VESTIBULO-OCULAR INTERACTIONS WITH BODY TILT:
GENDER DIFFERENCES AND AFFERENT-EFFERENT INTERPLAY

By

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ABSTRACT

This dissertation investigated the importance of information from various sensory receptors on the perception of self-orientation. In five experiments, we systematically manipulated the relative orientation between the gravitational inertial forces and the body.

The first experiment was originally designed to evaluate the effect of body inversion on the perception of straight-ahead. Interestingly, when participants were inverted, females presented a greater footward bias in the perception of straight-ahead than males. Two follow-up experiments revealed that whole-body rotation and altered blood-distribution could not explain the gender differences in the perception of straight-ahead. As a result, we attributed the gender differences in the perception of self-orientation to differences in the use of afferent information from stable gravireceptors (i.e., otoliths).

A fourth experiment examined the contribution of perceptual strategy to the perception of self-orientation. Once again, females exhibited a greater footward bias than males in the perception of straight-ahead. However, this bias was reduced slightly when female participants were instructed to focus on cues arising from inside the body. This finding indicates that, at least to some extent, strategy mediates gender differences in perceptual decision-making.

The final experiment was designed to examine the importance of limb movement on the perception of spatial orientation. Five response modes were used to gradually increase the motor demands associated with perceptual judgments about self-orientation. This study was designed to test a theory of visual information processing (i.e., Milner & Goodale, 1995), which claims that the use of distinct visual processing modules depend on the motor demands of a visual perception task. Interestingly, we found that whole limb movements affect the perception of an egocentric illusion (i.e., oculogravic illusion; see Graybiel, 1952).

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PREAMBLE

The research presented in this dissertation investigated the importance of various sources of afferent and efferent information, as well as individual differences, on the perception of spatial orientation. Six experiments are organized into three manuscripts. The first manuscript deals with the biological foundation for the perception of self-orientation. The second manuscript is related to the influence of perceptual strategy on the perception of self-orientation. The last manuscript deals with the effect of response mode (e.g., verbal vs. motor) on the perception of spatial orientation. Although the investigation of individual differences in the perception of self-orientation was not the original purpose of this research, gender was found to affect perceptual decision-making about spatial orientation. Thus, gender differences in the perception of self-orientation is a theme in the first two papers.

An extended introductory section precedes the three manuscripts. This section is intended to introduce the reader to some of the larger theoretical issues relevant to the material presented in each of the papers. Sections on internal representations and frames of reference set the stage for an overview of the neurobiology of different types of visual coding and some of the background on visual illusions. As well, some material illustrating the strategic differences between males and females in spatial decision-making is presented before introducing the specific goals associated with each of the three pieces of work.

Following the presentation of the empirical work, a general summary/conclusion section completes the dissertation. In this section, we return to some of the larger theoretical and philosophical issues presented in the introduction. The goal of this last section is to place the contribution of this thesis into a larger theoretical context, than would be appropriate for a domain-specific empirical journal.

GENERAL INTRODUCTION

The relative importance of nature and nurture in determining what we experience has been a major debate from the time Auguste Compte and Immanuel Kant forwarded their respective theories. Comte's "positivism" theory (Comte, 1838) states that the development of a complex system (e.g., the human brain) depends on the integration of environmental information. This view espouses the importance of the environment in what we experience (i.e., nurture). At the other end of the continuum, Kant's "idealism" theory (Kant, 1838) suggests that sensory experience depends on brain structure and organization. This perspective gives greater importance to our biological nature in determining sensory experience. Even today, the relative importance of biology and experience remains an important issue for research in motor control and learning (Howe, Davidson, & Sloboda, 1998; Singer & Janelle, 1999). Thus, one of the goals of the present dissertation was to investigate the relative importance of nature and nurture on the perception of spatial orientation with body tilt. Regardless of the relative importance of environmental and biological influences on the development of perceptual-motor behaviour, a fundamental problem pertains to how we integrate the information available to us from various environmental sources.

Descartes (1637; reproduced in Gilson, 1967) was one of the early philosophers to consider how environmental features are integrated into our consciousness. Descartes considered many aspects of life as he tried to discover the fundamentals of living on this planet. He suggested that what we perceive might be a construct of our brain. This reasoning was based on the fact that our senses can easily be biased. Thus, what we are conscious of, either awake or asleep, might not really exist. Sometimes, it is even difficult to know the difference between being awake and being asleep. This difficulty in differentiating what is real and what is not real leaves open the possibility that the world as we perceive it might not actually exist and could simply be the object of our imagination. However, the fact that we are able to imagine suggests that we do exist. This perspective led Descartes to forward the well-known citation: “I think, therefore I am”. For now, assume that the present text really exists. Based on this assumption, we can consider the following argument as a modified version of Descartes’ argument. Specifically, it is possible that what you perceive from the letters forming the text you are currently reading is totally different from what someone else perceives from the same letters. This occurs regardless of the words that the letters form. In the same vein, our experiential construct of any observed environment might well be totally different for someone else’s. However, we still achieve very similar behaviours in response to similar environments. For example, the letter below this “D” appears to be a “***d***” for everybody, regardless of the knowledge of the alphabet. That ***d***oes not mean that what you perceive from the letter is similar to what someone else perceives but everybody perceives a “***d***” below the “D”. Thus, the spatial relationship between the letters seems to be encoded similarly across individuals. As a result, there seems to be a common spatial frame of reference, which is important for organized behaviour in our environment.

Frames of reference

Coding of spatial information can be performed in a Cartesian or a vectorial system. A Cartesian frame of reference combines three planes orthogonally oriented to each other and yields a three dimensional space in which the location of any point in space can be identified relative to each plane. In order to determine the position of a point in space in a Cartesian system, one must determine a value for each of the three spatial dimensions (i.e., X, Y, & Z). A vectorial frame of reference requires two values (i.e., direction and amplitude) to encode the location of any point in a three-dimensional space. Although it is not the goal of the present dissertation to discuss the theoretical relevance of each spatial frame of reference (i.e., Cartesian and vectorial), it is important to mention that it has been recently suggested that humans rely on a vectorial system to perform precision limb movements in three-dimensional space (Vindras & Viviani, 1998).

In order to behave normally in our environment, regardless of the system we use (Cartesian or vectorial), we need to have some sort of spatial reference. A frame of reference can be defined as an imaginary spatial organization of the environment. As well, a frame of reference is stable even if we are not. As we move in our environment, the actual afferent information is not always congruent with what we perceive. Indeed, when the eyes move, the visual field moves on the retina in the opposite direction. This should create the perception of a moving environment. However, we seldom perceive the environment as moving. For example, when riding on a roller coaster, people might experience difficulty in knowing up from down but they never perceive the whole planet revolving around their body. The latter observation implies that information about the environment is spatially organized in a structure, which is not necessarily centred/anchored with respect to the viewer . This is evidence for the use of a frame of reference. Interestingly, after many rides, people may still perceive themselves as moving when they are stationary but yet also identify that this perception is inaccurate. Thus, it is only after integrating multiple sources of afferent and efferent information that we perceive ourselves either stable or moving in our environment (see Gielen, 2001).

Different types of spatial information can be used to anchor each frame of reference. A frame of reference can be anchored on the point of gaze, where the position of an object is encoded relative to the focal point (i.e., retinally-centred). It can also be anchored on the viewer, independent of her/his point of gaze (i.e., viewer-centred). In fact, the anchoring point of a frame of reference can be associated with the spatial organization of the cells in different modules of the visual system. For example, the layers of the superior colliculus are organized in a retinal-centred fashion, respecting the spatial organization of the retina. Other modules in the parietal, temporal, and cerebellar cortices are spatially organized into head-centred or viewer-centred maps.

Dorsal and ventral visual streams

Following the identification of different brain modules for visual processing (Ungerleider & Mishkin, 1982), Milner and Goodale (1995) attempted to identify the functions of the ventral and the dorsal visual streams. Neurons of the ventral stream project from the primary visual cortex to the inferior temporal cortex. Neurons of the dorsal stream project from the primary visual cortex to the posterior parietal cortex. Perception of an object's spatial location and motion is highly associated with the posterior parietal cortex. For example, some specific cells in the middle parietal cortex respond when a stimulus moves in one specific direction (Salzman & Newsome, 1994). As a result, the dorsal stream (i.e., parietal) is specialized for the perception of stimulus motion, producing a 'viewer-centred' view of the stimulus (i.e., egocentric frame of reference). The use of an egocentric frame of reference implies that spatial information about an object is encoded relative to the observer. Conversely, the ventral stream is associated more with the perception of shape and with the intrinsic properties of the observed object. For example, specific cells in the inferior temporal cortex (i.e., ventral stream) only respond to a specific shape (Kobatake & Tanaka, 1994). The ventral stream produces an 'object-centred' view (i.e., allocentric frame of reference) and codes the intrinsic properties of the stimulus (e.g., its use). The use of an allocentric frame of reference implies that spatial information about an object is encoded relative to another object. The association between each visual stream (i.e., ventral and dorsal) and a particular frame of reference (i.e., allocentric and egocentric) has been supported by clinical research with humans (Milner & Goodale, 1995).

Milner and Goodale (1995) have used the case of D.F. to argue for an important dissociation in visual processing. D.F. suffers from ventral stream damage caused by anoxia. Although D.F. is unable to perform perceptual tasks, she is able to sucessfully complete motor tasks involving similar visual stimuli. From example, when asked to match the perceived orientation of a straight line with another straight line, she displayed very poor accuracy. However, when asked to insert an envelope into a slot matching the orientation of the same straight line, she exhibited normal performance. Thus, it appears that D.F. cannot perceptually identify the orientation of a slot but she can coordinate her movement appropriately to the same visual stimulus. In terms of frame of reference, the comparison of the two stimuli requires the use of an allocentric frame of reference (i.e, the ventral stream), but the inserting task requires an egocentric frame of reference (i.e., the dorsal stream). These results are in line with Milner and Goodale's (1995) model of visual perception. This model is also consistent with research involving neurologically healthy participants.

Aglioti, Goodale, and DeSouza (1995) measured grip size (i.e., distance between index and thumb) to evaluate the perceived diameter of poker chip disks surrounded by Titchener-Ebbinghaus circles. Generally, the perception of size of two identical circles is biased by the surrounding circles (i.e., circle surrounded by large circles is perceived smaller than circle of same size surrounded by small circles). When simply scaling their grip to the poker chip (i.e., without a reaching movement), participants were affected by the size of the surrounding circles. However, the same grip component during a reach and grasp movement was found to be unaffected by the illusion. Milner and Goodale's (1995) interpretation of these results was that the perceptual task involves the use of the ventral stream, which encodes in an allocentric frame of reference and is susceptible to visual illusions. The reach and grasp task involves the dorsal stream, which encodes in an egocentric frame of reference. The dorsal stream is immune to this type of visual illusion. Fundamental to Milner and Goodale's (1995) neurophysiological distinction between the ventral and the dorsal stream is the dissociation between perception and action (cf. Franz, 2001).

Neurophysiological correlates

One can directly observe a segregation of visual information by simply looking at the anatomy of the retina. Different combinations of rods and cones lead to the formation of two types of ganglion cells in the retina: magnocellular and parvocellular (the names reflect their size; magno = large, parvo = small). The fibers from the parvo and magno ganglion cells are segregated, from the optic nerve to the lateral geniculate nucleus (LGN) in the thalamus. This segregation between magno and parvo cells diminishes in the primary visual cortex in the occipital lobe (i.e., V1 or Brodmann's area 17). Although the parvo and magno cells were previously associated with the dorsal and ventral streams, respectively (Livingstone & Hubel, 1988), pyramidal and nonpyramidal cells interconnect parvo and magno cells to different visual modules (e.g., columns and blobs) in the primary visual cortex. Thus, both parvo and magno cells contribute to the two visual streams. More specifically, it has been shown that eliminating the input from the parvo cells does not affect dorsal stream function, whereas eliminating either the parvo or magno input substantially reduces ventral stream function (Wurtz & Kandel, 2000a, b). Thus, the segregation in visual processing can still be identified beyond the

LGN and establishes the existence of parallel neural pathways for visual processing. Dissociations between perception and action are assumed to reflect these structural partitions. However, these visual streams are not completely separate and independent structures.

When one examines the neuroanatomy of the visual system, it is clear that the optic nerve projects to different brain areas in addition to the thalamus (i.e., LGN). Indeed, there are retinal projections to the superior colliculus (SC) and the pretectum (PT). While the function of the PT is usually associated with the pupil reflex, it also has a role to play in smooth pursuit eye movements (Büttner-Ennever & Horn, 1997). The SC controls saccadic eye movements and also integrates different sources of afferent information. The superficial layers of the SC include a retinotopic map. These layers are directly fed by the retina whereas the deeper layers are associated with other afferent sources such as vestibular, auditory, and somatosensory information. Interestingly, the distribution of the cells on each layer of the SC follows the relative spatial distribution of the layer fed by the retina (i.e., retinal-centred). In addition to feeding the oculomotor system, the SC sends neural projections to control head and neck movements as well as neural projections to the cerebellum. Further, "it is notable that most if not all of the dorsal-stream areas send projections to the superior colliculus" (Milner & Goodale, 1995, p.56). Interestingly, there is little reference to the cerebellum and the basal ganglia in the work of Milner and Goodale (1995) although these structures also contribute to movement control and learning (see Stein & Glickstein, 1992 for a review). Perhaps the dorsal and ventral distinction alone fails to appreciate the complexity as well as the symbiotic nature of the human brain. At the very least, we should acknowledge that many motor behaviours require continual cross-talk between the ventral and dorsal streams.

Evidence for dorsal-ventral interactions?

Marteniuk, MacKenzie, Jeannerod, Athenes, and Dugas, (1986) demonstrated that the transport phase of a grasping movement can be affected by the nature of the target (i.e., tennis ball or light bulb) even if the targets are of the same size and located at the same distance from the participant. In this situation, processing associated with the ventral stream affected the dorsal stream function. Specifically, the object properties associated with ventral stream processing affected the reaching movement thought to be under the control of the dorsal stream. Evidence of such cross-talk is neither sparse in the literature nor surprising considering the important network of interconnections between the two streams.

One of the goals of this thesis was to examine whether dissociations between perception and action stem from the cognitive vs. action demands of the task per se or the particular frame of reference a response mode engenders. As demonstrated in Aglioti et al. (1995), the illusion associated with the Titchener-Ebbinghaus circles requires the participant to adopt an allocentric frame of reference that involves consideration of the surrounding circles. However, reaching for the poker chip involves the use of an egocentric frame of reference. This egocentric frame of reference, associated with the dorsal stream, allows the performance to be unbiased by the perceptual illusion. In the case of Aglioti et al.'s (1995) protocol, the performer moves her/his limb in the environment. However, limb movements are not required for all types of egocentric judgments. For example, observers adopt an egocentric frame of reference both when perceiving an object moving relative to themselves and when perceiving themselves moving through the environment. As mentioned above, the efferent copy allows the observer to differentiate object motion from self-motion (Gielen, 2001). Thus, it may be that motor involvement alters egocentric spatial coding. In this dissertation, the effect of motor involvement on an egocentric perceptual illusion was investigated. If dissociation between perception and action stems from the independent contribution of the ventral and dorsal streams, respectively, then an egocentric illusion should not be affected by the response requirements. Conversely, if motor involvement affects the perception of an egocentric illusion, then an alternate explanation should be sought. The egocentric illusion investigated in the present work involves visual-vestibular interactions.

Illusion in the perception of self-orientation

Graybiel (1952) observed that the perceived location of a target in space is altered by the resultant of all the inertial forces applied to the body during centripetal acceleration (i.e., gravity + centripetal acceleration). The resulting misperception termed the oculogravic illusion is usually accompanied by a bias in perceived body orientation (see also Graybiel & Brown, 1951). Whiteside (1961) subsequently investigated the effects of variation in resulting inertial forces on manual aiming. He observed that limb movements can be affected by variation in the magnitude of inertial forces (i.e., muscle loading/unloading). However, it was found that the visual illusion associated with the altered inertial environment supercedes the muscle loading/unloading bias (see Cohen & Welch, 1992 for a review). This visual bias (i.e., oculogravic illusion) entails egocentric spatial coding and is associated with vestibulo-ocular interactions.

Schöne (1964) demonstrated that the key to the oculogravic illusion is the shear created in the otoliths (i.e., utricle and saccule of the vestibular system). Any variation in the direction and/or the magnitude of the inertial forces creates variations in forces tangential to the otoliths' surfaces, which alter the orientation of the hair cells. A bend in the hair cells modifies their firing rate, which directly affects oculomotor muscle commands (Fluur & Melmström, 1970a, b). Feedback from the otoliths to the extra-ocular muscles is fed mainly through the vestibular nuclei (see Büttner-Ennever, 1999). However, modification of gaze orientation under altered vestibular stimulation does not fully account for the observed perceptual biases.

Ebenholtz and Shebilske (1975) measured gaze orientation while participants were asked to estimate what they perceived to be straight-ahead under different body tilt conditions in the median plane. Their results indicated that there was a mismatch between eye orientation and perceived straight-ahead. Indeed, the eye position bias was smaller than the perceptual bias. Thus, this type of illusion combines both an ocular rotation, which stems from vestibular stimulation (i.e., neurophysiological), and an additional visual bias (i.e., perceptual). Similar findings were reported with the more accurate infrared oculography technology (Brandt & Fluur, 1967a, b). Interestingly, visual context can reduce or even eliminate this type of visual illusion (DiZio, Li, Lackner, & Matin, 1997; Stoper & Cohen, 1989). Moreover, misperceptions of spatial orientation can be created from purely visual stimulation.

Asch and Witkin (1948) asked participants in an upright position to adjust a target line to the objective vertical while viewing it in a tilted environment (Rod-and-Frame Test: RFT). The results of this study revealed that the perception of verticality was biased in the same direction as the tilt in the visual environment, and therefore, away from the postural orientation (Asch & Witkin, 1948). Such bias in the perceived vertical can be explained by a vestibular and somatic affordance for being tilted. Further, females are usually more influenced by a tilted visual frame than males during perceptual decision-making about the true vertical (Witkin, Lewis, Hertzman, Machover, Bretnall Meissner, & Wapner, 1977). Thus, before investigating the influence of motor involvement on the perception of an egocentric illusion, we explored how perception of an egocentric illusion varies with gender. All of our investigations required participants to make judgments about the true straight-ahead position under different body tilts in the median plane.

Study 1- Gender Differences in the Perception of Self-Orientation

The first study included three experiments designed to distinguish between the effects of whole-body rotation, altered direction of inertial forces (i.e., gravity), and variations in blood distribution on perceived straight-ahead in both females and males. In the first experiment, we evaluated the combined effects of whole-body rotation and variation in the direction of inertial forces on the perception of straight-ahead. This stimulation was created by rotating the participant from a horizontal to an upright or an inverted position. In the second experiment, we isolated the effect of whole-body rotation on perceived straight-ahead. Participants were submitted to two conditions in which they estimated their straight-ahead in a horizontal supine position. In one condition, they were stable throughout a block of trials. In the other condition, they were rotated backwards from an upright orientation prior to each trial. Comparing the results of the first two experiments allowed us to discriminate between the effect of whole-body rotation and the effect of variation in the direction of inertial forces on the perception of straight-ahead. In the third experiment, the relative contribution of whole-body rotation and altered direction of inertial forces on perceived straight-ahead was evaluated in a within-participant design. In addition to replicating the previous studies, this experiment allowed us to control for the influence of baroreceptors (i.e., blood pressure receptors) on gender differences in the perception of straight-ahead. Indeed, it has been shown that stimulation of the baroreceptors can influence the perception of spatial orientation (Vaitl, Mittelsteadt, & Baisch, 1997). Thus, perceived straight-ahead was measured both in a 45° and a 135° orientation, with or without whole body rotation prior to a block of trials. It was expected that the 135° orientation would induce greater variations in blood distribution than the 45° orientation. These three studies were designed to determine the relative importance of whole body rotation, variation in the direction of inertial forces and variation of blood distribution on the perception of an egocentric illusion in both female and male participants.

Study 2 - Gender Differences in Perception of Self-Orientation: Software or Hardware?

The goal of the second study was to investigate the contribution of a perceptual strategy to the perception of straight-ahead. Based on the importance of vestibular afferent information for the perception of the oculogravic illusion (Schöne, 1964) and on gender differences in the size of the otoliths (Sato, Sando, & Takahashi, 1992), it could be argued that gender differences in the perception of straight-ahead stem from "hardware" differences between males and females. Indeed, the fact that males have larger otoliths might allow them to be less biased by variation in the direction of inertial forces than females. However, evidence that the focus of attention can alter perception of verticality (i.e., RFT) in female participants (Reinking, Goldstein, & Houston, 1974) highlights the potential contribution of "software" in perceptual decision-making. In this second study, we evaluated the importance of perceptual strategy on the perceived straight-ahead. With and without instructions to focus on internal or external sensory cues, males and females were asked to make perceptual decisions about their straight-ahead both in an upright orientation and a 45° body tilt. Thus, in contrast to the physiological determinants of our perceptual judgments (i.e., study 1), study 2 explored how these judgments might be mediated by strategy.

Study 3 - Afferent and Efferent Interplay for Perception and Action

In the final study, perceived straight-ahead was examined in participants using different response modes. Each response mode required a different degree of motor involvement. Because we were dealing with an egocentric illusion instead of more common allocentric illusions (e.g., Titchener-Ebbinghaus circles), this study was designed to determine if the contribution of efferent control is independent of the frame of reference adopted for perceptual decision-making. In addition to the perceived straight-ahead task, participants were required to complete a modified version of the RFT. This second part of the study allowed us to test Witkin's idea that the visual stimulus of a RFT can induce a vestibular and/or a somatic affordance of being tilted (see Goodenough, Oltman, & Cox, 1987).

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Gender Differences in the Perception of Self-Orientation

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Abstract

We investigated gender differences in the integration of afferent information for the perception of self-orientation. Male and female participants were asked to identify their Perceived Straight-Ahead (PSA) in different body orientations relative to gravity (i.e., pitch). Only the females presented a footward bias in PSA in an inverted condition as compared to an upright condition. However, when tested in a horizontal orientation, with or without prior whole body rotation, both males and females presented a footward bias in PSA. Further, using a 45° and 135° body tilt, gender differences were found only in the 45° conditions. Moreover, gender explained a significant amount of the variance in PSA when body rotation was not involved. These results are interpreted with reference to the literature on frame dependence (45) and circular vection (11, 27). We suggest that the otoliths represent the best candidate to explain gender differences in the perception of spatial orientation (35).

1.0 Introduction

Multiple sensory systems contribute to most of the perceptual judgements we make during our daily lives. Relevant to the work presented here, the perception of self-orientation is influenced by both visual information and the inertial forces that affect our vestibular system. For example, the perception of the true vertical (i.e., earth's vertical) is biased by a tilted visual environment (1, 44) and by variations in the direction and/or magnitude of inertial forces acting on the body (14, 22, 24, 26, 43). Interestingly, males and females appear to integrate afferent information for the perception of self-orientation somewhat differently.

Early work by Witkin and colleagues established gender differences in the perception of verticality using the Rod-and-Frame Test (RFT). The RFT requires the participant to orient a rod to the true vertical while a surrounding frame is tilted. As a general rule, "the perceived upright was always much closer to the visual than the postural vertical" (see 1, p.335). This bias in perceived orientation was explained by a vestibular and a somatic affordance of being tilted when the visual environment is tilted. The effect of frame tilt on perceived upright is termed frame dependence. Interestingly, females appear to be more frame-dependent than males (45). Gender differences also exist for other spatial tasks (see 29). As well as these visually-induced biases, gender differences in the perception of verticality can also be found with direct vestibular stimulation with a tilting chair (24, 34). In sum, the above literature shows that males and females integrate afferent information for the perception of the true vertical differently, whether the information is from a real or an illusory tilt.

Another example of gender differences in the perception of self-orientation comes from the work on visually-induced perception of body rotation (i.e., circular vection: 11, 27, 41). The methodology used to create circular vection requires a participant to sit in a stable chair, which is surrounded by a rotating drum. Usually, after observing the drum rotate for a certain time, participants perceive themselves moving in the opposite direction to the drum even though they remain stationary. The onset of this optokinetic illusion (i.e., circular vection) usually occurs earlier for females than for males. Once again, gender mediates visual-vestibular interactions (11). Similar gender effects were also found by inducing an illusion of self-rotation with a unilateral caloric stimulation (i.e., cold water irrigation) of the inner ear (41). The latter experiment indicates that gender differences stem from the vestibular system. Thus, gender differences are found for the perception of verticality and the perception of self-orientation.

Although females appear to be more frame dependent and more susceptible to circular vection than males, the strategic and neural processes associated with making perceptual judgements in these situations are quite different. Specifically, misjudgements in the RFT depend on the observer adopting an object-centred or allocentric frame of reference. For visual information, this type of context-dependent decision-making involves the ventral visual stream, which projects from the primary visual cortex to the inferotemporal cortex (33). In contrast, the illusion of self-motion induced by a moving environment requires a viewer-centred or egocentric frame of reference. This type of visually-induced bias in self-orientation is usually associated with the dorsal stream, which projects from the visual cortex to the posterior parietal areas (33). Thus, "visual vertical settings … are mediated by a separate processing channel" than perception of self-orientation (see 26, p.421), and gender differences are apparent for both types of perceptual decision-making.

Gender differences have been found for visually-induced (45) and body tilt-induced (24, 34) biases in the perception of verticality (i.e., allocentric). However, for misperceptions associated with an egocentric frame of reference, gender differences have only been found for visually-induced biases in the perception of self-orientation (11, 27). The main goal of the present work was to determine if gender differences also extend to visual biases induced from direct vestibular stimulation. We examined the influence of whole body tilt on Perceived Straight-Ahead (PSA). Inducing a whole body tilt has been shown to affect the PSA (16). More specifically, body tilt in the median plane leads to a footward bias in the perception of straight-ahead. The presence as well as the orientation of the visual environment can mediate this bias. This is the case both for the perception of verticality (1) as well as the perception of eye-level (31, 38). The neurophysiological and perceptual mechanisms that contribute to these visual-vestibular interactions are still not well understood.

Altering the direction of inertial forces acting on the participant should modify the afferent signal from all gravireceptors. For example, the otoliths (i.e., utricle and saccule) provide us with information for oculomotor control and self-perception. Specifically, hair cells located on different parts of otoliths' macula are associated with different oculomotor responses (17-18). Thus, altered inertial forces (i.e., direction and/or magnitude) modify the firing rate of hair cells in the utricle and the saccule. This afferent information is integrated by the vestibular nuclei and results in an oculomotor command (4). The ensuing eye rotation displaces the visual field on the retina. Consequently, when the magnitude and/or the direction of the inertial forces are altered, an individual misperceives her/his eye-level as well as the height of a target (5, 9-10, 13, 36, 42-43). This is true even in a static condition such as a supine position. Although this effect is associated with the doll reflex (16) and ocular counterrolling (12, 30), we prefer to use the term oculogravic illusion (20)[1]. A rotation from one orientation to another stimulates the semi-circular canals. Eye position following a whole body rotation could be influenced by variations in other sources of afferent information than the semi-circular canals (see 28). As well, besides the angular velocity and the body rotation period, eye position biases from the stimulation of the semi-circular canals depends on the ocular axis (e.g., vertical, horizontal, torsional; see 25). In short, angular accelerations usually induce an oculomotor response and an associated perceptual bias. This effect is termed the oculogyric illusion. The visual illusion arising from body tilt stems partially from a vestibulo-ocular bias (see 36). However, the ocular bias actually underestimates the magnitude of the perceptual effect (2-3, 16). Thus, biases in PSA entail both a vestibulo-ocular and an additional perceptual component (see Figure 1). In this work, we investigated gender differences in perception of self-orientation that encompass these two components. As well, we considered how afferent input from the baroreceptors affects the perception of self-orientation (40).

It is still unclear whether the gender differences in the perception of self-orientation are associated with one or more sources of afferent information or if they stem from the manner in which the information is integrated. The neural locus of such integration may be the posterior parietal cortex. This system is known to map many sources of afferent information for the perception of self-orientation (37). Interestingly, the same cortical system is implicated in the integration of visual information, which could explain the vestibular affordance of being tilted induced by a tilted visual environment. Thus, although it is still not possible to identify the specific source of afferent information responsible for the observed gender differences, there is a potential neurophysiological explanation for the similarities between biases in the perception of self-orientation resulting from vestibular and visual manipulations.

The purpose of the first protocol was to explore gender differences in the PSA associated with a whole body tilt. As a starting point, we examined conditions that resembled real-life situations. Specifically we employed whole body rotation that entailed variation in the direction of inertial forces. Obviously, such conditions stimulate most of the body receptors (19). In terms of vestibular influence, these conditions involve not only the stimulation of the semi-circular canals but also stimulation of the otoliths. Thus, this type of rotation is subject to both the oculogyric and the oculogravic illusions, respectively. Perception of straight-ahead in males and females was evaluated in an inverted and an upright orientation. Whole body rotation from a horizontal starting position preceded each trial. These extreme conditions were used to maximize PSA biases. Indeed, between the upright and the inverted conditions, the variation in the direction of inertial forces stimulating the otoliths is maximal (i.e., 180°), and the direction of the rotation stimulating the semi-circular canals is opposite (i.e., backward and forward). We anticipated that any difference in PSA between males and females would be most pronounced under these extreme conditions.

The purpose of the second protocol was to explore the relative importance of whole body rotation and the direction of inertial forces on gender differences in the perception of straight-ahead. In this second protocol, the only difference between the two experimental conditions was the presence of a whole body rotation prior to each trial. Thus, testing was performed in the same body orientation for both conditions (i.e., horizontal). As a result, the direction of the inertial forces acting on the body receptors was the same in the two situations. In terms of vestibular stimulation, these conditions involve similar otolithic stimulation but different semi-circular stimulation. This protocol was designed to evaluate the contribution of whole body rotation to gender differences on PSA.

In the last protocol, we attempted to evaluate the contribution of shifts in blood volume (i.e., baroreceptor stimulation) to gender differences in the perception of straight-ahead. While being inverted, a heavier participant is submitted to a greater upper body pressure than a lighter participant, which in turn, could lead to a different perceptual bias (40). In addition, this protocol allowed us to replicate the conditions of protocol one and two using a within-subjects design. Thus, we measured PSA both immediately after a whole body rotation and in a stable condition. We expected to account for the effect of shifts in blood volume (i.e., stimulation of the baroreceptors), as well as the oculogravic and oculogyric illusions, on gender differences in PSA.

2.0 Method

2.1 Participants

In each protocol, 20 members of the McMaster community (10 females, 10 males) participated in exchange for a financial compensation ($5). All participants had normal or corrected-to-normal vision and were unaware of the goal of the experiment. In protocol one, the mean age of the group was 21.9 years old (SD = 2.9 years) and all participants but one male were right-handed. In the second protocol, the mean age of the group was 19.9 years old (SD = 1.8 years) and all participants but one male and one female were right-handed. In the third protocol, the mean age of the group was 21.6 years old (SD = 2.3 years) and all participants but three males and one female were right-handed.

2.2 Apparatus

The equipment consisted of a straight-ahead perception device and an inverting device. For protocols 1 and 2, the straight-ahead perception device consisted of a series of 32 LEDs (4.5 cm intervals) installed on a track of 1.4 m long linked to a Bassin timer

(Lafayette Instrument Co.) and a handheld switch. The LED track was installed on a custom made pivot to allow manipulation of track orientation (i.e., upright and inverted). The pivot was fixed on a stand to allow height adjustments. The LED track was placed 1 m from the participant. The LED lighting sequence always started above the visual field (i.e., towards the feet). The Bassin timer was set with a preparation time of 0.5 sec. and a speed of 0.45 m/s (i.e., 1 mph) and provided timing performance to the nearest millisecond. Data provided from the Bassin timer were entered into a spreadsheet on a portable PC.

In the second protocol, two modifications were made to the straight-ahead measurement device. Specifically, the series of LEDs was installed over the inverting device (i.e., 0.9 m from the participant) and 27 LEDs were used (i.e., track length = 1.17 m).

In the third protocol, we employed a straight-ahead measurement device that consisted of an arc with a radius of 53.5 cm. In the centre, we placed a round, smooth manipulandum equipped with a potentiometer and a laser pointer (see Figure 2). The arc was made of a 4.5 cm wide piece of polymer painted in black. The potentiometer was linked through an Analog-to-Digital converter (Dataq DI-220) to a computer (586 Pentium 75), which acquired data with the Windaq program (Dataq Instruments). The potentiometer input was sampled at 100 Hz and provided a spatial resolution of 0.08 degrees. The manipulandum allowed the participants to adjust the position of the laser beam at perceived straight-ahead on the arc in a self-paced manner. This arc-manipulandum was installed on a 7 cm by 107 cm piece of plywood that could be moved along the saggital and longitudinal axis of the participant in such a way that the shaft of the potentiometer could be centred with the participant's eyes. This device was attached to the bed on the right-hand side of the participant. This equipment eliminated the timing component present in protocols 1 and 2.

The inverting device consisted of a bed rotating around its transverse axis, which was installed on a supporting frame secured to the wall (see Figure 3). The participant was secured on the bed by the means of a waist harness (KBOUM) and a set of carabiners. Spine board straps (FERNO) were used to stabilize the shoulders and a pair of Velcro straps was used for the feet. An adjustable cervical immobilization collar (WIZLOC) restricted head movements. The bed was equipped with an 8 cm thick foam mattress for comfort.

Following the study of Vaitl et al. (40), one of the goals of the third protocol was to evaluate the importance of shifts in blood volume on PSA. Because it was necessary to allow blood pressure to build up in the upper body, participants had to stay in an inclined orientation for more than a few seconds. For ethical reasons, two pitched positions were used instead of the inverted orientation: 45 degree and 135 degree supine. Accordingly, two pairs of straps were used to maintain the bed in the appropriate positions.

2.3 Tasks & Procedures

Before the experimental session, the participant provided informed consent according to the rules and guidelines of the ethics board of McMaster University. Afterward, the participant was secured to the bed with the above-mentioned pieces of equipment. Two experimenters were required for the experimental session. One experimenter manipulated the participant's body orientation by adjusting the bed while the other experimenter collected data about objective and perceived straight-ahead. The objective straight-ahead was measured prior to the experimental trials. For the experimental trials, the participants were asked to make perceptual judgments of their perceived straight ahead. The participant was instructed to keep her/his eyes still for all trials. In protocols 1 and 2, they were asked to press the hand held switch when the LED perceived to be straight-ahead was lit. In protocol 3, they were asked to position the laser on the arc at PSA.

In the first protocol, a typical trial started with the participant in a horizontal orientation with a small source of light (40 W light bulb). As depicted in Figure 4a, the participant then was asked to close her/his eyes and was moved into the appropriate orientation (i.e., inverted or upright) at approximately 20 degrees per second (i.e., 90° in 4.5 seconds). During this period, the lamp was shut off. A lock pin was used to secure the bed orientation during the trial. As soon as the participant was in the appropriate orientation, the experimenter said "ready" and "go". This delay between the achievement of the position and the "go" signal was 1.5 to 2.0 s. The participant was instructed to open her/his eyes at the "ready" signal and to look straight-ahead. On the "go" signal, the Bassin timer was activated for the preparation period (0.5 s) that was followed by LED lighting sequence and the participant's response. The delay between the initiation of the timer and the participant's response averaged 2.60 s. Thus, on average, there was a delay of 4.35 s between the end of the whole body rotation and the response. During each trial, only the LEDs were visible in an otherwise dark environment. After the response, participants were instructed to close their eyes and the second experimenter moved them back into the resting horizontal orientation for 5 s before the next experimental trial. However, for ethical reasons, the participant was allowed to request a longer intertrial interval if she/he felt nauseous or light-headed. This occurred in less than 5% of the trials. During that waiting period, the room was lit for the experimenter to record the data. This protocol included four sets of ten trials. Each participant was randomly assigned to a sequence. Half of the participants (5 males and 5 females) performed 10 trials in the inverted orientation followed by 10 trials in the upright orientation, and repeated that sequence twice. The other half of the participants started in the opposite orientation (i.e., upright) and also alternated between conditions.

In the second protocol, the task and procedure were similar to those of the first except for the following. Participants performed ten trials in each of the two conditions. In the first condition (Rotation), the participant was kept in a stable upright orientation for at least 15 s before being rotated backwards at approximately 20°/s to the horizontal orientation for an experimental trial (see Figure 4b). In the other condition (Stable), the participant was kept in a steady horizontal orientation throughout the 10 trials with at least 15 s between each trial. Participants were randomly assigned to a sequence. Half of the participants (5 males, 5 females) performed 10 trials in the stable condition and then performed 10 trials in the rotation condition. The other participants were submitted to the alternate sequence starting with the rotation condition.

In the third protocol, a typical trial was as follows. One experimenter placed the manipulandum in a random position. From trial to trial, this position was alternated between upward and downward from objective straight-ahead. Then, the same experimenter gave a "GO" signal to the participant. At that point, participants were allowed to open their eyes and place the laser beam at the PSA. The laser beam on the arc was the only source of visual information. The participants were asked to complete their response within 5 seconds. When the response was completed, the participant gave an "OK" signal. On that signal, a second experimenter triggered a marker on the data collection program. At the same time, participants closed their eyes in preparation for the next trial. Prior to each set of trials, unless described otherwise, a delay of 90 s was introduced in order to eliminate all remaining stimulation from the semi-circular canals. All participants were first placed in vertical upright orientation for 10 trials. Then, half of the participants were pitched at the 45° orientation while the other half were pitched to 135°. Because the sequence of events was identical, only the testing sequence starting with the 45° orientation is described (see Figure 5). Thus, after being positioned at the 45° orientation for 10 trials (Pitch 45), participants were rotated to the 135° orientation for another 10 trials (Pitch 135). Afterwards, the arc-manipulandum was placed at the marked position for the 45° condition before rotating the participant to that angle. Immediately after being rotated forward from 135° to 45°, participants performed 10 trials (FRotation). Afterwards, they performed another 10 trials in the same orientation (Post-FRotation). Then, the arc-manipulandum was adjusted to repeat the same sequence for the 135° position (BRotation and Post-BRotation). Thus, this set of conditions combined PSA measurements with or without whole body rotation prior to the trials. This occurred with both normal (45° conditions) or unusual (135° conditions) blood distribution. As well, in order to control for any potential after-effect of the oculogyric illusion, PSA performance was measured following a 90 s delay, both before and after a whole-body rotation (i.e., Pitch 45 and Post-FRotation, as well as Pitch 135 and Post-BRotation).

2.4 Analyses

For the first and second protocols, the temporal difference between the participant's response and the illumination of the straight-ahead LED was read from the Bassin timer's display (to the nearest millisecond). This temporal measure was then transformed into a spatial error according to the subject's objective straight-ahead measured prior to testing. For the third protocol, the accuracy of straight-ahead perception was determined by the angular difference between the calibrated true straight-ahead and the achieved position of the potentiometer. For all protocols, separate factorial analyses of variance were conducted and significant interactions were further analysed with the Tukey's HSD procedure ($p < .05$).

For the first protocol, a 2 Gender (Female, Male) by 2 Orientation (Inverted, Upright) by 20 Trials (1-20) mixed analysis of variance was conducted on the PSA error. For one participant, the room was accidentally lit during the inverted condition. As a structured background influences eye-level perception (37), the data from that participant were removed from the analysis. Also, two other participants revealed variability in timing error greater than two standard deviations from the group's mean variability. Such a pattern could be explained either by an inconsistent strategy or a failure to understand the task. Unfortunately, all of the participants concerned were female, which left us with 10 males and 7 females for the analyses.

In the second protocol, a 2 Gender (Female, Male) by 2 Condition (Rotation, Stable) by 10 Trials (1-10) mixed analysis of variance was conducted on the PSA error. Again, some participants revealed variability in spatial error greater than two standard deviations from the group's mean. Thus, the results of 2 females and 1 male were removed from the analyses.

In the last protocol, we calculated the constant error (CE) in degrees from the spatial error measures and performed separate analyses of variance for each experimental orientation (i.e., 45° and 135°). Thus, separate 2 Gender (Male, Female) by 4 Condition (Upright, Pitch, Rotation, and Post-Rotation) by 10 Trials (1-10) mixed analyses of variance were conducted on the PSA error. For an unknown reason, one participant managed to insert his chin into the cervical collar, which in turn, failed to maintain his head in a stable position. Not surprisingly, the data of that participant presented variability greater than two standard deviations from the average variability of the group and were removed from the analyses.

3.0 Results

3.1 First protocol

The analysis yielded a main effect for Orientation, F (1, 15) = 11.80, $p < .01$, and an interaction between Gender and Orientation, F (1, 15) = 9.56, $p < .01$. The breakdown of the interaction revealed that females estimated their PSA more footward in the inverted than in the upright orientation while orientation did not affect males significantly (see Figure 6). There were no effects or interactions involving Trial.

3.2 Second protocol

As depicted in Figure 7, the analysis yielded a main effect for Condition, F (1, 15) = 5.47, $p < .05$, where the PSA was more footward in the rotation condition (-0.63 cm) than in the stable condition (6.23 cm). There were no main effects or interactions involving Trial or Gender.

3.3.0 Third protocol

3.3.1 45° orientation

This analysis yielded main effects for Condition, F (3, 51) = 6.86, $p < .001$, and for Trial, F (9, 153) = 7.11, $p < .001$, as well as an interaction between Gender and Condition, F (3, 51) = 3.69, $p < .05$. Overall, participants presented a more footward bias in the Pitch 45 (-11.46 cm), the FRotation (-12.04 cm), and the Post-FRotation (-14.52 cm) than in the Upright condition (-5.87 cm). However, the breakdown of the Gender by Condition interaction revealed that only the females had a greater PSA bias in the Pitch 45, the FRotation, and the Post-FRotation conditions than in the Upright condition (see Figure 8a). Further, participants showed less footward bias in the first (-9.01 cm) than in the fifth (-10.81 cm) trial. Likewise, there was a smaller footward bias in the second (-9.97 cm) and the third (-10.05 cm) than in the eighth (-11.78 cm) trial, which was similar to the last trial (-12.26 cm).

3.3.2 135° orientation

This analysis yielded main effects for Condition, $F\ (3, 51) = 14.42$, $p < .001$, for Trial, $F\ (9, 153) = 3.67$, $p < .001$, as well as a Condition by Trial interaction, $F\ (27, 459) = 4.15$, $p < .001$. As depicted in Figure 8b, straight-ahead perception was less biased in the Upright (-5.87 cm) than in the Pitch 135 condition (-13.11 cm), which was not different from the Post-BRotation condition (-14.20 cm) but less biased than the BRotation condition (-19.85 cm). Overall, trial one (-14.73 cm) revealed greater footward bias than trial eight (-12.27 cm), nine (-12.53 cm), and ten (-12.32 cm). Perceived straight-ahead on trial two (-14.40 cm) was also more biased than on trial eight. However, the post hoc analysis of the Condition by Trial interaction revealed a greater footward bias in the second (-15.16 cm) trial than in the eighth (-10.31 cm) trial of the Pitch 135. For the BRotation condition, we observed a greater footward bias in the first (-26.00 cm) than from the third (-21.01 cm) to the last trial, and also a greater footward bias in the second (-22.62 cm) than in the sixth (-17.92 cm), ninth (-17.65 cm), and tenth (-17.83 cm) trial (see Figure 9).

3.3.3 Correlational/regression analyses

Correlation/regression analyses were conducted to determine the relative contribution of gender and three indices of blood volume on straight-ahead perception. These indices were weight, height, and body mass index. Body mass index is calculated by dividing the mass by the squared height of the participant. In these analyses, we used the above-mentioned independent variables to predict PSA bias from upright for both blocks of trials in each condition (i.e., difference between average error in the experimental condition and the upright condition).

As would be expected from the inferential statistics, gender accounted for a significant amount of variance ($p < .05$) in PSA in both block of trials of the Pitch 45 and the Post-FRotations (Pitch 45: Block 1, $r_b = .57$, Block 2, $r_b = .63$; Post-FRotation: Block 1, $r_b = .54$, Block 2, $r_b = .57$). More specifically, females presented more footward biases than males. Gender did not have a significant impact on perceptual judgements in any of the other conditions. Moreover, PSA judgments at Pitch 45 and Post-FRotation were independent of all blood volume indices (i.e., for weight, height, and body mass index: $r < .35$).

Interestingly, while our indices of blood volume failed to explain the obtained gender differences in the 45° conditions, body mass index and perceptual bias were significantly correlated in the second block of the BRotation (i.e., 135° orientation) ($r =$

.48). Note that it is in the BRotation condition that both males and females exhibited the most footward bias. The relationship between body mass index and PSA indicates that people with lower body mass indices present larger footward biases than people with higher body mass indices. Thus, while the shifts in blood volume were sufficient to create an important perceptual bias in the 135° conditions, they did not contribute significantly to the observed gender effects found in the 45° conditions.

4.0 Discussion

4.1 First protocol

In line with our expectations, the two extreme conditions were sufficient to create a significant straight-ahead perception bias although this effect was true only for the females. More specifically, it was found that females estimated their PSA more towards their feet in the inverted orientation as compared to the upright orientation. The males did not present a consistent bias. Males were more variable than females in the inverted condition[2]. As a result, the inverted condition affected the perception of self-orientation differently for males and females. The observed gender differences in the inverted condition are consistent with the literature on circular vection (11, 27, 41), frame dependence (44), and perception of verticality with body tilt (24, 34). It seems that integration of information about self-orientation differs across gender, whether it is from whole body rotation or visual stimulation. Interestingly, there is anatomical evidence that the vestibular apparatus is larger for males than females (35). This is true for both the superior semi-circular canal and the otoliths. With respect to the vestibular contribution, the variation in the direction of the inertial forces on the otoliths and/or the associated whole body rotation stimulating the semi-circular canals could have led to the observed gender differences.

4.2. Second protocol

The PSA results from the second protocol were straightforward. Specifically, both females and males showed footward PSA biases in the rotation condition relative to the stable condition. Because the direction of the inertial forces acting on the otoliths was the same in both conditions, it was assumed that the whole body rotation led to the footward bias in straight-ahead perception. In terms of vestibular stimulation, this rotation associated with the semi-circular canals did not lead to any gender differences in PSA. Of course, there are other afferent differences between the two conditions. For example, information from the baroreceptors could also affect perception of self-orientation (39). Regardless, there was no difference in PSA between males and females when the direction of the inertial forces was not changed. It appears that whole body rotation affects straight-ahead perception differently for males and females only when the direction of inertial forces is varied.

4.3 Third protocol

In this protocol, females demonstrated a footward bias in PSA when submitted to the 45° conditions (i.e., Pitch 45, FRotation, and Post-FRotation) as compared to the Upright condition. Also, as in protocol 1, males were not significantly affected by the modification in the direction of inertial forces. Moreover, gender predicted PSA biases in the stable 45° conditions (i.e., Pitch 45 and Post-FRotation). This finding provides support for the idea that variation in the direction of inertial forces contributes to gender differences in straight-ahead perception. In terms of vestibular stimulation, it is only when the semi-circular canals were not stimulated that gender was significantly correlated with straight-ahead perception. However, this does not mean that all males are immune to the perceptual effects induced by variation in the direction of inertial forces. Indeed, between-subject variability was greater for males than females in the Pitch 45 condition ($\underline{Fmax}$ (8, 9) > 6, $\underline{p} < .05$, for both blocks of trials). Certainly, further investigation of individual differences in the perception of self-orientation is required.

Interestingly, when submitted to the 135° conditions, both males and females presented a significant footward bias in PSA as compared to the upright orientation. Following the work of Vaitl et al. (40), these results support the idea that blood distribution in the body influences the perception of self-orientation. It appears that the 135° conditions (i.e., Pitch 135, BRotation, and Post-BRotation) induced stimulation from the baroreceptors, which led to significant footward biases both for females and males. Thus, in cases where the direction of inertial forces were modified, no gender differences in PSA were observed if there was time for blood to be redistributed.

With respect to when a straight-ahead judgement was made, it was found that even after 90 s in the Pitch 45 condition, the PSA bias continued to increase. Conversely, after a similar delay without whole body rotation, PSA error in the Pitch 135 condition appeared to decrease. Although variations in the magnitude of the perceptual bias is expected to vary with time (see 7), the direction of these variations simply reflect the Aubert and Müller effects associated with body tilt in the median plane (15). For the BRotation condition, it seems that the trial effect results from a gradual but incomplete reduction of the vertical nystagmus created by the rotation[3].

5.0 Conclusion

Gender differences have been found for many spatial tasks (29) including very cognitive tasks such as providing driving directions from a fictional map (32). As well, gender differences have been reported for visually-induced biases in the perception of self-orientation (RFT & Circular Vection). In the present study, we demonstrated that there were also gender differences for the perception of self-orientation associated with the modification of the direction of inertial forces. Our findings provide support for the proposition that gender differences stem from visual-vestibular interactions. They are consistent with studies on circular vection (11, 27, 41), the RFT (45), and perception of verticality with body tilt (24, 34). Our results demonstrated that a variation of the direction of the inertial forces without modification in blood distribution led to the observed gender differences. Without blood redistribution, gender predicted the perceived straight-ahead only if whole body rotation was not involved prior to performance (see Protocol 3). Although we did not control for each source of gravireception for the perception of self-orientation (e.g., neck proprioception; see 8), we suggest that the otoliths are responsible for the observed gender differences in the perception of straight-ahead.

Several lines of evidence support the latter proposition. First, whether it is from vestibular affordance created by a visual stimulus (e.g., RFT and circular vection) or from direct vestibular stimulation (e.g., caloric stimulation and body tilt), gender differences in the perception of self-orientation appear to stem from the same system. As an example, we have recently shown that there is significant correlation between visually-induced and body-tilt-induced biases in the perception of self-orientation (i.e., RFT and PSA with 45° body tilt: see 39). These common visual-vestibular influences may be associated with the posterior parietal cortex, which integrates afferent information for the perception of self-orientation (37). However, gender differences have not only been found for the perception of self-orientation (i.e., egocentric) but also for the perception of verticality (i.e., allocentric) (24, 34, 45). Thus, the posterior parietal cortex is an unlikely neurophysiological candidate to explain the observed gender differences found under both allocentric and egocentric frames of reference. This observation highlights the importance of the afferent signals from the gravireceptors. As gender differences in circular vection appear to be associated with the vestibular system (11), vestibular afference is a good candidate. For example, Welch et al. (41) found that perception of self-motion occurs earlier for females than males from caloric stimulation of the inner ear. Thus, given that: (a) gender differences in the perception of spatial orientation seem to stem from the sources of afferent information rather than the higher order structures involved in sensory integration, (b) visual-vestibular interactions differ with gender, and (c) variation in the direction of inertial forces alone leads to gender differences in straight-ahead perception, it is suggested that variations in afferent information from the otoliths are responsible for gender differences in the perception of self-orientation. Accordingly, the same source of afferent information would be responsible for the observed gender differences in perception of verticality (24, 34, 45).

In the first and third protocol, we found important gender differences in PSA. However, the males were more heterogeneous than females in the same conditions. Thus, stating that the perception of self-orientation is less biased for males than for females when varying the stimulation of the gravireceptors is misleading. Instead, we propose that the use of afferent information from the gravireceptors for the perception of self-orientation differs between individuals. As an example, if the observed gender differences in this work stem from anatomical differences in the size of the otoliths (35), then these size differences should more accurately predict the perception of self-orientation than gender. From this perspective, it may be appropriate to consider individual differences other than gender in future visual-vestibular research.

In summary, regardless of underlying mechanisms, variation in the direction of inertial forces affects the perception of self-orientation differently in females and males. Moreover, gender differences can be found for both visually-induced and body-tilt-induced biases in the perception of self-orientation. As well, they can also be observed whether the task requires an allocentric or an egocentric frame of reference. These gender differences not only have important implications for understanding the processes responsible for skilled perceptual-motor performance, but also for the design of educational, recreational, and work environments.

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Footnotes

[1] The use of the term doll reflex (16) is sparse in the current literature. As well, it would be inadequate to use the term ocular counterrolling (12, 30) as there is an ocular torsional aspect associated with counterrolling and we did not measure eye position. The term elevator illusion is associated with variations in the magnitude of inertial forces (see 10). Thus, we employed the term oculogravic illusion, which is associated with the otoliths (23). Any variation in the shear of the otoliths is expected to lead to a bias in eye-level perception (36), which includes static conditions. In fact, Clark and Graybiel (7) measured the delay for the oculogravic illusion to appear. This implies that this illusion is associated with the static perceptual bias of the target found after that delay (i.e., in a constant altered inertial environment; see 6) and not the apparent motion of the target. Although most work on the oculogravic illusion by Graybiel and colleagues involved manipulation of both the direction and the magnitude of the inertial forces (6-7, 20-23), variation in the direction of inertial forces is sufficient to lead to a shear in the otoliths (e.g., 36) and therefore, an oculogravic illusion.

[2] A F-max test revealed greater variance for the males than for the females for the inverted condition (F-Max (9, 6) = 10.83, $p < .01$).

[3] Note that the greatest effect of the whole body rotation appears on the very first trial. On average, this measurement was made 3.5 seconds after the end of the whole

body rotation, which is shorter than the average delay employed for the first and second protocols.

Figure Captions

Figure 1. Illustration of the vestibulo-ocular and perceptual components of straight-ahead perception bias.

Figure 2. Illustration of the arc-manipulandum installed on the inverting bed.

Figure 3 Illustration of the experimental inverting device.

Figure 4. Illustration of the experimental conditions employed in: (A) Protocol 1 and (B) protocol 2.

Figure 5. Illustration of the experimental conditions employed in Protocol 3.

Figure 6. Constant spatial straight-ahead perception error and standard error (cm) as a function of Gender and Orientation (Protocol 1).

Figure 7. Constant spatial straight-ahead perception error and standard error (cm) as a function of Gender and Orientation (Protocol 2).

Figure 8. Constant spatial straight-ahead perception error and standard error (cm) as a function of Gender and Condition in: (A) the 45 degree conditions and (B) the 135 degree conditions of Protocol 3.

Figure 9. Constant spatial straight-ahead perception error (cm) as a function of Trial for the 135° conditions (Protocol 3).

Figure 1

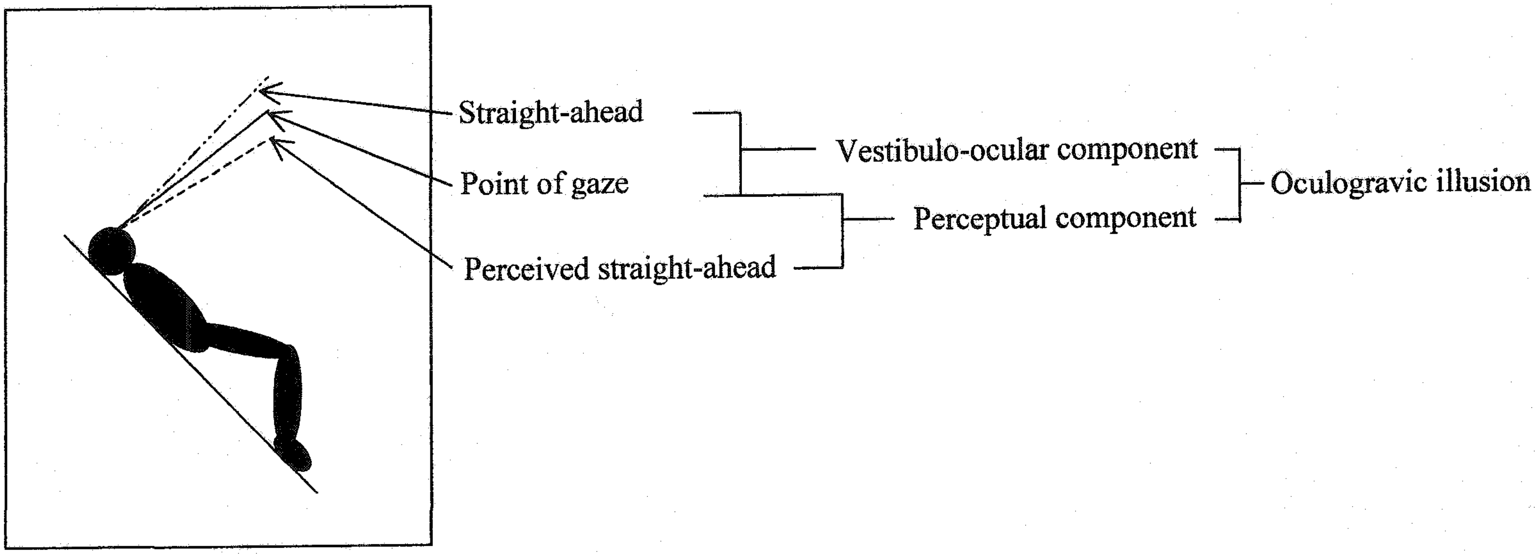

Straight-ahead
Point of gaze
Perceived straight-ahead
Vestibulo-ocular component
Perceptual component
Oculogravic illusion

Figure 2

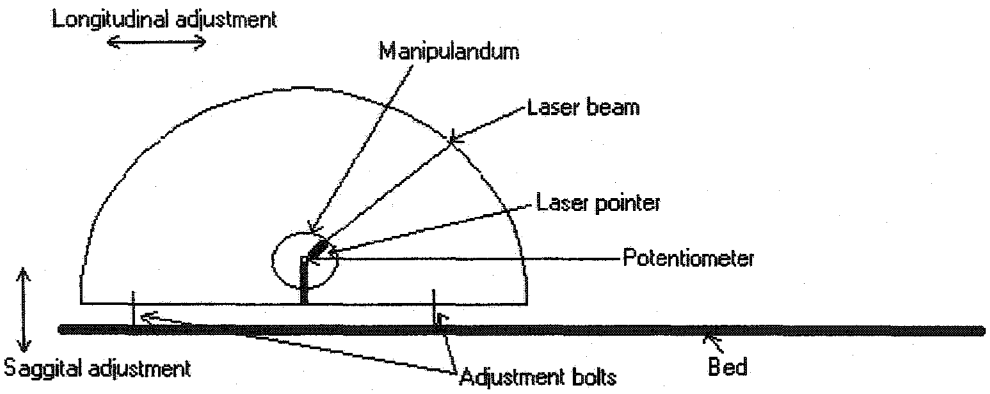

Longitudinal adjustment
Manipulandum
Laser beam
Laser pointer
Potentiometer
Saggital adjustment
Adjustment bolts
Bed

Figure 3

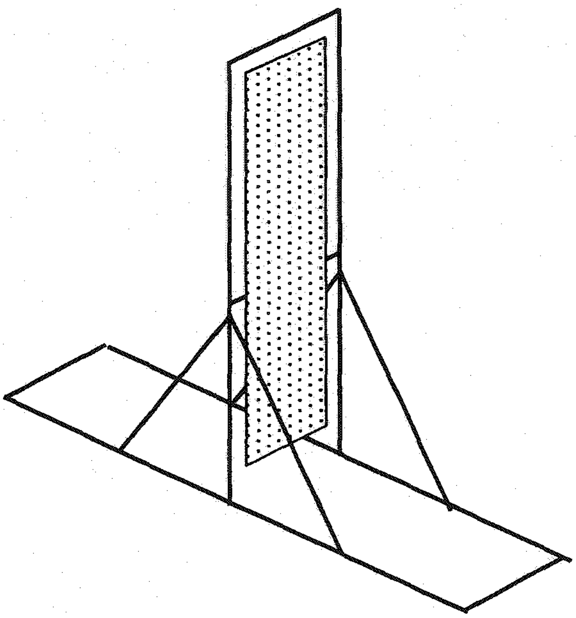


Figure 4

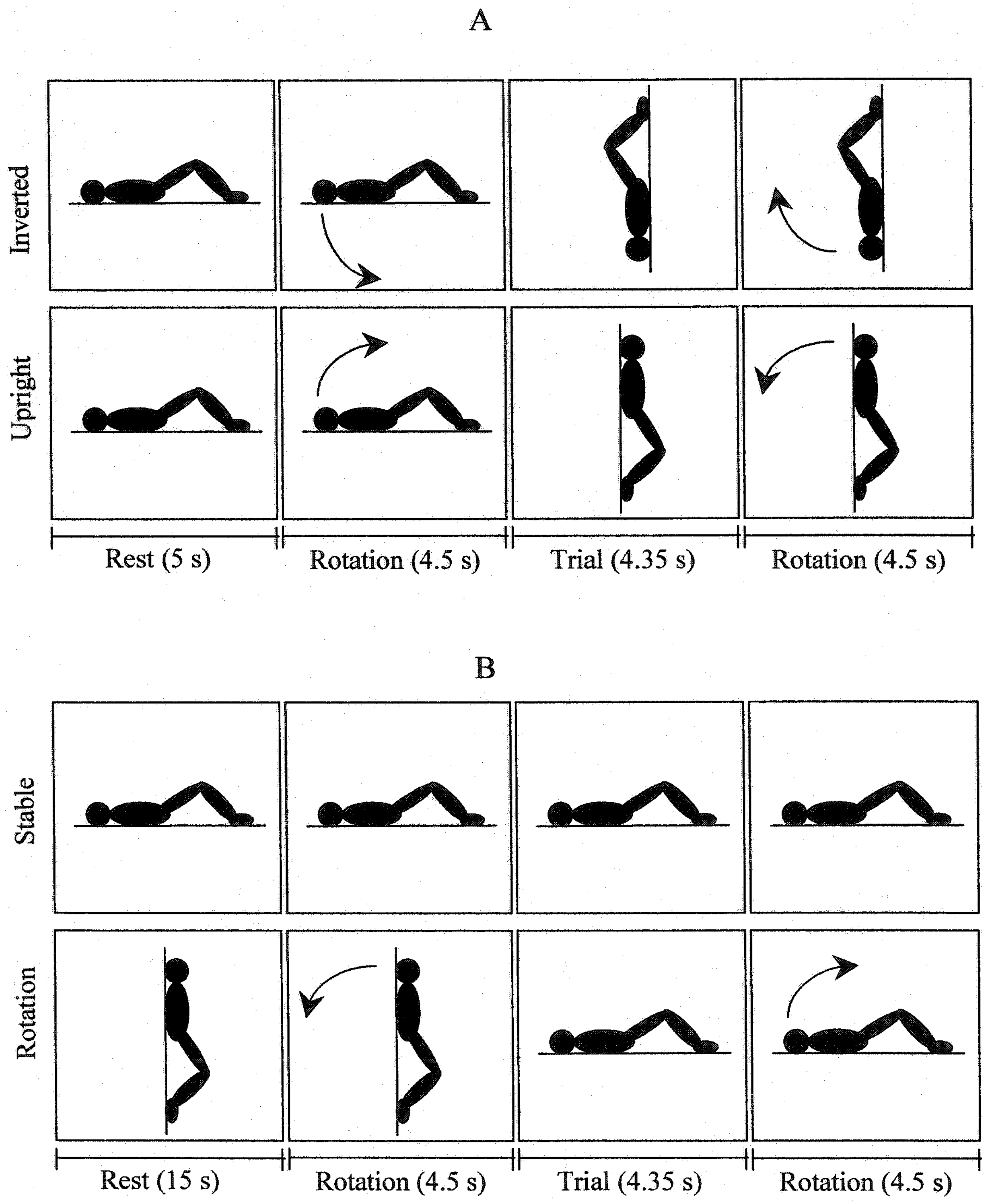
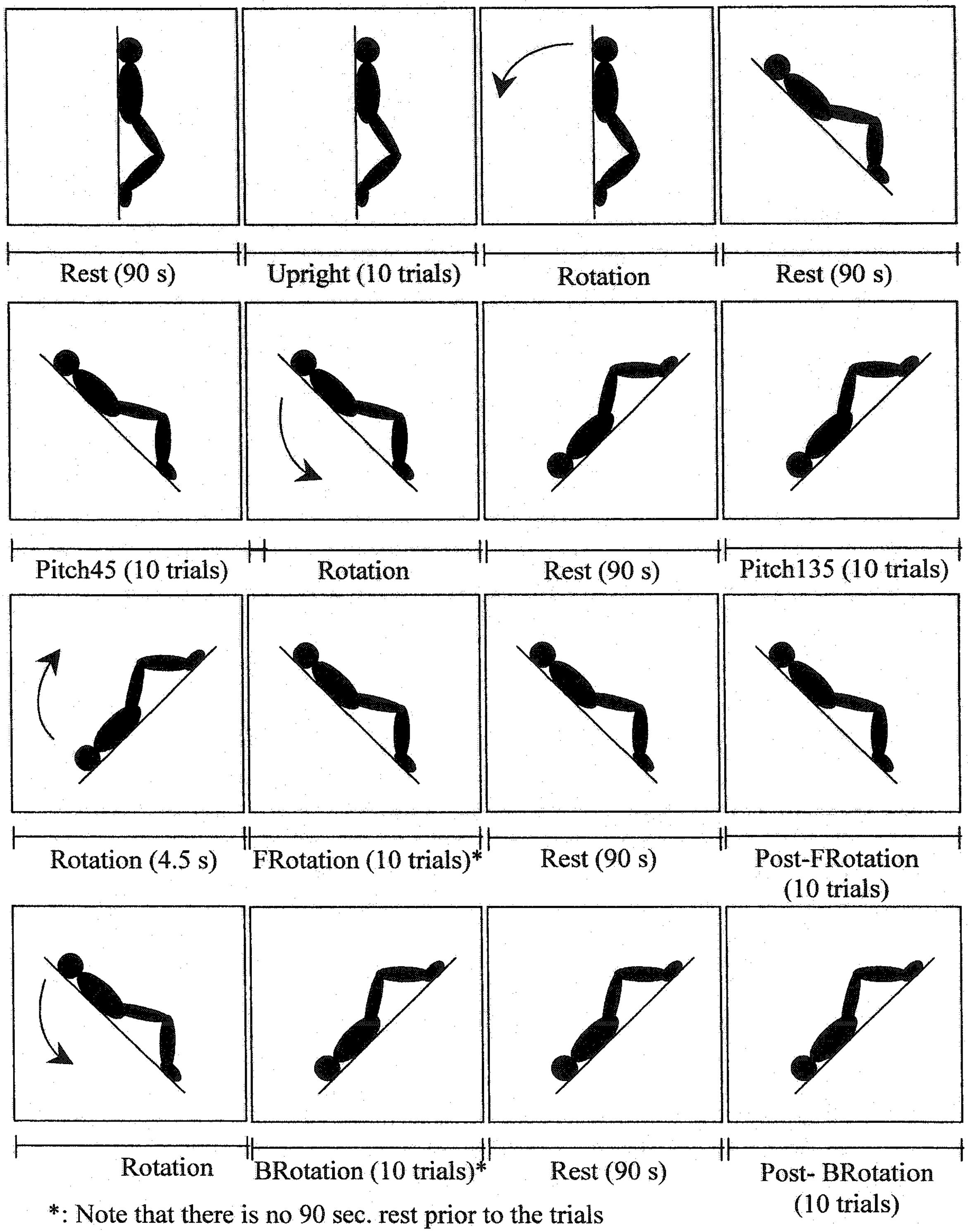

A
Inverted
Upright
Rest (5 s)
Rotation (4.5 s)
Trial (4.35 s)
Rotation (4.5 s)
B
Stable
Rotation
Rest (15 s)
Rotation (4.5 s)
Trial (4.35 s)
Rotation (4.5 s)

Figure 5



*: Note that there is no 90 sec. rest prior to the trials

Figure 6

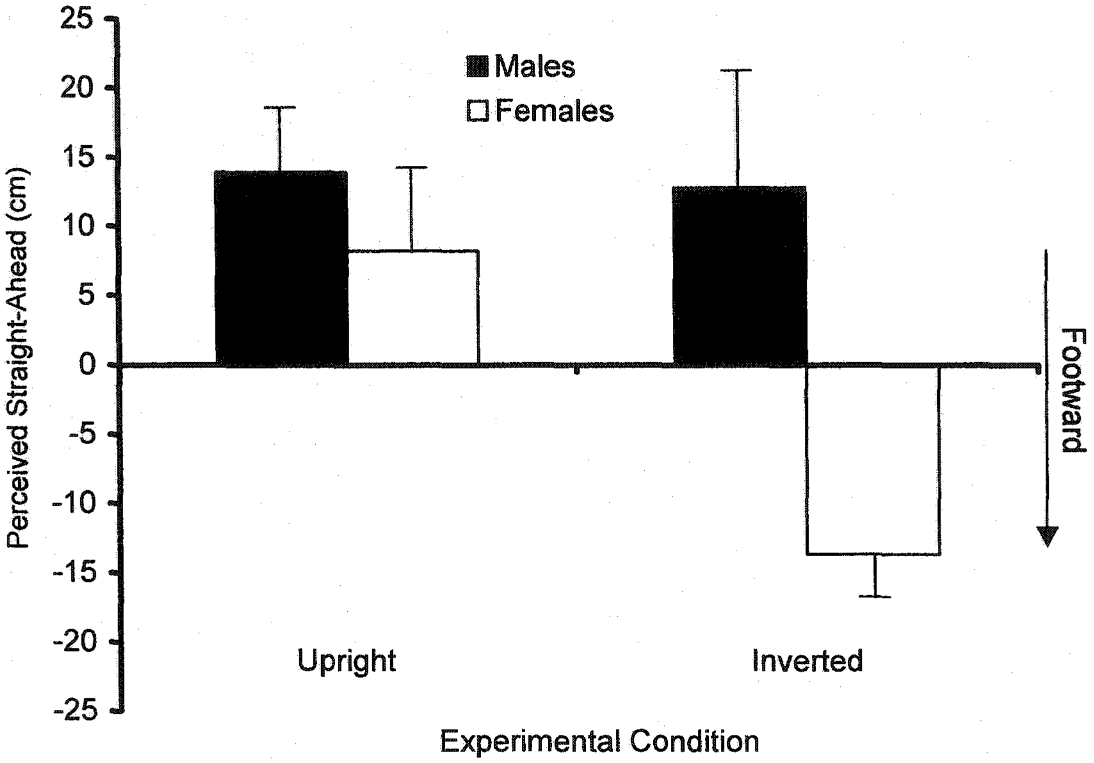

25
20
15
10
5
0
-5
-10
-15
-20
-25
Perceived Straight-Ahead (cm)
■ Males
☐ Females
Upright
Inverted
Experimental Condition
Footward

Figure 7

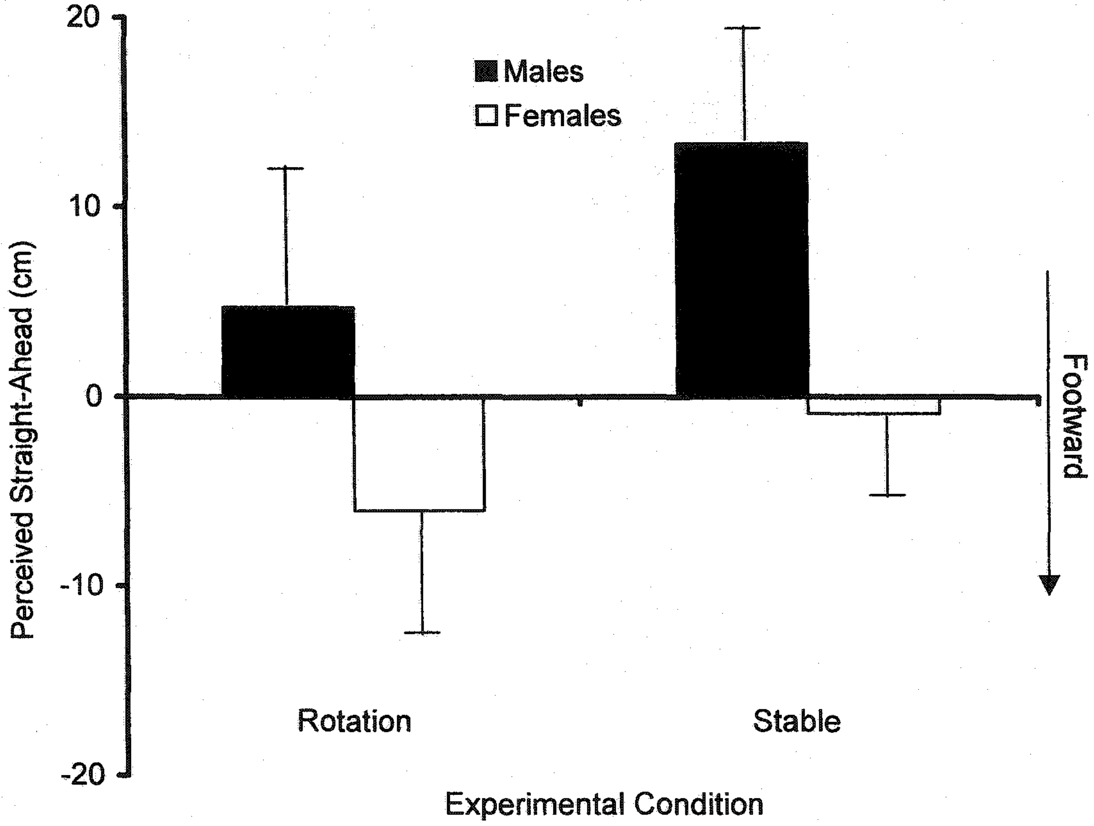

■ Males
□ Females
20
10
0
-10
-20
Perceived Straight-Ahead (cm)
Footward
Rotation
Stable
Experimental Condition

Figure 8

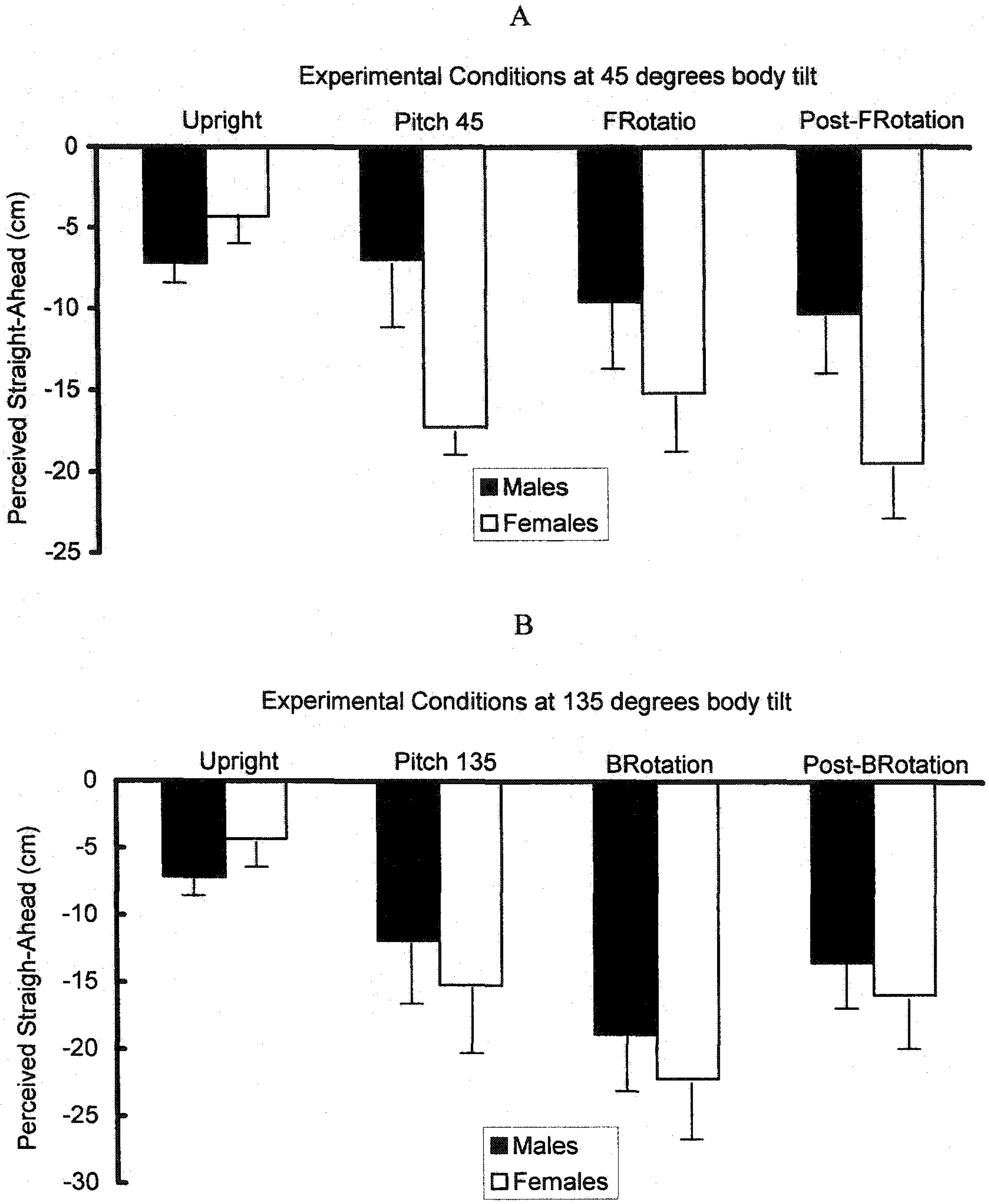
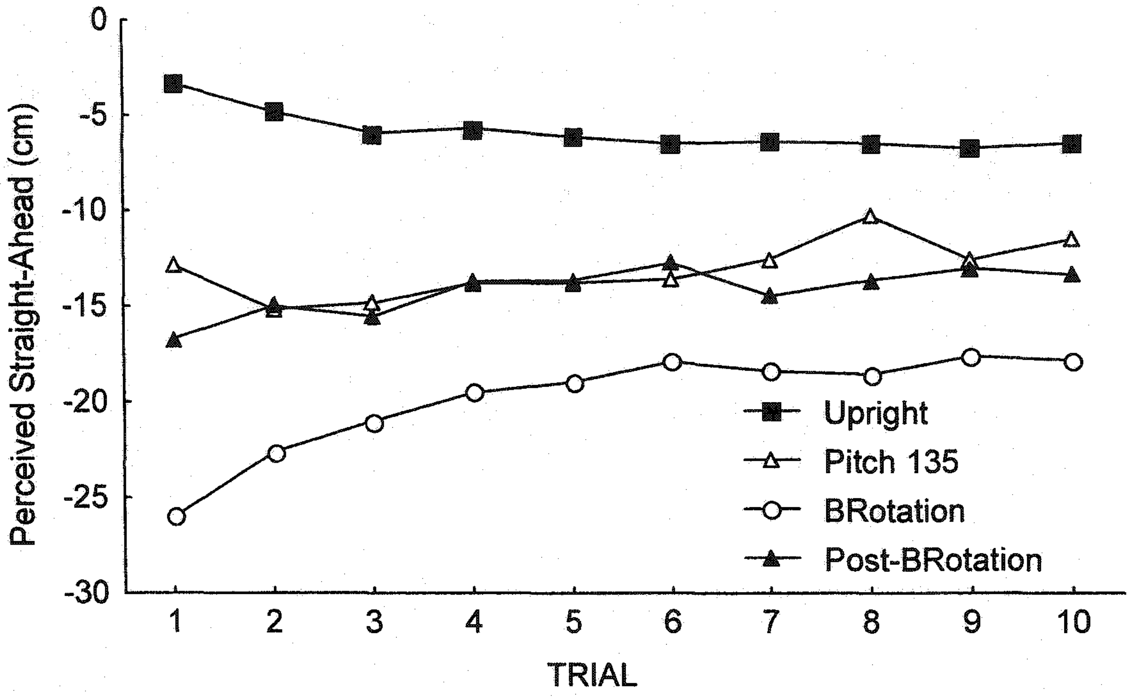

A
Experimental Conditions at 45 degrees body tilt
Upright
Pitch 45
FRotatio
Post-FRotation
Perceived Straight-Ahead (cm)
0
-5
-10
-15
-20
-25
■ Males
☐ Females
B
Experimental Conditions at 135 degrees body tilt
Upright
Pitch 135
BRotation
Post-BRotation
Perceived Straigh-Ahead (cm)
0
-5
-10
-15
-20
-25
-30
■ Males
☐ Females

Figure 9


0
-5
-10
-15
-20
-25
-30
Perceived Straight-Ahead (cm)
1
2
3
4
5
6
7
8
9
10
TRIAL
Upright
Pitch 135
BRotation
Post-BRotation

STUDY TWO

I was the major contributor to every aspect of this research project including experimental design, pilot testing, testing, data analyses, and write-up of the study. This paper has been submitted to Perception.

Running head: PERCEPTION OF SELF-ORIENTATION

Gender Differences in Perception of Self-Orientation: Software or Hardware?

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Abstract

In this study, we evaluated the contribution of attentional strategy to the perception of self-orientation with or without a body tilt in the median plane. Reinking, Goldstein, and Houston (1974) found that the frame-dependence of females on the rod-and-frame test (RFT) could be mediated by instructions prompting them to focus on internal cues (i.e., arising from inside of the body). Here, we measured the influence of attentional instructions on the perception of straight-ahead. Eleven females and thirteen males estimated their straight-ahead in an upright and a 45° body tilt in the median plane under three instruction conditions. All participants first performed without attentional instructions. Then, participants performed under both internal and external attentional instructions. For females, but not for males, perception of straight-ahead was more footward in the supine than in the upright orientation. Although instructions did not eliminate gender differences, internal instructions allowed females to reduce their perceptual bias in the supine orientation.

Gender Differences in Perception of Self-Orientation: Software or Hardware?

The incidence of scientific investigations on gender differences has recently increased and the area of perceptual-motor behaviour is no exception. Indeed, it is important to identify how females and males differ with respect to complex motor behaviours in order to appropriately design recreational and work environments. In this context, it is appropriate to determine the degree to which perceptual-motor differences between males and females stem from physiological vs. psychological sources. More specifically, it seems relevant to determine if gender differences in perception stem from differences in the neural structures involved in the sensory processing required to make perceptual judgments (e.g., visual system) or in the cognitive processes employed (e.g., attentional focus). Research on the rod-and-frame test generated a debate on the source of gender differences for spatial orientation tasks.

The rod-and-frame test (RFT: Asch & Witkin, 1948) requires the participant to orient a rod to the objective vertical. On some trials, a surrounding frame is upright, tilted clockwise (C), or counterclockwise (CC). As a general rule, participants tend to estimate the true vertical less accurately when the frame is tilted than when it is upright. The direction of this error depends on the orientation of the frame (i.e., Aubert effect or Muller effect: see Ebenholtz & Shebilske, 1973 and Wenderoth, 1977). Although both males and females exhibit this perceptual bias, frame dependence is generally more pronounced for females than for males (see Witkin, Lewis, Hertzman, Machover, Meissner, & Wapner, 1977, Ch.8).

One explanation of frame dependence is that the tilted frame creates a vestibular affordance (see Goodenough, Oltman, & Cox, 1987). More specifically, when a participant is trying to orient the rod to the true vertical, a tilted frame creates the self-perception of being tilted. Thus, it seems that biases in visual information (i.e., tilted frame) can induce a bias in the vestibular system (i.e., perception of being tilted). However, this "vestibular affordance" explanation of visually-induced biases in the perception of self-orientation was recently challenged.

Scholan and Smith (1990) conducted a RFT in which they restricted the size the visual display to central vision (i.e., less than 10°). The reduction of the visual stimulus to central vision was expected to prevent the visual-vestibular interactions, which can induce biases in the perception of self-orientation. Although the small display failed to induce a perceptual bias for males, female participants still exhibited frame dependence. Based on this gender difference, Scholan and Smith (1990) claimed that frame dependence is not associated with a vestibular affordance (cf. Goodenough et al., 1987).

Recently, we tested the vestibular affordance proposition more directly (Tremblay & Elliott, Study 3 of the present thesis). We first required participants to complete a RFT similar to the one used by Scholan and Smith (1990) (i.e., visual display of less than 10°). The same participants were also asked to make perceptual jugments about their self-orientation (i.e., straight-ahead) with body tilt in the median plane. The latter task does not present any visual bias but induces altered vestibular stimulation. Interestingly, we found that the perception of rod orientation with a small visual display in the RFT was significantly correlated with perception of self-orientation with body tilt[1]. In contrast to Scholan and Smith (1990), we argue that visual stimulation within central vision can lead to a bias in the perception of self-orientation. Thus, our data support the notion of vestibular affordance introduced by Witkin (see Goodenough et al., 1987) to explain gender differences in the RFT.

Gender differences in perception of spatial orientation can be found with other tasks. In a recent study examining the effect of body tilt on the perception of straight-ahead, we found that perception of self-orientation varied with gender (Tremblay & Elliott, Study 1 of the present thesis). We asked participants to evaluate their perceived straight-ahead in different body orientations relative to gravity, with or without whole body rotation prior to the perceptual judgment. Although one can expect the vestibulo-ocular reflex to lead to eye position biases with body tilt, there is an additional perceptual bias, which leads to an oculogravic illusion (Brandt & Fluur, 1967a, b; Ebenholtz & Shebilske, 1975) (see Figure 1). In our study (Tremblay & Elliott, Study 1 of the present thesis), females perceived their straight-ahead more footward than males when the direction of the inertial forces was changed. However, gender explained a significant amount of the variance only when no whole body rotation was involved prior to a trial and when the blood distribution remained normal (i.e., without stimulation of the baroreceptors: see Vaitl, Mittelsteadt, & Baisch, 1997). Other researchers (Groberg, Dustman, & Beck, 1969; Pitblado, 1976) have also reported gender differences in the perception of verticality with body tilt. In summary, gender differences have been found for visually-induced or body-tilt-induced biases in the perception of verticality and for visually-induced and body-tilt-induced biases in the perception of self-orientation. Both structural (i.e., hardware) and cognitive (i.e., software) explanations have been offered to explain these gender differences in the perception of spatial orientation.

The hardware explanation

Using a computed-assisted three-dimensional reconstruction of the human vestibular system from the temporal bones, Sato, Sando, and Takahashi (1992) found that some elements of the vestibular apparatus differ in size between males and females of all ages (from 1 day to 76 years old). More specifically, it was shown that the otoliths and the superior semi-circular canals are significantly larger for males than for females. As hair cell density is constant across gender (Merchant, Velasquez-Villasenor, Tsuji, Glynn, Wall, & Rauch, 2000), the otoliths of the average male contain more hair cells than the otoliths of the average female. Perhaps these additional hair cells in males provide the basis for a more dominant vestibular signal in males than in females. The relative contribution of the vestibular and visual signals could lead to the observed gender differences in the perception of verticality or self-orientation when the two sources of afferent information are in conflict (e.g., RFT). The latter proposition is supported by a recent finding (Tremblay & Elliott, Study 1 of the present thesis), which revealed that when only the direction of inertial forces was manipulated (e.g., otoliths), gender explained a significant amount of the variance in perceived straight-ahead. Thus, gender differences in spatial orientation tasks (e.g., RFT) may stem from differences in the size of the otoliths. However, differences in perceptual strategy may also explain gender differences in perception of spatial orientation.

The software explanation

Focus of attention is known to affect frame dependence (Reinking, Goldstein, & Houston, 1974). For example, instructing female participants to direct their focus of attention to internal cues can reduce frame dependence in the RFT. That is, when asked to pay attention to cues arising from the environment, participants were more biased by the visual frame than participants who were asked to pay attention to stimuli arising from their body. Thus, it appears that an attentional strategy can affect perception of spatial orientation.

In the present work, we attempted to identify the importance of an attentional strategy to gender differences in the perception of self-orientation with body tilt. Three sets of instructions were used to alter participants' focus of attention (i.e., no instructions, focus on internal cues, and focus on external cues). For each set of instructions, a perception of straight-ahead test was conducted both in an upright and a 45° supine position. In the no instructions condition, females were expected to demonstrate a significantly greater footward bias than males in the supine position (Tremblay & Elliott, Study 1 of the present thesis). Focusing on either internal or external cues should affect the perception of straight-ahead. Following Reinking et al. (1974), our first expectation was that perceived straight-ahead would be less biased if participants paid attention to internal cues. We expected only females to be affected by this strategy, because body tilt does not usually influence the perception of straight-ahead for male participants (Tremblay & Elliott, Study 1 of the present thesis). Thus, the goals of this study were to determine if an attentional strategy can: (a) reduce or eliminate the effect of variation in the direction of inertial forces on perception of self-orientation and (b) reduce or eliminate gender differences in the perception of self-orientation.

Method

Participants

Twenty-four members of the McMaster community (11 females,13 males) participated in this study in exchange for financial compensation ($5). Each participant provided written informed consent according to the rules and guidelines of the ethics board of McMaster University. All participants had normal or corrected-to-normal vision and all but one male were right-handed. As well, they were unaware of the purpose of the experiment.

Apparatus

The experimental session occurred in a dark room and involved an inverting device and apparati designed to measure perceived straight-ahead. The inverting device consisted of a bed that could be rotated around its transverse axis. The device was installed on a supporting frame secured to the wall (see Figure 2). The participant was secured on the bed by the means of a harness (KBOUM) and a set of carabiners. Spine board straps (FERNO) were used to stabilize the shoulders and a pair of Velcro straps was used for the feet. Further, an adjustable cervical immobilization collar (WIZLOC) restricted head movements. The bed was equipped with an 8 cm thick foam mattress for comfort.

The perceived straight-ahead measurement device consisted of an arc with a radius of 53.5 cm. It was 4.5 cm wide and painted black. In the center of the arc, there was a smooth round manipulandum equipped with a potentiometer and a laser pointer (see Figure 3). The potentiometer was linked through an Analog-to-Digital converter (Dataq Instruments – Model 220) to a computer (586 Pentium 75), which acquired data with the Windaq program (Dataq Instruments). The potentiometer input was sampled at 200Hz and provided a spatial resolution of 0.08 degrees. The manipulandum allowed the participants to adjust the position of the laser beam at perceived straight-ahead on the arc in a self-paced manner. This arc-manipulandum was installed on a 7 cm by 107 cm piece of plywood that could be moved along the saggital and longitudinal axis of the participant in such a way that the shaft of the potentiometer could be centered with the participant's eyes. This device was attached to the bed on the right-hand side of the participant.

Task & Procedure

After providing informed consent, the participant was secured to the bed with the above-mentioned pieces of equipment. The setup minimized head displacement or rotation. For the experimental trials, the participants were asked to make perceptual judgments of their straight-ahead. The participant was instructed to keep her/his eyes still for all trials (i.e., not to follow the displacement of the laser on the arc). The task was performed in the dark because visual context can influence evaluations of spatial orientation (Stoper & Cohen, 1989).

The experimental session included six sets of ten trials combining three sets of instruction (no instructions, external, and internal) with two positions (upright and 45° supine). All participants began with the no-instruction set as the internal and external instruction sets were expected to affect performance. Afterwards, performance with the internal and the external sets of instruction was counterbalanced across participants. The following instructions, derived from Reinking et al. (1974; p. 809), were read to the participant prior to performance according to the experimental condition: "In the next trials, it is important that you pay close attention to stimuli arising from [outside or inside] your body. The cues necessary to successfully perform the next set of trials lie [out there in your environment or in your body]. So remember, pay very close attention to [your environment or your body] and use the data you find there in making your decision about your straight-ahead." All participants were first tested in the upright orientation and then in the 45° supine orientation. Each set of ten trials was preceded by a 90 s waiting period during which participants were reminded of the attentional instructions. This period in a stable position was to eliminate perceptual effects associated with whole-body rotation (i.e., oculogyral illusion).

Each trial was performed as follows. First, the laser was positioned in such a way that the participant could not see it (i.e., either headward or footward). Then, the experimenter gave a signal that allowed the participant to open her/his eyes and perform the trial. At that point, the participant grasped the manipulandum and positioned the laser at the perceived straight-ahead, giving a verbal signal to the experimenter when the final position was achieved. At this signal, the experimenter inserted a marker in the data collection program, which was used later to establish perceived straight-ahead. Afterwards, the experimenter instructed the participant to close her/his eyes, move the laser either headward (i.e., up) or footward (i.e., down), and release the manipulandum before the next trial.

Analyses

The average perceived straight-ahead bias was calculated for each orientation under each instruction set. As male participants previously demonstrated greater between subject variability than females for the perception of straight-ahead with body tilt (see Tremblay & Elliott, Study 1 of the present thesis), we first performed separate preplanned analyses for both males and females. In order to identify if any perceptual bias was due to body tilt, we contrasted straight-ahead perception biases in the upright and the 45° supine orientation. Other sets of preplanned analyses were conducted to examine the importance of instructions on perceived straight-ahead. Specifically, for both females and males, separate analyses were performed to contrast each instruction condition (i.e., internal and external) to the no instruction condition. During data collection, data were lost for two male participants due to a computer failure.

Results

The first planned comparisons revealed that, regardless of the attentional instructions, females estimated their straight-ahead more footward in the 45° supine orientation than in the upright orientation ($\underline{F}$ (1, 20) = 5.14, $\underline{p} < .05$). This was not true for males ($\underline{F}$ (1, 20) = 0.28, $\underline{p} > .6$). The second set of planned comparisons contrasted no instruction judgments in the supine orientation with judgments of the two attentional sets of instructions. These analyses revealed that neither males nor females were significantly affected by the internal instructions (Males: $\underline{F}$ (1, 20) = 1.45, $\underline{p} > .24$; Females: $\underline{F}$ (1, 20) = 2.50, $\underline{p} > .12$) or by the external instructions (Males: $\underline{F}$ (1, 20) = 0.50, $\underline{p} > .48$; Females: $\underline{F}$ (1, 20) = 0.35, $\underline{p} > .56$). Thus, only females presented a greater footward straight-ahead perception bias in the supine than in the upright orientation. This occurred regardless of the attentional instructions (see Figure 4).

Although there was no influence of strategy in the original analysis, it is possible that the order in which participants were instructed to focus on internal vs. external cues affected the straight-ahead judgments. For example, as is apparent in Table 1, the smallest difference in perception of straight-ahead was found between the second block of trials of the upright and the supine orientation for the female participants starting with and performing under internal instructions. To investigate this possibility, we decided to run an additional analysis in which the order of testing (i.e., order of instructions) was included as a factor, along with trial block. As well as the anticipated main effect for Gender ($\underline{F}$ (1, 18) = 5.32, $\underline{p} < .05$), this analysis revealed a 5-way interaction between

Gender, Order, Instructions, Orientation, and Block of trials ($F(2, 36) = 5.77$, $p < .01$). Selected post hoc comparisons (Tukey HSD, $\alpha < .05$) revealed that female participants who performed under the internal set of instructions first were not more biased in the second block of trials in the supine orientation than in the first ($p > .06$) and the second ($p > .42$) block of trials in the upright orientation when performing with the internal set of instructions. As well, comparing the straight-ahead biases found in the supine orientation for the females who were first submitted to the external instructions, there was a smaller perceptual bias in the first block of trials under the internal instructions than both blocks of trials performed with the external instructions (Block 1: $p < .01$; Block 2: $p < .01$) and the first block of trials performed without instructions ($p < .05$). Thus, at least to some extent, instructions mediated the footward straight-ahead perception bias typically found for females. However, in the supine orientation, female participants estimated their straight-ahead more towards their feet than males regardless of the instruction presentation order, the instructions employed, and the block of trials ($p < .05$).

In order to determine the relative contribution of Gender and Instructions to the perception of self-orientation, Gender by Instruction analyses were conducted on the data from the 45° body tilt condition. Gender explained 25 times more variance in the perception of straight-ahead than Instructions (Gender: $\omega^2 = .129$; Instruction: $\omega^2 = .005$).

Discussion and Conclusion

The goal of this study was to determine if an attentional strategy could reduce or eliminate the effect of variation in the direction of inertial forces on perception of self-orientation and thus reduce or eliminate gender differences in the perception of self-orientation. First, we have some evidence that strategy can affect the perception of straight-ahead with body tilt. Specifically, females who first performed under external instructions demonstrated a smaller straight-ahead perception bias in the first block of trials with the internal instructions than in both blocks of trials with the external instructions and the first block of trials without attentional instructions. Also, the females who performed under internal instructions before external instructions exhibited no more bias on the second block of trials in the supine orientation than in the upright orientation. It appears that an internal but not an external focus of attention allowed female participants to eliminate their straight-ahead perception bias between an upright and a supine position. Thus, gender differences in the perception of self-orientation were at least slightly reduced when participants performed with internal instructions. However, while strategy has some influence, it does not eliminate gender differences in the perception of self-orientation. As a result, it seems that gender differences in the perception of spatial orientation stem largely from "hardware" and not "software" differences.

Anatomical differences in the vestibular apparatus have been found between males and females (Sato et al., 1992). More specifically, the otoliths and superior semi-circular canals are larger in males than in females. As suggested above, this size difference could result in a more dominant vestibular signal for males than for females. As variation in the direction of inertial forces leads to gender differences in the perception of self-orientation (Tremblay & Elliott, Study 1 of the present thesis), it could be that difference in the size of the otoliths between males and females is responsible for gender differences in the perception of spatial orientation. Indeed, if there are gender differences only in the vestibular but not in the visual system, the relative contribution of visual and vestibular information differs between males and females. Interestingly, this "hardware" difference also explains why females are influenced by visually-induced biases in spatial orientation such as circular vection (Darlington & Smith, 1998; Kennedy, Hettinger, Harm, Ordy, & Dunlap, 1996) and the RFT (Witkin et al., 1977).

In conclusion, it appears that physiological differences supersede the effects of strategy (i.e., internal focus of attention) in determining gender differences in the perception of self-orientation. However, the possibility that the relative contribution of vestibular and visual afferent information for the perception of spatial orientation differs across gender raises an important issue about perceptual judgments under different environmental conditions. Indeed, under normal gravity circumstances, it has been observed that tasks performed in visually-deprived or biased environments, influence females more than males (Darlington & Smith, 1998; Kennedy et al., 1996; Witkin et al., 1977). If this differential effect of visual cues for the perception of self-orientation in males and females reflects the relative use of vestibular information over visual information, then females may have an advantage over males while performing tasks under reduced vestibular stimulation (e.g., microgravity conditions of a space flight). On the other hand, it should also be considered that the visual environment is more likely to be unusual in microgravity conditions, which would then suggest that females could be more affected than males in altered gravity circumstances. At least, it appears that the ability to adapt to different environmental conditions should be examined as a function of gender.

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Footnotes

[1] It should be noted that it was only when there was no frame around the rod or when the frame was in the same orientation as the rod that performance at the RFT was significantly correlated with perception of self-orientation with body tilt. There was a little relationship between the RFT performance and perception of straight-ahead during body tilt when the rod and the frame were in different orientations. Thus, even though restricting a display to central vision appears to reduce field dependence in the RFT (i.e., Scholan & Smith, 1990), information restricted to central vision can still induce a biased perception of self-orientation (i.e., a visually-induced vestibular affordance).

Table 1

Perceived straight-ahead bias (deg) as a function of Gender, Order, Instructions, Orientation, and Block of trials

		No Instructions				External Instructions				Internal Instructions			
		Upright		Supine		Upright		Supine		Upright		Supine	
Gender	Order	1	2	1	2	1	2	1	2	1	2	1	2
Females	External 1st	-8.5	-9.7	-17.1	-17.7	-7.5	-8.8	-18.9	-18.8	-7.5	-6.8	-12.5	-15.9
	Internal 1st	-11.0	-11.5	-17.8	-17.8	-9.8	-9.8	-14.2	-14.7	-9.8	-10.7	-15.3	-13.9
Males	External 1st	-6.2	-6.4	-7.6	-8.6	-2.2	-3.3	-4.9	-6.4	-3.2	-5.0	-3.3	-3.0
	Internal 1st	-3.6	-4.3	-6.2	-7.0	-5.6	-5.4	-7.6	-5.4	-5.3	-4.7	-7.2	-7.2

Figure Captions

Figure 1. Drawing of the perceptual and vestibulo-ocular components of the oculogravic illusion.

Figure 2. Drawing of the experimental inverting device.

Figure 3. Drawing of the arc-manipulandum installed on the inverting bed.

Figure 4. Perceived straight-ahead (deg) as a function of Gender, Instructions, and Orientation.

Figure 1

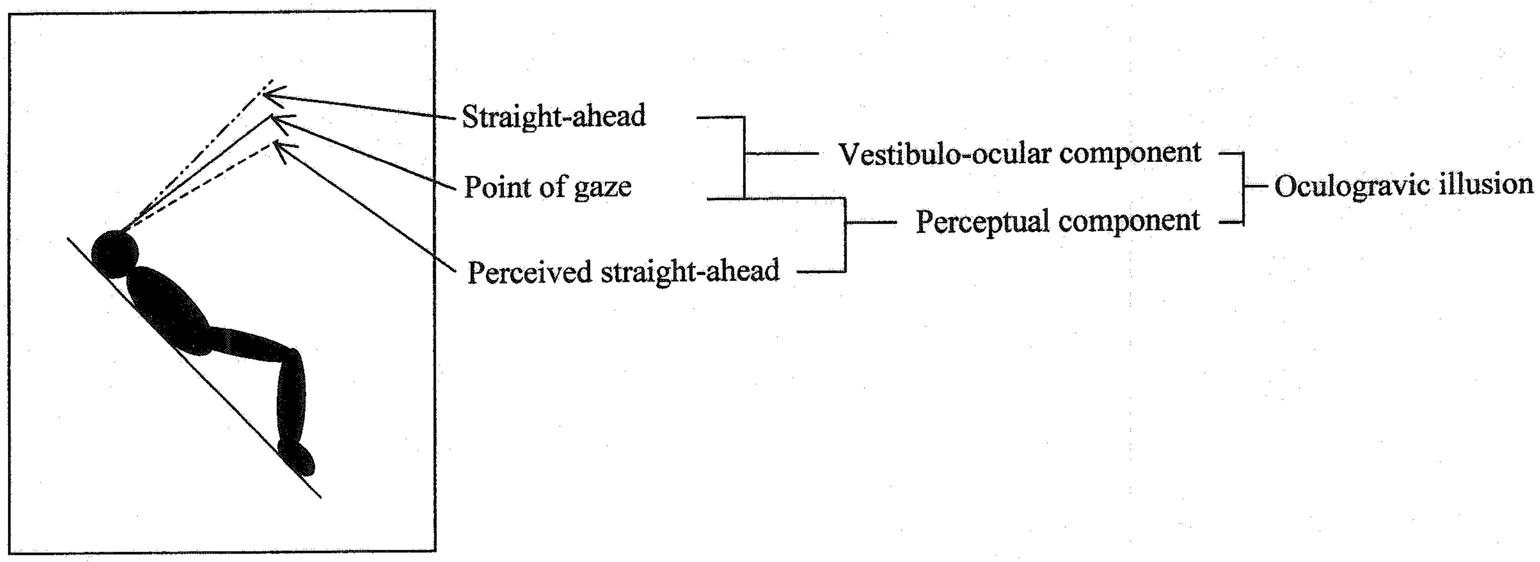

Straight-ahead
Point of gaze
Perceived straight-ahead
Vestibulo-ocular component
Perceptual component
Oculogravic illusion

Figure 2

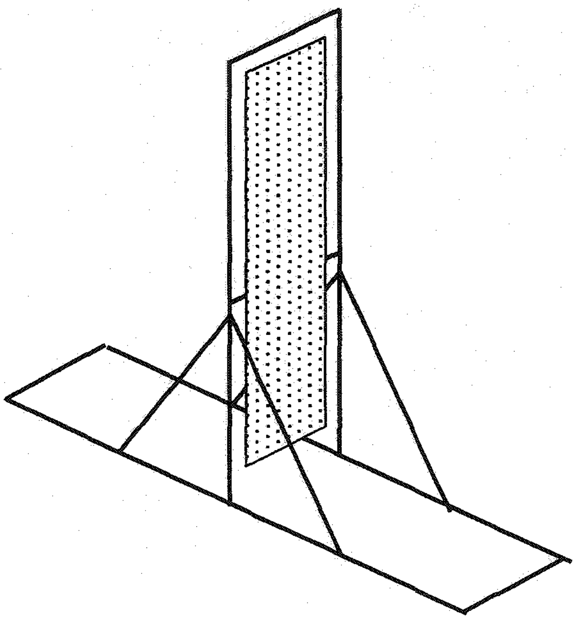


Figure 3

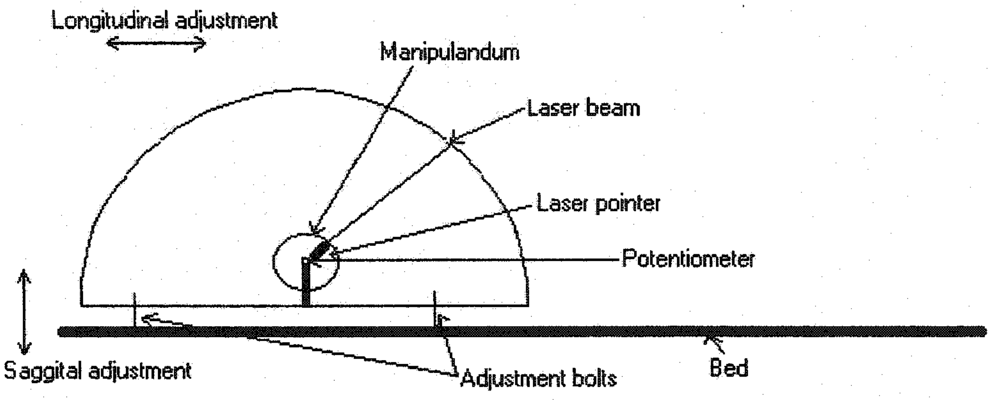
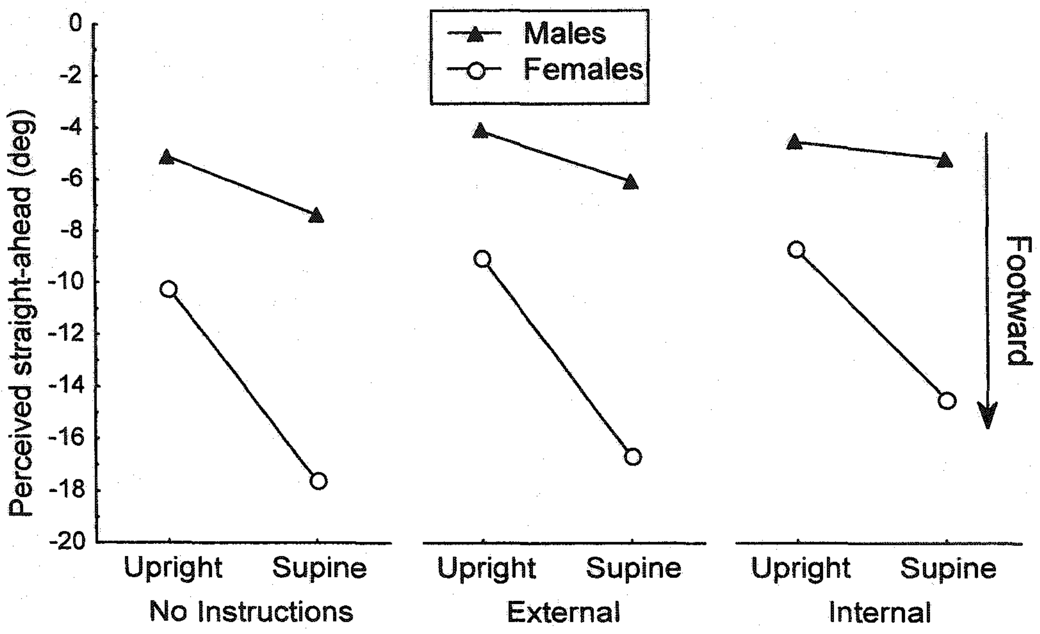

Longitudinal adjustment
Manipulandum
Laser beam
Laser pointer
Potentiometer
Saggital adjustment
Adjustment bolts
Bed

Figure 4


Males
Females
Perceived straight-ahead (deg)
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
-20
Footward
Upright
Supine
No Instructions
Upright
Supine
External
Upright
Supine
Internal

STUDY THREE

This manuscript has been submitted for publication to Experimental Brain Research. I was the major contributor to every aspect of this research project including experimental design, pilot testing, testing, data analyses, and write-up of the study.

Running head: PERCEPTION AND ACTION

Afferent and Efferent Interplay for Perception and Action: The Influence of Response Mode on an Egocentric Illusion

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Abstract

Milner and Goodale (1995) forwarded a model of visual organization that accounts for differences between perception and action via the use of two visual streams (i.e., ventral and dorsal) specialized for specific types of visual coding (i.e., allocentric and egocentric). In this study, we evaluated the effect of action on the perception of an egocentric illusion. Eighteen participants were asked to perform two tasks. First, they estimated their straight-ahead under two body tilts in the median plane (i.e., pitch) using five different response modes. The response modes varied in the degree of efferent and cognitive involvement. The participants were also asked to perform a custom rod-and-frame test. Differences in straight-ahead perception between the two body tilts were significant only when proximal limb control was not involved. Further, there was a significant correlation between estimations of perceived straight-ahead with body tilt and estimations of rod orientation in the RFT (i.e., without body tilt). These results are discussed in terms of cerebellar involvement rather than ventral-dorsal stream interactions (e.g., Milner & Goodale, 1995).

Afferent and Efferent Interplay for Perception and Action: The Influence of Response Mode on an Egocentric Illusion

Researchers interested in perceptual-motor behaviour have traditionally been concerned with how particular perceptual experiences influence the organization and control of movements. The typical procedure used to investigate sensorimotor interactions has been to manipulate perceptual variables and to observe their impact on motor behaviours. In the last decade however, researchers have accumulated a large body of evidence to indicate that the type of motor or cognitive response a person makes influences the very nature of the perceptual experience. In the same vein, it has been shown that the availability of efferent information affects the manner in which afferent information is acquired, interpreted, and remembered.

In the case of visual perception, efferent information about eye movements (i.e., corollary discharge) is needed for the perceptual system to distinguish between environmental motion and self-motion (see Gielen, 2001). This type of distinction has been identified at the single cell level for the integration of afferent and efferent information about head position. For example, Roy and Cullen (2001) demonstrated that a subclass of vestibular neurons (i.e., vestibular-only neurons) respond to semi-circular canal stimulation only when accompanied by efferent information about neck movements. Indeed, the sensitivity of vestibular-only neurons to head movements was reduced only when those head movements were voluntary. Conversely, vestibular-only neurons responded normally when head movements were passive. Thus, the interplay between efferent and afferent information appears to be crucial for determining the spatial location and orientation of both the observer and objects in the environment. It appears that the importance of such afferent-efferent interplay extends from using efferent information about head movements to maintain visual constancy to remembering manual positioning movements based on non-visual information.

In a study that involved remembering a limb position over a brief retention interval, Lee and Hirota (1980) demonstrated that passively encoded movements (i.e., experimenter controlling the participant's limb) were best remembered when they were reproduced passively. Actively encoded movements were reproduced best under active retrieval conditions. Thus, the withdrawal and even the addition of efferent information about limb control disrupted performance during retrieval. It appears that in addition to sensory processes, motor processes affect our perceptual judgements.

A number of recent studies have shown that susceptibility to certain visual illusions depends on the response requirements associated with the perceptual judgements. For example, Aglioti, Goodale, and DeSouza (1995) used grip size (i.e., distance between index and thumb) to evaluate the perceived diameter of poker chip disks surrounded by Titchener-Ebbinghaus circles. When simply estimating the size of the poker chip with their grip size, participants were affected by the size of the surrounding circles. However, during a reach and grasp movement, the same grip component was found to be unaffected by the illusion. Similar dissociations between cognitive and motor judgements have been reported for the Müller-Lyer illusion (Daprati

& Gentilucci, 1997). Milner and Goodale (1995) have used this type of finding, as well as clinical and animal evidence, to forward a neurophysiological model of visual processing (see also Livingston & Hubel, 1988; Schneider, 1969; Ungerleider & Mishkin, 1982).

Milner and Goodale (1995) suggested that there are two distinct visual streams. These streams are associated with different types of perceptual judgements and response requirements. The ventral stream, which projects from the visual cortex to the inferotemporal cortex, is specialized for form perception and object recognition. These perceptual judgements require an 'object-centred' view of the stimulus as well as the encoding of its intrinsic properties (e.g., its use). This 'object-centred' view implies that visual information is spatially encoded in a frame of reference centred on the object. The response mode associated with the ventral system is usually cognitive and language-based. The dorsal stream extends from the visual cortex to the superior parietal areas. This stream is associated with more action-based perceptual judgements, which require the control of limb and body movements (e.g., moving to a location in space, intercepting a moving object). The dorsal stream provides a 'viewer-centred' perspective of the stimulus. Thus, visual information is spatially encoded in a frame of reference centred on the viewer. This is sometimes referred as 'egocentric coding'. In 'object-centred' (i.e, ventral) perceptual decision-making individuals adopt, what has been termed, an allocentric frame of reference. In the case of visual illusions (e.g., Aglioti et al., 1995), an allocentric frame of reference entails consideration of the target stimulus in the context of the objects around it (e.g., the surrounding circles in the Titchener-Ebbinghaus illusion). However, when participants actually reach for an object, they adopt an egocentric perspective in which the encoding of object size is independent of the visual surround. Interestingly, Glover and Dixon (2001) reported that there can be a transition between these frames of reference within a single perceptual-motor task.

Glover and Dixon (2001) observed that the initial reaching component of a grasping movement was affected by a visual illusion but that the terminal phase of the movement was not. These results led Glover and Dixon (2001) to suggest that movement planning was based on allocentric coding (i.e., ventral) but that on-line control processes employ an egocentric frame of reference (i.e., dorsal). In the research described above, visual illusions associated with allocentric coding disappeared with greater motor involvement (i.e., an egocentric frame of reference). Thus, it appears that resistance to visual illusions with increased efferent control stems from a shift in the frame of reference adopted by the performer (i.e., allocentric to egocentric).

McIntyre, Berthoz, and Lacquaniti (1998) suggested that gravity “can potentially be used to align the different frames of reference” (p.146). This gravity-based alignment involves an ongoing calibration procedure based on gravitoinertial forces. Interestingly, this calibration procedure may also affect the way people make perceptual judgements (cf. Milner & Goodale, 1995).

Aglioti et al. (1995) observed that a reaching movement towards an object mediated the perception of the object’s size. In the case of the Titchener-Ebbinghaus’ circles, the perceptual illusion stems from an allocentric frame of reference. This perceptual bias disappeared when the task required a reaching movement –an egocentric frame of reference. While in this case, a transition from an allocentric to egocentric frame of reference reduced the impact of the illusion, the response mode can also influence our spatial judgement within a frame of reference. Indeed, a number of visual illusions are egocentric in nature and may also be affected by response mode. For example, the elevator illusion is a misperception of the height of a target when the magnitude of the inertial forces acting on the body is changed. Investigations on the elevator illusion led Cohen and Welch (1992, p.162) to suggest that "If subjects' limbs are not restrained and supported before and between pointing trials, changes in the apparent weight of the limbs might inform the subjects of the nature of the gravitational-inertial environment". Referring back to McIntyre's et al. (1998) proposition, it seems that integration of gravitational information provided during the movement of the arm (e.g., forces required to move the arm in a particular direction and the resulting feedback) allowed for proper calibration of the spatial environment. Thus, response mode appears to be an important determinant of perception/misperception. In contrast to the empirical work associated with Milner and Goodale's (1995) model of visual perception, changes in spatial judgements do not require a transition from one frame of reference to another. In this theoretical context, the purpose of the present study was to investigate the influence of motor involvement on perceptual judgements about the location of a point in egocentric space.

In work involving an egocentric frame of reference, Whiteside (1961) reported that manual aiming was greatly affected by the manipulation of kinesthetic and/or vestibular afferent information. The aiming apparatus used in this research consisted of a planar surface located in front of the participant and a mirror placed between the aiming surface and the participant. The mirror provided a virtual target and prevented the participants from seeing their limb during the execution of the movement. Whiteside (1961) used parabolic flight and a centrifuge to manipulate vestibular and/or kinesthetic information. He also submerged the participant's body under water (but not the head) to manipulate kinesthesis. Aiming accuracy was significantly altered in all situations compared to aiming under normal conditions. In the submerged condition, participants overshot the target (i.e., terminated their movement above the target). Overshooting probably occurred because the magnitude of the motor command necessary to reach the target under normal gravity (i.e., 1G or $9.8 m/s^2$) is greater than under water. This interplay between limb inertia and the necessary motor commands is termed muscle loading/unloading. When the gravitational forces are increased (i.e., macrogravity) or decreased (i.e., microgravity) in magnitude, the required efferent command to bring the limb to the same endpoint is increased or decreased, respectively. However, in both the parabolic flight (i.e., microgravity) and the centrifuge (i.e., macrogravity), the movement endpoints were lower and higher than the target, respectively. These results are opposite to the expected muscle loading/unloading effects. Indeed, Whiteside (1961) found that the visual illusion was strong enough to supercede muscle loading/unloading effects (i.e., pointing higher under 0G and lower under 2Gs: see Cohen & Welch, 1992 for a review). It should be noted that this oculogravic illusion (Graybiel, 1952; Graybiel & Brown, 1951) is usually unconscicous[1] and entails egocentric spatial coding (i.e., spatial relationship between the observer and a point in space). Interestingly, perception of verticality is also influenced by the direction of the inertial forces acting on the body (Wiktin, 1950). Further, these perceptual biases are associated with vestibulo-ocular interactions.

Schöne (1964) identified the underlying mechanisms that explain the effects of gravity on perception. Although associated with the vestibulo-ocular reflex, Schöne (1964) demonstrated that the key to the oculogravic illusion is the shear created in the otoliths. When the direction and/or the magnitude of the inertial forces are modified, the resulting bend of the hair cells, created by the tangential forces to the surface of the otoliths, mediates the firing rate of the hair cells. In turn, the firing rate of hair cells in different locations in the otoliths alters the oculomotor muscle commands (Fluur & Melmström, 1970a, b). These vestibulo-ocular interactions are associated with variations in eye-level perception and oculogravic illusions. However, modification of gaze orientation under altered vestibular stimulation does not fully account for the observed perceptual biases.

Ebenholtz and Shebilske (1975) photographed the eyes of participants in a calibrated structure while they were estimating the perceived straight-ahead in different body tilts in the median plane. Interestingly, the difference between the perceived and true straight-ahead was greater than the eye orientation bias created by the vestibular stimulation. As depicted in Figure 1, this type of illusion combines both an ocular rotation, which stems from vestibular stimulation (i.e., neurophysiological), and a visual bias (i.e., perceptual). Brandt and Fluur (1967a, b) reported similar findings when measuring eye position using infrared oculography. For example, for a gaze shift of 300 minutes of arc, there was an associated perceptual bias of more than 600 minutes of arc. Thus, when inertial forces are altered in direction and/or magnitude, one should observe a variation in eye position as well as a perceptual bias. It is also important to note that while vestibular stimulation has an important influence on visual perception, the contribution of vestibular input is mediated by the visual context in which perceptual judgments are made (see also DiZio, Li, Lackner, & Matin, 1997; Stoper & Cohen, 1989).

Misperceptions of spatial orientation can also be created by purely visual stimulation. For example, it is possible to create the illusion of being tilted by having a tilted visual display in front of an upright individual. Asch and Witkin (1948) asked participants in an upright position to adjust a target line to the objective vertical while viewing it in a tilted environment (Rod-and-Frame Test: RFT). With a frame tilted at 22°, the perceptual biases were in the direction of the environmental surround. Indeed, "the perceived upright was always much closer to the visual than the postural vertical" (Asch & Witkin, 1948, p.335). The tilted visual frame is thought to induce a vestibular and a somatic affordance of being tilted (Goodenough, Oltman, & Cox, 1987; cf. Scholan & Smith, 1990). Thus, orientation biases are induced in a solely visual manner.

Milner and Goodale's (1995) model of visual perception and the empirical work on illusions used to support this model do not consider the contribution of the vestibular system in visual perceptual decision-making. The primary focus of the present research is on how response mode interacts with direct vestibular input (i.e., body tilt) to influence the perceptual judgements we make about spatial orientation. A second purpose of the present research is to determine if spatial judgements associated with direct stimulation of the vestibular apparatus predict orientation biases induced in a solely visual manner (i.e., no direct vestibular input). If there is a relationship between spatial judgments involving direct vestibular and visual inputs and spatial judgments involving visual inputs only, it could mean that the same neural mechanisms are involved in these two types of spatial decision-making.

Method

Participants

Eighteen members of the McMaster University community (9 females and 9 males) took part in the experiment (Mean age = 25.3 years, SD = 3.9 years) in exchange for a small financial compensation (i.e., $10). Each participant provided informed consent according to the guidelines of the ethics board of McMaster University. The participants were unaware of the purposes of the experiment.

Apparatus

The oculogravic illusion apparatus included a tilting device to incline the participant and a device to record perceived straight-ahead. The tilting device was installed in a dark room (7' X 14' approx.). The device consisted of a bed that could rotate around its transverse axis (see Figure 2). The participant was secured to the bed by the means of a waist harness (KBOUM). Spine board straps (FERNO) and Velcro straps were used to stabilize the shoulders and the feet, respectively. Head movements were restricted by an adjustable cervical immobilization collar (WIZLOC). The bed was equipped with a 8 cm thick foam mattress for comfort.

The perceived straight-ahead measurement device consisted of an arc with a radius of 53.5 cm. It was 4.5 cm wide and painted black. In the centre of the arc, a smooth round manipulandum was equipped with a potentiometer and a laser pointer (see Figure 3). The potentiometer was linked through an Analog-to-Digital converter (Dataq Instruments – Model 220) to a computer (PC compatible, AMD450MHz processor), which acquired data with the Windaq program (Dataq Instruments). The potentiometer input was sampled at 200Hz and provided a spatial resolution of 0.04°. The same straight-ahead measurement device was used to obtain perceptual judgments about the straight-ahead with five different response modes. The participants were able to adjust the position of the laser beam (or just their limb depending on the response mode) at perceived straight-ahead in a self-paced manner without gravitational influences other than their own limb weight. This could be done by using the manipulandum alone

(Outside diameter = 12.0 cm, grip diameter 7.3 cm) or when the device was equipped with a counterbalanced aiming rod (42 cm). As well, it was possible to engage a switch-controlled DC motor against the manipulandum, which moved the laser at 41.30°/s or 4.55°/s. The fastest speed was used by the experimenter to place the laser away from the participant's field of vision. The slowest speed, controlled by another spring-loaded switch, allowed either the experimenter or the participant to adjust the position of the laser at the perceived straight-ahead. The link between the motor and the manipulandum was added or withdrawn according to the experimental task. This arc-manipulandum was installed on a 7 cm by 107 cm piece of plywood that could be moved along the saggital and longitudinal axis of the participant in such a way that the shaft of the potentiometer could be centred with the participant's eyes. This device was attached to the bed on the right-hand side of the participant.

The RFT was run on a PC (AMD450MHz processor) with the E-Prime software (Psychology Software Tools Inc., Beta 5 version) using a 17 inch monitor (AOC, Spectrum 7Glr). The spatial resolution of the framed and unframed visual stimulus bitmaps was the maximum allowed by the E-Prime software (1280 X 1024 pixels). The frame consisted of two parallel lines of equal length (500 pixels long by 10 pixels wide or 11.0 cm by 0.2 cm) and the rod was a single line (400 pixels long by 10 pixels wide or 8.8 cm by 0.2 cm) centred in the frame. Both were white and presented on a black background in an otherwise dark environment. The participant sat at least 70 cm from the monitor on a 45 cm high chair. The centre of the screen was at 110 cm from the floor. A stimulus including both a rod and a frame viewed 70 cm away subtended a visual angle of less than 10°.

Task and Procedure

The participant was secured to the bed with the above-mentioned pieces of equipment. For the experimental trials, the participants were asked to make perceptual judgments of their own eye-level by looking straight ahead. The participant was instructed to keep her/his eyes still during all trials.

The experimental session included five response modes performed in two different body orientations. The first response mode was verbal (Verbal) where the DC motor allowed the experimenter to control the position of the laser. The second response mode involved the same DC motor but the switch was controlled by the participant (Switch). The third response mode involved the use of the smooth manipulandum alone (Wrist). For the fourth and fifth response modes, the aiming rod and its counterweight were installed on the manipulandum. In these response modes, the arm of the participant was almost fully extended and the rod's position was manipulated with the index finger. In the fourth response mode, the laser was shut off and the participant was required to aim her/his index finger at eye-level (Arm w/o Laser). The fifth response mode was similar to the fourth except that the laser was turned on (Arm). Although the presentation of the response modes was sequential (i.e., from Verbal to Arm), half of the participants performed each response mode in the 15° body orientation first while the other half always started with the body 75° body orientation.

Each trial was performed as follows. The direction of the laser was oriented footward and outside the participant's field of view before each trial even if it was shut off (i.e., Arm w/o Laser). Then, the experimenter gave a signal that allowed the participants to open their eyes and perform the trial. The participants were instructed to keep their eyes still during the trial and to position the laser and/or finger at perceived straight-ahead, giving a verbal signal to the experimenter when the final position was achieved. This signal was used by the experimenter to insert a marker in the data collection program and determine perceived straight-ahead. Afterwards, the manipulandum/aiming rod was moved footward (i.e., down), outside the field of view before the next trial. For each trial, a measure of perceived straight-ahead (i.e., signed angle value) was obtained from the potentiometer at the marker inserted upon the participant's signal.

The RFT consisted of 90 trials. Each trial started with a fixation point (1 sec) followed by presentation of the target rod (140 ms), a delay including a fixation point (3 sec), a comparison rod (140 ms), and a delay allowing the participant to respond (3 sec) (see Figure 4 for protocol description). A frame accompanied the target rod on 83.3% of the trials but never accompanied the comparison rod. The participant was asked to indicate whether the comparison rod was in the same orientation, rotated Clockwise (C) or Counter Clockwise (CC) relative to the target rod. The response was recorded through the E-Prime software with the numbers 1, 2, and 3 of the keypad of a standard keyboard and was spatially compatible (i.e., left key = CC, middle key = same, right key = C). For the target rod, the six frame conditions (no frame, 0°, 15° C, 15° CC, 75° C, 75° CC) were combined with five rod orientations (0°, 15° C, 15° CC, 75° C, 75° CC). Each of the 30 possible combinations were presented 3 times in order to present each of the possible associated comparison rod, which could be at the same orientation, 3° C, or 3° CC from the target rod.

Analyses

The average perceived straight-ahead was calculated for each block of five trials, for each orientation (i.e., 15° and 75°) and in each response mode. This led to a 2 Gender (Female, Male) by 5 Response Mode (Verbal, Switch, Wrist, Arm w/o Laser, Arm) by 2 Position (15°, 75°) by 2 Block (1-5 trials, 6-10 trials) analysis of variance with repeated measures on the last three factors. Similar analyses were conducted for the standard deviations of the perceived straight-ahead measures. Significant effects were further analysed with the Tukey HSD post hoc procedure. Alpha was set at .05 for both the ANOVAs and the post hoc analyses.

The accuracy of spatial orientation judgments for the RFT was scored as a function of congruency. Averaging the results for two types of display, we calculated the percentage of trials in which participants correctly identified the relative orientation between the target and comparison rods. The first type of display was termed incongruent as it included all the trials in which the target rod was accompanied by a frame in a different orientation from the rod. The second type of display was termed congruent and it included the trials in which the rod was presented alone or with a frame in the same orientation.

The relationship between performance on the straight-ahead perception task and the RFT was examined using correlational analyses. More specifically, we examined the relationship between performance on the straight-ahead perception task in the 15° and the 75° positions for each response mode and performance on the different displays of the RFT: discordant display (i.e., different orientations) or congruent display (i.e., no frame or frame in same orientation as the rod).

Results

The analysis of mean perceived straight-ahead revealed significant effects for Response Mode, F (4, 64) = 36.07, $p < .001$, and Position, F (1, 16) = 7.22, $p < .05$, as well as a Response Mode by Position interaction, F (4, 64) = 24.11, $p < .001$[2]. The post hoc analysis of the interaction revealed a significant difference in straight-ahead perception between the 15° and the 75° orientation for all response modes except for the Arm. As evident in Figure 5, participants perceived their straight-ahead more footward in the 15° orientation than in the 75° orientation with the Verbal, Switch, and Wrist response modes. When participants aimed without the laser, their perception of straight-ahead was more headward in the 15° orientation than in the 75° orientation. In the Arm response mode, there was no difference in the perceived straight-ahead between the two orientations. When the impact of response mode was examined within the 75° orientation, participants exhibited greater footward bias in the Arm w/o Laser response mode than in the other response modes. For the 15° orientation, straight-ahead was evaluated more footward with the Verbal and Arm w/o Laser response modes than with the Switch, Wrist, and Arm response modes.

Analysis of the standard deviations of perceived straight-ahead yielded main effects for Response Mode, F (4, 64) = 7.83, $p < .001$, Position, F (1, 16) = 12.95, $p < .01$, and Block of trials, F (1, 16) = 27.46, $p < .001$ (see Table 1). Breakdown of the Response Mode effect showed that participants were more variable in the Arm w/o Laser response mode than in the Switch, Wrist and Arm situations. Further, they were more variable in the Verbal response mode than in the Wrist response mode. Also, participants were more variable in the 15° orientation than in the 75° orientation and in the first than in the second block of trials.

Correlation coefficients were significant between performance with Congruent stimuli of the RFT and the Wrist (r (16) = .64: see Figure 6a) and the Arm (r (16) = .52: see Figure 6b) Response Modes of the perceived straight-ahead task in the 75° orientation (see also Table 2).

Discussion and Conclusion

Before examining the influence of response mode on the perception of self-orientation during body tilt, it is important to identify the frame of reference that the participants chose to adopt. In order to make this determination, we first examined the relationship between spatial judgments under direct stimulation of the vestibular apparatus and orientation biases induced in a solely visual manner (i.e., no direct vestibular input). The perception of rod orientation in the RFT was significantly correlated with the perception of self-orientation during body tilt. More specifically, people who were less accurate in their estimations of the rod orientation in the congruent condition of the RFT also perceived their straight-ahead more footward in the 75° orientation with the Wrist and Arm response modes. Thus, biases created by vestibular and somatic affordance in the perception of rod orientation were significantly correlated with self-orientation judgments under direct vestibular stimulation. Interestingly, this was the case even if the visual stimulus was presented for a brief period in the central visual field (cf. Scholan & Smith, 1990). This was true when there was no allocentric mismatch (i.e, congruent stimuli). Thus, participants adopted an egocentric frame of reference in both the RFT and the straight-ahead perception task.

The primary purpose of this study was to determine the influence of response mode on an egocentric illusion. Participants judged the straight-ahead to be more footward in the 15° conditions than in the 75° conditions[3], but only with a verbal response mode or when the actual movement demands of the decision were minimal (i.e., use the switch to move the laser and simple wrist rotation). There was no difference between the two orientations when a laser beam provided visual information about the position of the limb during a whole arm movement. Thus, it appears that the response mode influenced perceived straight-ahead. Interestingly, when aiming to the perceived straight-ahead without visual information, participants exhibited greater footward bias than with any other response mode. Moreover, they actually perceived the straight-ahead more footward in the 75° orientation than in the 15° situation[4].

In one way our findings are similar to other work examining the influence of response mode on perceptual decision-making. That is, participants were less influenced by a visual illusion when the perceptual judgments involved the use of whole limb movements. However in the work associated with Milner and Goodale's (1995) model of visual processing, the perceptual illusions occurred when participants adopted an allocentric frame of reference and disappeared when the motor requirements of the task necessitated the use of an egocentric frame of reference (Aglioti et al., 1995; Glover & Dixon, 2001). In the context of Milner and Goodale's model, this reflects a shift from ventral to dorsal stream processing. In the work reported here, we have demonstrated that action can influence perceptual judgments within a particular frame of reference. Specifically, participants exhibited an illusory footward bias while making cognitive, but not motor judgments. In all cases, judgments were made relative to the participant's body (i.e., an egocentric frame of reference). In terms of ventral vs. dorsal stream processing, there are two potential explanations for these findings.

One possibility is that the ventral stream, which has been shown to be important for cognitive judgements, can also encode in an egocentric frame of reference. The involvement of a motor response elicits dorsal stream involvement, in which egocentric encoding is more accurate than in the ventral stream. Alternatively, it could be that the ventral-dorsal dichotomy is not the best theoretical framework for understanding how response mode affects the accuracy of our perceptual decision-making.

Following the argument forwarded by Glover and Dixon (2001), the fact that the cursor was visually available in the Arm response mode should have allowed participants to correct for the perceived illusion by "using a separate visual representation that encodes only spatial charateristics of the target and that is largely independent of the context" (p. 571). However, there was a significant difference in perceived straight-ahead between the 15° and the 75° orientation for two response modes involving the laser (i.e., Switch and Wrist). According to Glover and Dixon (2001), on-line processing of the displacement of the laser, regardless of the response mode should have allowed for the on-line correction in the perceptual judgments. However, the illusory bias was only eliminated when proximal control was involved. Thus, the present experiment casts some doubt on a strict ventral-dorsal dissociation for perception and action.

The ventral and dorsal streams are not the only neural systems that could be responsible for dissociations between perception and action. Studies involving normal participants as well as patients with cerebellar pathologies have made it clear that any normal reaching gesture requires extensive involvement of the cerebellum –and the basal ganglia– (see Stein & Glickstein, 1992). In fact the cerebellum contains more than half of the neurons of the human brain, and it maps multiple sources of afferent input, including the types of vestibular input important for the perceptual judgments made in this study. Descending efferent commands are necessarily routed through the cerebellum. As well, afferent information from the muscle spindles and Golgi tendon organs is encoded in the cerebellum in conjunction with the afferent visual and vestibular information. As discussed earlier, it is not the processing of afferent information alone that determines veridical perception but rather the integration of this information with the intended movement consequences (i.e., efference). Rather than the dissociation between perception and action being due to ventral-dorsal involvement, it is possible that cerebellar involvement in the perceptual-motor process makes perceptual decision-making less susceptible to visual illusions. Thus, the cerebellum is a good candidate to explain the dissociation between perception and action.

To conclude, the availability of afferent and efferent sources of information appears to mediate dissociation of perception and action. Whether this dissociation stems from dorsal-ventral stream or cerebral-cerebellar interactions, increased motor involvement appears to reduce the salience of visual illusions. Interestingly, the cerebral-cerebellar explanation incorporates illusions regardless of their availability to consciousness or their mapping (i.e., allocentric or egocentric). From an evolutionary perspective, it is clear that the ability to move and acquire objects in the environment developed long before neural systems associated with more cognitive decision-making. In this context, it is rather comforting to realize that the perceptual biases associated with many cognitive judgments do not interfere with more basic survival behaviour. Perhaps, in order to improve human-machine interfaces as well as our ability to perform in novel complex environments, such as piloting a car, a plane or a spacecraft, we need to understand when greater motor involvement will facilitate perceptual-motor performance. In doing so, we allow the integral and symbiotic functioning of all parts of the human brain. Otherwise, specific perceptual-motor training may be necessary to improve processing flexibility under the specific circumstances.

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Footnotes

[1] While using a fixed target, which appears to move when the magnitude and direction of inertial forces are altered, Graybiel (1952) demonstrated that the participants were aware of the illusion. Such awareness is not possible without a visual reference (i.e., a visual background).

[2] While females tended to exhibit greater footward bias than males, the main effect for gender was not significant ($\underline{p} > .14$). This was expected, as gender differences are usually found when comparing perceived straight-ahead perception in an upright and a tilted body orientation.

[3] Ebenholtz and Shebilske (1975) demonstrated that the straight-ahead perception bias is more footward with a 60° than with a 15° body tilt in the median plane. The direction of perceptual bias is actually opposite to our findings. However, their results were obtained while using 4 trials with a different starting position of the visual stimulus (i.e., starting above and below the visual field). In the present study, we used 10 trials and only one direction of the visual stimulus. In another experiment performed in our lab, the starting position of the cursor was varied between trials. Using data from a 45° body tilt condition, the effect of stimulus direction on perceived straight-ahead appeared to interact with the number of trials. More specifically, on the first trials, upward stimulus direction led to a slightly more footward bias then a downward stimulus direction while this effect was reversed for the last trials. Further, in a study investigating

the well known Aubert and Muller effects, Ebenholtz and Shebilske (1973) demonstrated that the perception of the vertical was biased in a different direction when participants were tilted at 25° in the median plane than when they were tilted at 75°. Thus, the number of trials, the stimulus direction, and the body tilt (i.e., Aubert and Muller effects) appear to interact with the perception of spatial orientation.

[4] Perhaps in the absence of vision, the footward estimation of straight-ahead reflects a kinesthetic bias toward the horizon.

Table 1.

Standard deviations of straight-ahead estimations (deg)

	Position			
	15°		75°	
Task	Block 1	Block 2	Block 1	Block 2
Verbal	2.37	1.38	2.49	2.40
Switch	1.72	1.57	2.65	2.25
Wrist	1.64	1.11	2.19	1.72
Arm w/o Laser	2.88	1.59	2.91	2.68
Arm	1.63	1.63	2.32	2.14

Table 2.

Correlation coefficients between perceived straight-ahead for each response mode and each body tilt, and RFT performance for each display mode.

Body tilt		Response Mode				
		Verbal	Switch	Wrist	Arm w/o Laser	Arm
15°	Discordant RFT	0.13	0.23	0.21	0.17	0.18
	Congruent RFT	0.17	0.24	0.28	0.43	0.36
75°	Discordant RFT	-0.01	0.00	0.21	0.03	0.20
	Congruent RFT	0.22	0.20	0.64*	0.46	0.52*

*: significant at $p < .05$

Figure Captions

Figure 1.	Drawing of the perceptual and vestibulo-ocular components of the oculogravic illusion.
Figure 2.	Drawing of the experimental inverting device.
Figure 3.	Drawing of the arc-manipulandum installed on the inverting bed.
Figure 4.	Visual stimuli presentation scheme for the RFT.
Figure 5.	Task by Position interaction for the average straight-ahead perception bias (deg).
Figure 6.	Correlation between the proportion of correct responses at the RFT with the congruent displays and perceived straight-ahead in the 75° body tilt conditions with (A) the Wrist response mode and (B) the Arm response mode.

Figure 1

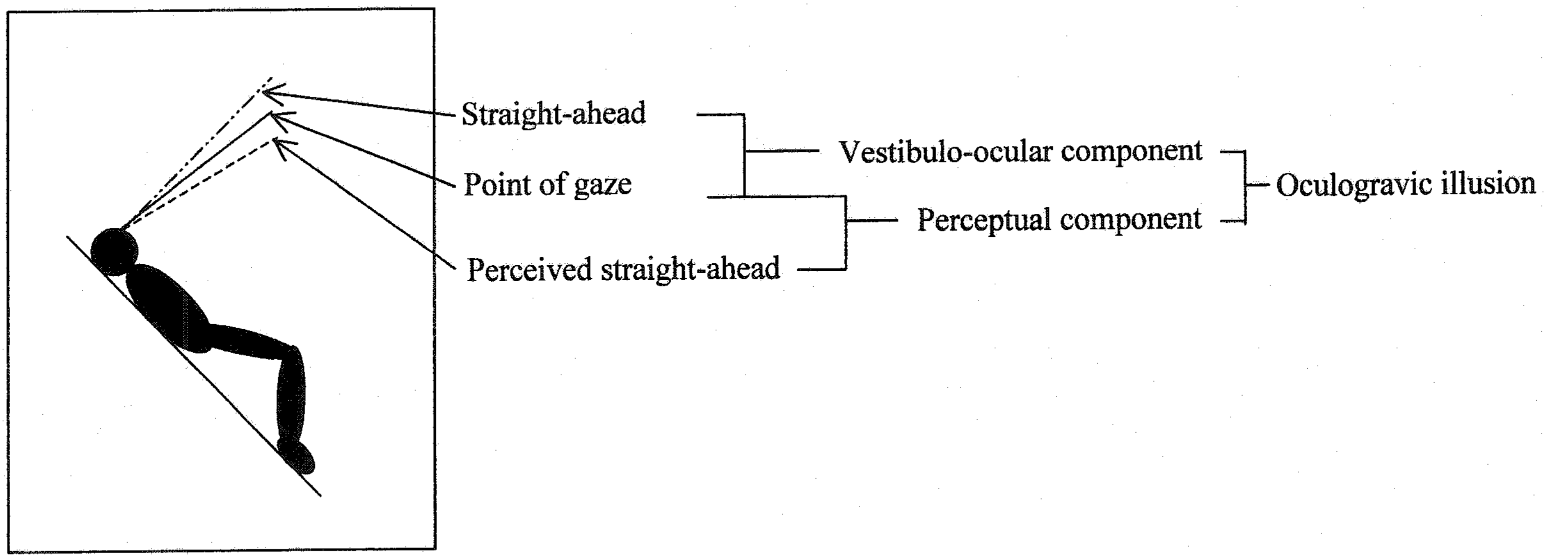

Straight-ahead
Point of gaze
Perceived straight-ahead
Vestibulo-ocular component
Perceptual component
Oculogravic illusion

Figure 2

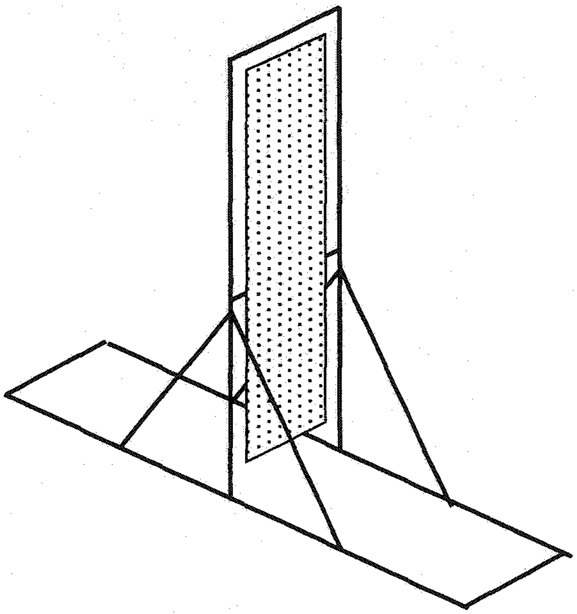


Figure 3

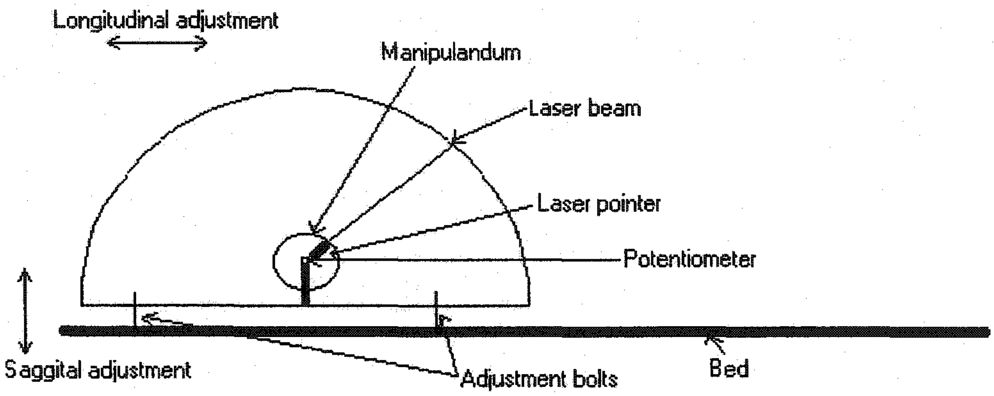

Longitudinal adjustment
Manipulandum
Laser beam
Laser pointer
Potentiometer
Saggital adjustment
Adjustment bolts
Bed

Figure 4

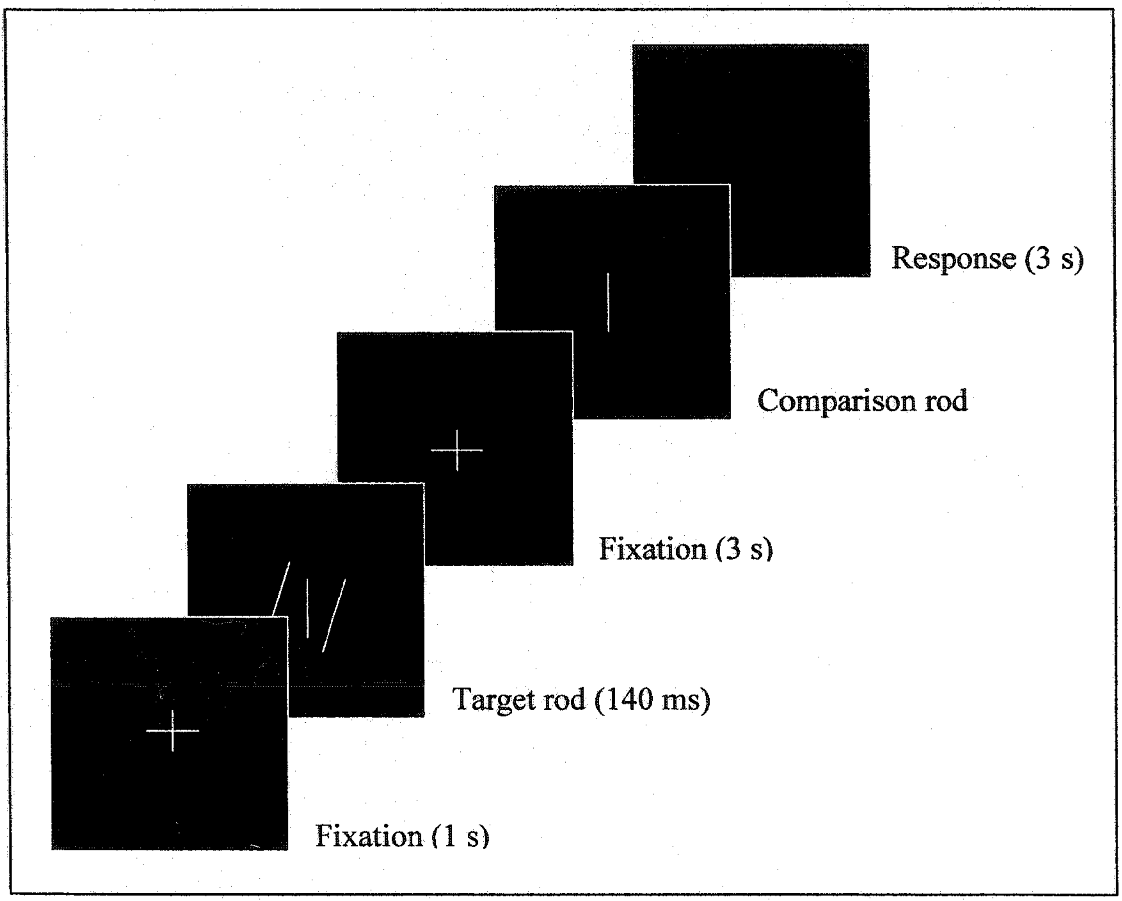
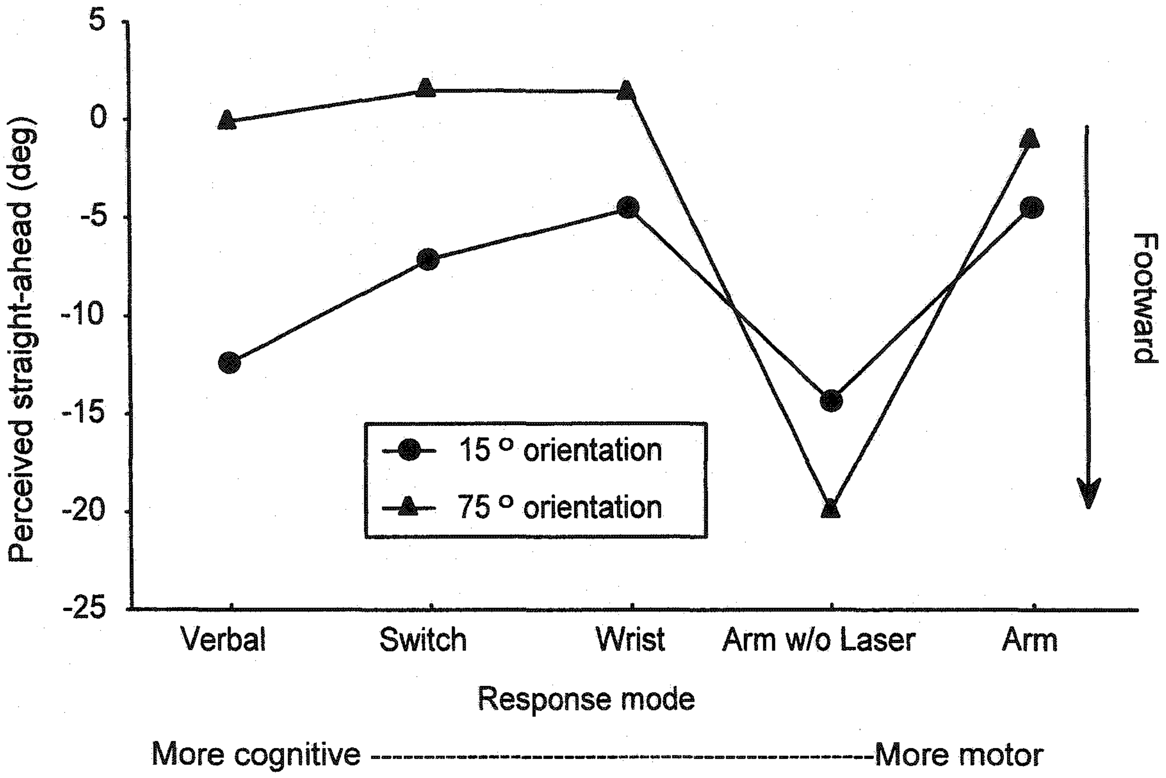
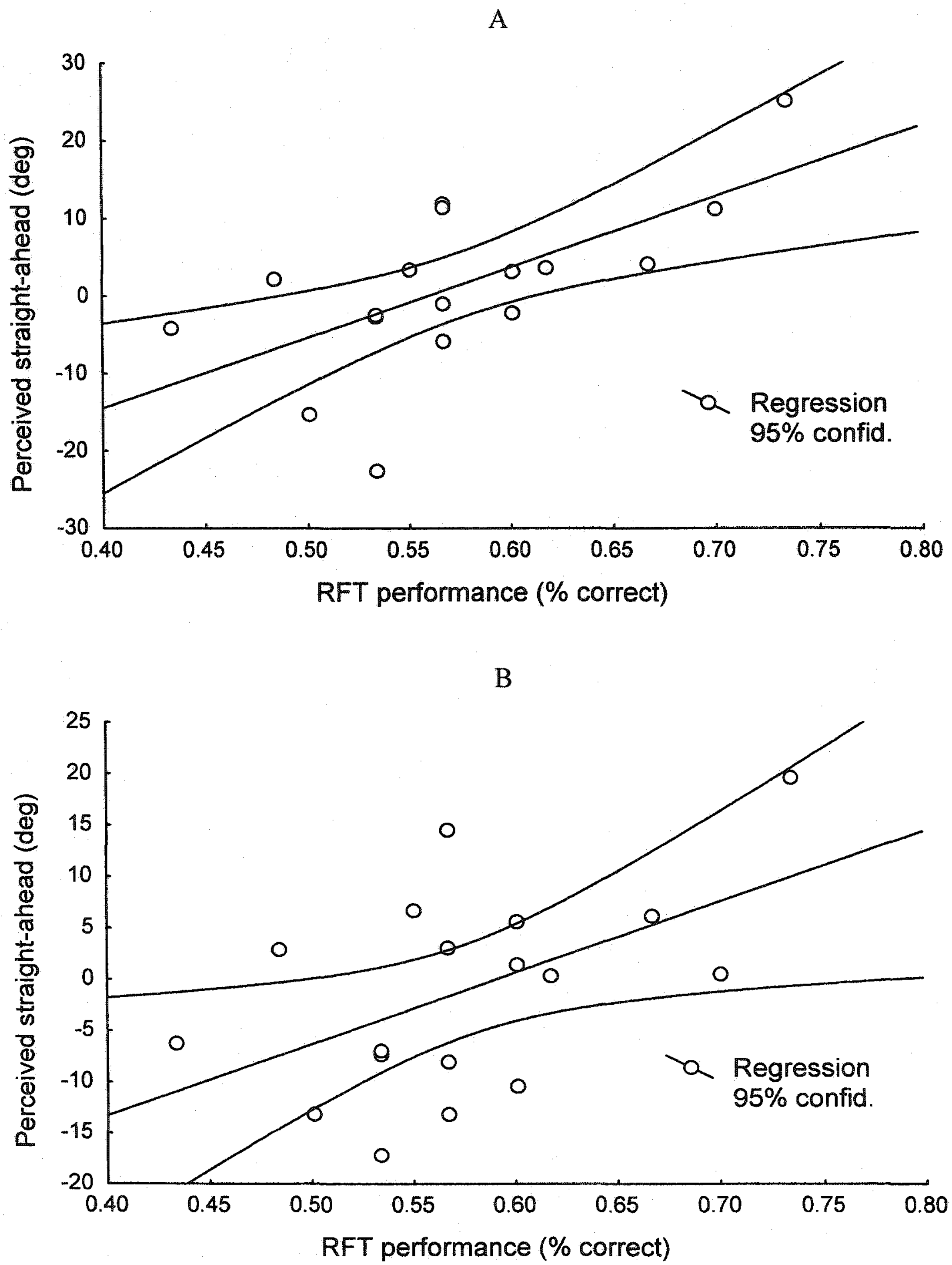

Response (3 s)
Comparison rod
Fixation (3 s)
Target rod (140 ms)
Fixation (1 s)

Figure 5



5
0
-5
-10
-15
-20
-25
Perceived straight-ahead (deg)
15 ° orientation
75 ° orientation
Footward
Verbal
Switch
Wrist
Arm w/o Laser
Arm
Response mode
More cognitive --More motor

Figure 6


A
30
20
10
0
-10
-20
-30
Perceived straight-ahead (deg)
0.40
0.45
0.50
0.55
0.60
0.65
0.70
0.75
0.80
RFT performance (% correct)
Regression
95% confid.
B
25
20
15
10
5
0
-5
-10
-15
-20
Perceived straight-ahead (deg)
0.40
0.45
0.50
0.55
0.60
0.65
0.70
0.75
0.80
RFT performance (% correct)
Regression
95% confid.

GENERAL CONCLUSION

The overall goal of the present work was to examine some of the mechanisms that mediate the perception of spatial orientation and self-orientation. In particular, we investigated how variations in the body orientation relative to gravity, attentional strategy, and efferent limb control affect the perception of self-orientation. As presented in Table 1, perception of self-orientation differs across gender, attentional instruction, and response mode.

In the first study, we demonstrated that whole body rotation, variation in the direction of inertial forces, and modification of blood distribution affects the perception of self-orientation with body tilt. More specifically, backwards whole body rotation, body tilt in the median plane, and greater upper body blood pressure induced a footward bias in the perception of straight-ahead. When only the direction of inertial forces acting on the body was changed, the footward bias was evident for females but not for males. Because the otoliths are specialized to encode the direction of inertial forces and because there are gender differences in the size of the otoliths (Sato, Sando, & Takahashi, 1992), we suggested that gender differences in the perception of spatial orientation stem from the otoliths. This suggestion of "hardware" differences does not conflict with evidence of "software" differences between males and females for the perception of spatial orientation (Miller & Santoni, 1986; Reinking, Goldstein, & Houston, 1974).

In the second study, we observed that an attentional strategy prompting participants to focus on internal cues (i.e., arising from inside the body) allowed female participants to reduce their perceived straight-ahead bias normally induced by body tilt. On the other hand, this reduction of perceptual biases for the females did not eliminate gender differences in the perception of self-orientation with body tilt in the median plane. Thus, it appears that an attentional strategy (i.e., "software") can affect perception of spatial orientation. However, strategy does not fully account for the gender differences observed in the first study. As a result, it is still possible to explain gender difference in the perception of straight-ahead with the "hardware" explanation (i.e., size of the otoliths). From the philosophical perspective presented in the introduction of this dissertation, it appears that both Compte's "positivism" (1838) and Kant's (1838) "idealism" theories contribute to the understanding of the perceptual-motor behaviour.

The third study was designed to shed more light on the interactions between perception and action. By comparing perceived straight-ahead judgments associated with the five response modes, we observed that efferent control of the whole arm allowed participants to reduce the perceptual bias. These results are not consistent with Milner and Goodale's (1995) explanation of dissociation between perception and action. At least for the specific egocentric illusion employed in the present work (i.e., oculogravic illusion), an alternate explanation was sought. Neurological evidence suggests that the cerebellum is involved in proximal control (Stein & Glickstein, 1992) and maps visual, kinesthetic, and vestibular information (Ghez & Thach, 2000). The involvement of the cerebellum during whole limb movement might induce corrections of the perceptual biases and/or allow the dorsal visual stream to integrate the response-produced feedback and affect the perception of spatial features. This effect of response-produced feedback on perceptual processes highlights the possibility that gravity is used to align our different frames of reference (McIntyre, Berthoz, & Lacquaniti, 1998). Indeed, the inertial forces acting on our limbs dictates the amount of force required to move the limb to a certain position. Moreover, this afferent-efferent interplay, that can explain dissociation between perception and action, necessitates the involvement of the cerebellum. As Helmholtz suggested over a century ago, how we perceive the world involves more than simple sensory processing (see Gielen, 2001). Interestingly, the integration of afferent and efferent sources of information seems not to differ between males and females as the effect of limb movement on the perception of spatial orientation was the same across gender.

In sum, this thesis sheds some light on gender differences in perception of spatial orientation by identifying a potential source of afferent information responsible for those differences (i.e., the otoliths). Gender differences can be influenced, but perhaps not eliminated, by adopting a different attentional strategy. Thus, both anatomical (i.e., hardware) and strategic (i.e., software) explanations appear to play a role in gender differences in the perception of self-orientation. This perception of self-orientation is affected by efferent limb control similarly for both males and females and probably reflects a re-alignment of the internal frames of reference (McIntyre et al., 1998).

Referring back to the universal frame of reference described by Descartes (1637, translated by Gilson 1967), it seems that its use can be affected by our limb movements. Thus, the well-known citation of Descartes: “I think, therefore I am”, could also read: “I move, therefore I am”.

Table 1.

Summary of all experiments

Study	Main findings
1 (exp. 1)	Whole body rotation to upside down affects females but not males. (Gender X Orientation Interaction)
1 (exp. 2)	Whole body rotation to horizontal affects both females and males. (Main effect for Condition)
1 (exp. 3)	Whole body rotation and altered blood distribution affects both males and females. Stable body tilt affects females but not males. (Gender X Condition X Orientation Interaction)
2	Instruction can affect females but not males. (Gender X Instructions Interaction)
3	With stable body tilts (15° and 75°), limb movements affects the perception of self-orientation. (Main effect for Response Mode)

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