (see Andersen et al. (1997) for a review).

3.3. *Conclusion*

Our results from saccadic and tactile estimates of gravity provide evidence that these measures, which do not involve visual feedback, will yield overestimates of gravity in response to physical tilt of ±60°, and that these are also affected by tilt of the visual environment. Leftward biases relative to gravity and the longitudinal axis of the head could be related to other reported leftward biases in shape perception. We suggest that visual, somatosensory, and vestibular/eye orientation information is used in updating separate egocentric and allocentric frames of reference. We further suggest that these frames of reference are accessible for both saccadic and tactile estimates of perceived self-orientation.

4. Experimental procedures

4.1. *Participants*

Nine male participants (seven right-handed) aged 24–44 years participated in this study and gave their informed written consent according to the guidelines of the York University Research Ethics Board. Participants reported having no visual, vestibular, or other neurological disorders. All participants were familiar with making observations in psychophysics experiments. Seven participants were naïve with respect to the purpose and design of the experiments and all participants were unaware of the order of presented trials. Participants received no feedback regarding their performance in the experiment.

4.2. *Vestibular–visual apparatus (York Tumbling Room facility)*

Participants sat in a chair that could be rotated in the roll plane around an axis at the level of their necks. They were secured using a five-point harness and padded chest plate to confine the torso, padding and straps for the legs and feet, as well as laterally mounted head pads and a bite bar to restrict head movements. A fixation point was generated using a laser that was mounted to the chair and thus fixed relative to the participant (Fig. 6A).

The visually indicated direction of gravity was manipulated using the York University Tumbling Room. The room was 2.4 m on each side and decorated as an ordinary room with many objects placed in their natural intrinsic relationships with each other (Figs. 6B–D). The wallpaper had a strongly polarized pattern of chickens and other farm animals; there were books on the bookshelves, place settings on a table, and a mannequin seated in front of the observer. The room could be rotated about the same axis as the chair. The configuration enabled us to present an upright or tilted participant with an upright or tilted visual environment. Participants were instructed to keep their eyes closed between trials and did not see the room move from one position to another.

4.3. *Egocentric and allocentric directions*

Prior to the commencement of the experiments, participants were given clear instructions defining vertical. For allocentric tasks, the direction of gravity was defined as the direction in which an object would fall if dropped. For egocentric tasks, the longitudinal axis of the head was defined as an axis down the midline of the head.

4.4. *Measurement of perceived directions: Tactile rod task*

Participants manipulated an unseen tactile rod (ROD) (25 cm long, 0.5 cm diameter) using their right hands to align the tactile rod with their perception of the required direction. The rod was mounted on the chest plate at the height of the participants' stomachs and pivoted about the roll axis. A potentiometer recorded the angular position of the rod with a resolution of 0.4°. One end of the rod was covered in masking tape and participants were instructed to point using this end in the following manner: *upward* when responding relative to gravity, the top of their head when responding to the longitudinal axis of their head. The rod was moved to a random orientation before each trial. Participants were given as much time as they needed to adjust the rod to their satisfaction. When participants were satisfied they pressed a response button mounted near their left hand at the side of the chair. The experimenter manually recorded the angular position of the rod from a calibrated digital readout outside the room. The participant was then asked to set the rod to a new random orientation – change in rod orientation was confirmed by the experimenter – before the next trial. For each task, two recordings of the rod's position were taken and averaged to be used as the defined perceived direction of each measurement. The repeated trials were randomly interleaved amongst other tasks such that they did not occur sequentially.

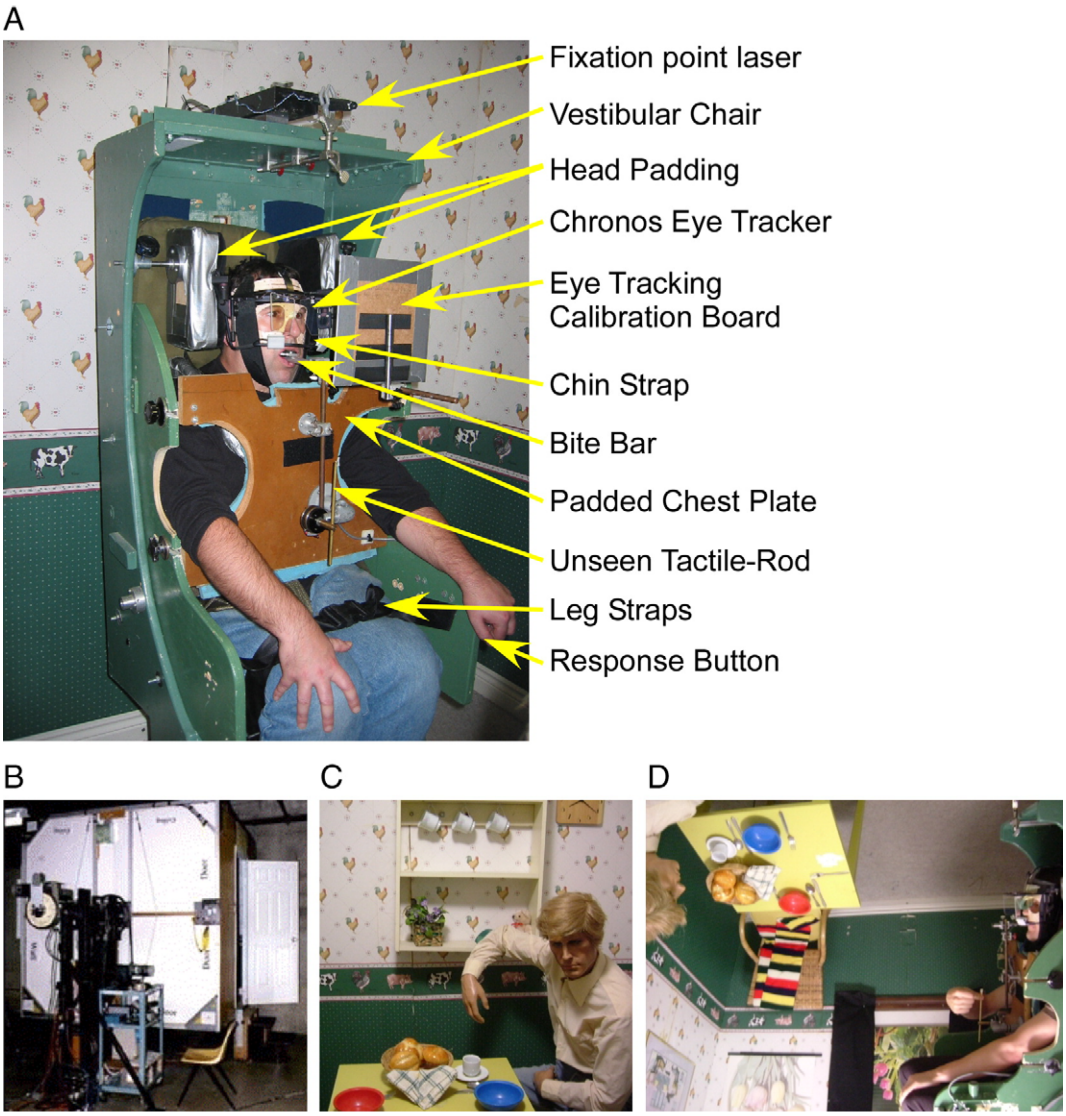


Fig. 6 – Apparatus. (A) Participant shown seated in the vestibular chair inside the York Tumbling Room. (B) shows outside and (C and D) show inside views of the York Tumbling Room. D shows a participant oriented at −60° (CCW) relative to gravity within the room oriented at −140° (CCW) relative to gravity (i.e. room tilted 80° counter-clockwise relative to the participant). The participant is shown attempting to align the tactile rod with the direction of gravity (this configuration was used for photographic purposes only and was not a configuration used in testing).

4.5. *Measurement of perceived directions: Eye-movement task*

Participants made twenty voluntary, self-paced, back-and-forth saccadic eye movements (EM) of approximately 20° at about 1 Hz along an imaginary line aligned with the relevant direction starting from the straight-ahead position defined by the fixation point. During each EM trial, participants made their first saccade along one of the following directions: (1) the upward direction defined by gravity, and (2) the top of the head. After this, participants continued to make saccadic estimates along the required axis. The position of the left eye was recorded using video-oculography (Chronos Vision GmbH, Berlin, Germany. Beta Version 2. ETD v3703, resolution 0.1°, linearity: 0.5% (horizontal and vertical) and 2.0% (torsion) (Clarke et al., 2002)). This system recorded eye movements at a rate of 100 Hz in Fick coordinates relative to the straight-ahead gaze position (where + values correspond to downward, leftward, and clockwise rotations of the eye). The eye tracker was secured to the head with a custom-made chin strap in addition to the regular forehead strap which came with the Chronos eye tracker. Eye movements were calibrated at the beginning of each session by having participants make voluntary saccades between a target aligned with straight-ahead to four targets presented at ±10° along the cardinal axes relative to the head with the head in the vertical upright position.

4.6. *Protocol*

Participants were tested in three head orientations: upright relative to gravity (0°), and tilted by 60° to the left (−60°) or right side (+60°) and the order of head orientations was randomized across participants. For the ±60° orientations, participants were rotated from an upright orientation at a tilt velocity of 0.4°/s with their eyes closed. Once rotated to the desired orientation they waited at least 30 s prior to data collection. In the upright condition, participants were not rotated prior to the commencement of testing. Once the chair and room orientations were arranged, participants looked first at the laser dot projected straight-ahead of them onto the opposite wall of the room. For ROD trials, participants maintained fixation on the laser dot throughout the entire trial. For EM trials, participants initially fixated the laser dot. The dot was then extinguished to signal the start of each trial and participants moved their eyes to indicate the required direction. All data required for a given head orientation were obtained within 30 min. For the ±60° orientations participants remained tilted for the duration of all data collection (i.e., participants were not rotated within trial blocks). For each of the three head orientations tested, six visual configurations were used. The first visual condition consisted of testing in the dark. The other five conditions consisted of testing when the room was oriented at −120°, −60°, 0°, +60°, and +120° relative to gravity (where positive values = clockwise from participant's perspective). The order of room orientations was randomized across all head orientations and participants. However, the dark condition was always the first condition tested. Participants were arranged in one particular head/visual environment configuration and were asked to perform the various judgment tasks. In summary, participants made two estimates (longitudinal axis of the head and gravity) in three head orientations and in six visual configurations for a total of 36 estimates for each of the two assessment measures, ROD and EM.

4.7. *Data analysis*

Post-hoc analysis of EM data recorded at 100 Hz was performed using the Chronos Iris (2.1.7.1) software package. For all movements, rotation conventions follow the right-hand rule commonly used to describe eye movements from the participant's perspective where down, left, and clockwise are positive. Fig. 7 depicts the methods used in EM data analysis.

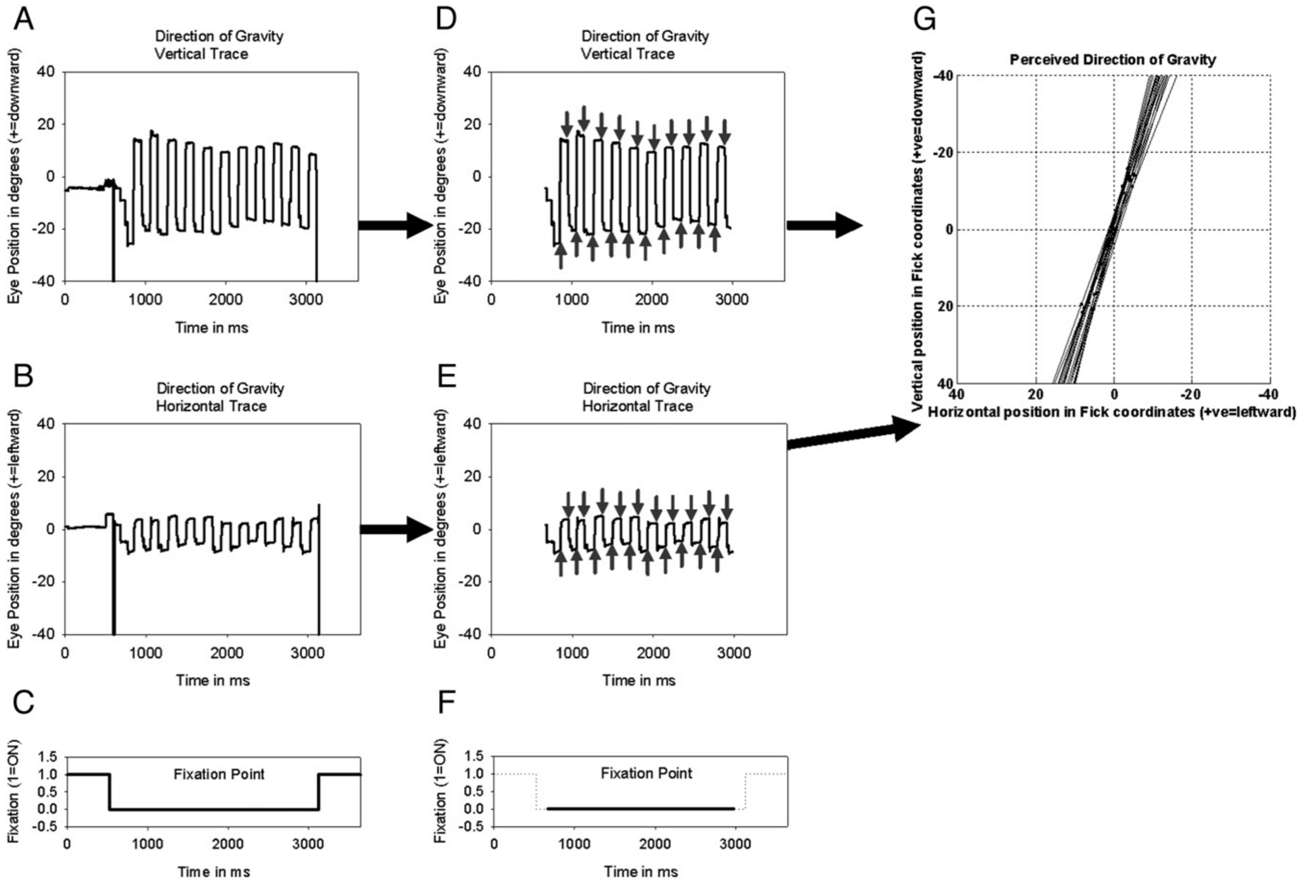


Fig. 7 – EM analysis. Example data taken from a participant with head at 0° and room at 60° for estimates of gravity. (A, B) Original eye-movement data recorded while a participant was moving his eyes relative to gravity. (C) Corresponding fixation point traces. (D, E) Corrected and cropped eye-movement data selected between 150 ms after the onset of movement and 150 ms prior to the termination of movement, where five data points prior to peak saccadic acceleration were selected for analysis (grey arrows). (F) Corresponding fixation point traces for corrected and cropped eye-movement data. (G) Horizontal and vertical eye movements plotted in 2D with each saccade fitted with a linear regression line used to define its orientation in head coordinates where the difference between the average trajectory angle and gravity (i.e., 0°) is reported as error in degrees relative to the head.

EM data were analyzed from 150 ms after the onset of the EM task to 150 ms prior to the termination of movement. Recording errors that arose when the video-oculography device lost track of the pupil – usually associated with a droopy eyelid or blinking – were removed from the analysis (5.2% data loss). To define the orientation of the saccadic trajectory relative to each target direction, EM data were double-differentiated to identify peak accelerations bounding each saccade. Five data points corresponding to each 'fixation period' (50 ms) (i.e., when the eye was stable between saccades) were selected from 10 ms prior to peak acceleration of each saccade. The fixation period occurring at the beginning of a saccade and the beginning of the next return saccade (ten data points total) were selected for regression analysis. Linear regression lines were fitted to each set of selected data points to define the average orientation of the saccadic trajectories for that condition. Ocular torsion was recorded in all trials. Torsional counterroll never exceeded 10% of head tilt (i.e., 6°) and during saccades torsional amplitude did not exceed 4°. Only positional horizontal and vertical eye-movement data and their respective regression fits are considered here.

Unless otherwise mentioned, the average orientation of saccadic trajectories from the EM data, and the ROD settings are expressed throughout as errors in degrees relative to each target axis (longitudinal axis of the head and gravity). Errors in the clockwise direction relative to each target axis are positive. Thus, in our convention, overestimates of gravity's direction when physically tilted to the left (counter-clockwise) are positive errors, and negative errors when physically tilted to the right (clockwise).

4.8. *Statistics*

Initial statistical analyses looking for the effect of head orientation in the dark and room orientation in the light were performed using one-way ANOVA for repeated measures. Bonferroni adjustments were made for pairwise comparisons between means. A series of one-way *t*-tests were performed to test for significant bias away from target directions. Bivariate Pearson's correlations were also performed to investigate the relationship between ROD and EM estimates. Correlations were performed between the average EM and average ROD settings for each subject.

Acknowledgments

This work was supported by the National Aeronautics and Space Administration Cooperative Agreement NCC9-58 with the National Space Biomedical Research Institute, the Canadian Space Agency, and the Natural Sciences and Engineering Research Council of Canada (NSERC). M. Barnett-Cowan was supported by a PGS-D3 NSERC Scholarship and a Canadian Institutes of Health Research Vision Health Science Training Grant. Thanks also go to Jeff Sanderson and Jim Zacher who helped conduct experiments, and to Carolee Orme and Jeff Sanderson for comments on an earlier version of this manuscript.

REFERENCES

Adams, W., Graf, E., Ernst, M., 2004. Experience can change the 'light-from-above' prior. Nat. Neurosci. 7 (10), 1057–1058.

Anastasopoulos, D., Haslwanter, T., Bronstein, A., Fetter, M., Dichgans, J., 1997. Dissociation between the perception of body verticality and the visual vertical in acute peripheral vestibular disorder in humans. Neurosci. Lett. 233 (2–3), 151–153.

Andersen, R., Snyder, L., Bradley, D., Xing, J., 1997. Multimodal representation of space in the posterior parietal cortex and its use in planning movements. Annu. Rev. Neurosci. 20 (1), 303–330.

Angelaki, D., Shaikh, A., Green, A., Dickman, J., 2004. Neurons compute internal models of the physical laws of motion. Nature 430 (6999), 560–564.

Asch, S., Witkin, H., 1948. Studies in space orientation. I. Perception of the Upright with displayed visual fields. J. Exp. Psychol. 38 (3), 325–337.

Aubert, H., 1861. Eine scheinbare bedeutende Drehung von objecten bei neigung des kopfes nach rechts oder links. Virchows Arch. 20 (3), 381–393.

Barnett-Cowan, M., Dyde, R., Harris, L., 2005. Is an internal model of head orientation necessary for oculomotor control? Ann. N. Y. Acad. Sci. 1039 (1), 314–324.

Bauermeister, M., Werner, H., Wapner, S., 1964. The effect of body tilt on tactual-kinesthetic perception of verticality Am. J. Psychol. 77 (3), 451–456.

Bisdorff, A., Wolsley, C., Anastasopoulos, D., Bronstein, A., Gresty, M., 1996. The perception of body verticality (subjective postural vertical) in peripheral and central vestibular disorders. Brain 119 (5), 1523–1534.

Bortolami, S., Pierobon, A., DiZio, P., Lackner, J., 2006. Localization of the subjective vertical during roll, pitch, and recumbent yaw body tilt. Exp. Brain Res. 173 (3), 364–373.

Bronstein, A., 1999. The interaction of otolith and proprioceptive information in the perception of verticality: the effects of labyrinthine and CNS disease. Ann. N. Y. Acad. Sci. 871 (1), 324–333.

Bronstein, A., Perennou, D., Guerraz, M., Playford, D., Rudge, P., 2003. Dissociation of visual and haptic vertical in two patients with vestibular nuclear lesions. Neurology 61 (9), 1260–1262.

Clarke, A., Ditterich, J., Drüen, K., Schönfeld, U., Steineke, C., 2002. Using high frame rate CMOS sensors for three-dimensional eye tracking. Behav. Res. Meth. Instrum. Comput. 34 (4), 549–560.

de Graaf, B., Bekkering, H., Erasmus, C., Bles, W., 1992. Influence of visual, vestibular, cervical, and somatosensory tilt information on ocular rotation and perception of the horizontal. J. Vestib. Res. 2 (1), 15–30.

Dyde, R., Jenkin, M., Harris, L., 2006. The subjective visual vertical and the perceptual upright. Exp. Brain Res. 173 (4), 612–622.

Gentaz, E., Baud-Bovy, G., Luyat, M., 2008. The haptic perception of spatial orientations. Exp. Brain Res. 187 (3), 331–348.

Groen, E., Jenkin, H., Howard, I., 2002. Perception of self-tilt in a true and illusory vertical plane. Perception 31 (12), 1477–1490.

Guedry, F., 1974. Psychophysics of vestibular sensation. Handbook of sensory physiology: the vestibular system, part 2: psychophysics, applied aspects and general interpretations. In: Kornhuber, H.H. (Ed.), Springer, New York, pp. 3–154.

Guerraz, M., Poquin, D., Ohlmann, T., 1998. The role of head-centric spatial reference with a static and kinetic visual disturbance. Percept. Psychophys 60 (2), 287–295.

Guerraz, M., Luyat, M., Poquin, D., Ohlmann, T., 2000. The role of neck afferents in subjective orientation in the visual and tactile sensory modalities. Acta Oto-Laryngol. 120 (6), 735–738.

Howard, I., Childerson, L., 1994. The contribution of motion, the visual frame, and visual polarity to sensations of body tilt. Perception 23 (7), 753–762.
Howard, I., Bergström, S., Ohmi, M., 1990. Shape from shading in different frames of reference. Perception 19 (4), 523–530.
Howard, I.P., 1982. Human Visual Orientation. John Wiley and Sons Ltd.
Jaggi-Schwarz, K., Hess, B., 2003. Influence of dynamic tilts on the perception of Earth-vertical. Exp. Brain Res. 149 (3), 340–350.
Jenkin, H., 2003. Relative role of visual and non-visual cues in determining the direction of “up”: experiments in the York tilted room facility. J. Vestib. Res. 13 (4), 287–293.
Kaptein, R., Van Gisbergen, J., 2004. Interpretation of a discontinuity in the sense of verticality at large body tilt. J. Neurophysiol. 91 (5), 2205–2214.
Luyat, M., 1997. Verticale posturale versus verticale subjective: une note sur létude de la perception de la verticale. LAnnée Psychol. 97 (2), 433–447.
Luyat, M., Gentaz, E., 2002. Body tilt effect on the reproduction of orientations: studies on the visual oblique effect and subjective orientations. J. Exp. Psychol. Hum. Percept. Perform. 28 (4), 1002–1011.
Mamassian, P., Goutcher, R., 2001. Prior knowledge on the illumination position. Cognition 81 (1), 1–9.
Mast, F., Jarchow, T., 1996. Perceived body position and the visual horizontal. Brain Res. Bull. 40 (5–6), 393–397.
McIntyre, J., Zago, M., Berthoz, A., Lacquaniti, F., 2001. Does the brain model Newton’s laws? Nat. Neurosci. 4 (7), 693–694.
Merfeld, D., Zupan, L., Peterka, R., 1999. Humans use internal models to estimate gravity and linear acceleration. Nature 398 (6728), 615–618.
Mittelstaedt, H., 1983. A new solution to the problem of the subjective vertical. Naturwissenschaften 70 (6), 272–281.
Mittelstaedt, H., 1986. The subjective vertical as a function of visual and extraretinal cues. Acta Psychol. 63 (1–3), 63–85.
Mittelstaedt, H., 1988. The information processing structure of the subjective vertical. A cybernetic bridge between its psychophysics and its neurobiology. Proc. Struct. Percept. Action 217–263.
Müller, G., 1916. Über das Aubertsche phänomen. Z. Sinnesphysiol. 49, 109–246.
Parker, D., Poston, R., Gulledge, W., 1983. Spatial orientation: visual–vestibular–somatic interaction. Percept. Psychophys 33 (2), 139–146.
Pettorossi, V., Bambagioni, D., Bronstein, A., Gresty, M., 1998. Assessment of the perception of verticality and horizontality with self-paced saccades. Exp. Brain Res. 121 (1), 46–50.
Poquin, D., Guerraz, M., Ohlmann, T., Marendaz, C., Brenet, F., Raphel, C., 1995. Visual disturbance and the Aubert effect Curr Psychol Cogn 14 (3), 231–253.
Schöne, H., Lechner-Steinleitner, S., 1978. The effect of preceding tilt on the perceived vertical: hysteresis in perception of the vertical. Acta Oto-Laryngologica 85 (1), 68–73.
Sharpe, J., 2003. What’s up, doc? Altered perception of the haptic, postural, and visual vertical. Neurology 61 (9), 1172–1173.
Stockwell, C., Guedry, F., 1970. The effect of semicircular canal stimulation during tilting on the subsequent perception of the visual vertical. Acta Otolaryngol. 70 (3), 170–175.
Van Beuzekom, A., Van Gisbergen, J., 2000. Properties of the internal representation of gravity inferred from spatial-direction and body-tilt estimates. J. Neurophysiol. 84 (1), 11–27.
Wade, N., 1970. Effect of prolonged tilt on visual orientation Q. J. Exp. Psychol. 22 (3), 423–439.
Wade, S., Curthoys, I., 1997. The effect of ocular torsional position on perception of the roll-tilt of visual stimuli. Vision Res. 37 (8), 1071–1078.
Witkin, H., Asch, S., 1948. Studies in space orientation: IV. Further experiments on perception of the upright with displaced visual fields. J. Exp. Psychol. 38 (6), 762–782.
Wood, S., Paloski, W., Reschke, M., 1998. Spatial coding of eye movements relative to perceived Earth and head orientations during static roll tilt. Exp. Brain Res. 121 (1), 51–58.
Yardley, L., 1990. Contribution of somatosensory information to perception of the visual vertical with body tilt and rotating visual field. Percept. Psychophys. 48 (2), 131–134.
Zago, M., Bosco, G., Maffei, V., Iosa, M., Ivanenko, Y., Lacquaniti, F., 2005. Fast adaptation of the internal model of gravity for manual interceptions: evidence for event-dependent learning. J. Neurophysiol. 93 (2), 1055–1068.
Zoccolotti, P., Antonucci, G., Goodenough, D., Pizzamiglio, L., Spinelli, D., 1992. The role of frame size on vertical and horizontal observers in the rod-and-frame illusion. Acta Psychol. (Amst) 79 (2), 171–187.
Zupan, L., 2005. Human ocular torsion and perceived roll responses to linear acceleration. J. Vestibular Res. 15 (4), 173–183.