EJN fens EUROPEAN JOURNAL OF NEUROSCIENCE

European Journal of Neuroscience, Vol. 31, pp. 1899–1907, 2010 doi:10.1111/j.1460-9568.2010.07199.x

Multisensory determinants of orientation perception: task-specific sex differences

M. Barnett-Cowan,[1,2,*] R. T. Dyde,[2] C. Thompson[1,2] and L. R. Harris[1,2]
[1]Multisensory Integration Laboratory, Centre for Vision Research, York University, Toronto, ON, Canada
[2]Department of Psychology, York University, Toronto, ON, Canada

Keywords: gender, gravity perception, perceptual upright, subjective visual vertical, visual dependence

Abstract

Females have been reported to be more 'visually dependent' than males. When aligning a rod in a tilted frame to vertical, females are more influenced by the frame than are males, who align the rod closer to gravity. Do females rely more on visual information at the cost of other sensory information? We compared the subjective visual vertical and the perceptual upright in 29 females and 24 males. The orientation of visual cues presented on a shrouded laptop screen and of the observer's posture were varied. When upright, females' subjective visual vertical was more influenced by visual cues and their responses were more variable than were males'. However, there were no differences between the sexes in the perceptual upright task. Individual variance in subjective visual vertical judgments and in the perceptual upright predicted the level of visual dependence across both sexes. When lying right-side down, there were no reliable differences between the sexes in either measure. We conclude that heightened 'visual dependence' in females does not generalize to all aspects of spatial processing but is probably attributable to task-specific differences in the mechanisms of sensory processing in the brains of females and males. The higher variability and lower accuracy in females for some spatial tasks is not due to their having qualitatively worse access to information concerning either the gravity axis or corporeal representation: it is only when gravity and the long body axis align that females have a performance disadvantage.

Introduction

Females have been shown to rely more on visual information than males in a number of spatial tasks related to perceived orientation (Witkin *et al.*, 1954; Linn & Petersen, 1985). Greater reliance on visual information in females has been particularly apparent when retinal and nonretinal information is in conflict during self-motion (Kennedy *et al.*, 1996; Darlington & Smith, 1998; Viaud-Delmon *et al.*, 1998) or when executing visually guided movements (Gorbet & Sergio, 2007). Given the long-established history of reports of increased visual dependence in females in perceptual orientation tasks, here we address the extent to which visual dependence is a general trait of the female brain and whether it arises from differences in how females and males integrate multisensory information.

In perceptual orientation tasks within a gravitational reference frame, observers combine visual information with vestibular and somatosensory cues of gravity's axis (see Howard, 1982; for a review) and with the internal representation of the body (the idiotropic vector: Mittelstaedt, 1983). Perhaps sex differences in this domain can be explained through males and females having qualitatively different information concerning a specific cue? Tremblay and colleagues (Tremblay *et al.*, 2004; Tremblay & Elliott, 2007) suggest that greater dependence on vision among females may be attributable to females having smaller otoliths (see also Sato *et al.*, 1992) rather than integrating sensory information differently (Viaud-Delmon *et al.*, 1998). If sex differences were attributable to anatomical differences then differences should be expected in all tasks involving the otoliths.

Dyde *et al.* (2006) demonstrated that we have at least two simultaneous perceptions of 'which way is up'. The subjective visual vertical (SVV; measured by judging the orientation of a line relative to the direction in which a ball would fall) is closely tied to the perceived axis of gravity. However, a second, related though functionally independent, measure of perceived orientation is the 'perceived upright' (Hock & Tromley, 1978): the orientation at which objects, faces and characters are most easily recognized (Rock & Heimer, 1957; Rock, 1973; Corballis *et al.*, 1978; Jolicoeur, 1985). Both the SVV and the perceptual upright (PU) are influenced by the relative orientation of ambient vision, gravity and the idiotropic vector (Groberg *et al.*, 1969; Mittelstaedt, 1983; Dyde *et al.*, 2006) but the SVV is dominated by gravity whereas the influence of these factors on the PU is more even (Dyde *et al.*, 2006). In the present paper both measures are used to assess differences in the relative contribution of visual and nonvisual cues to orientation perception among females and males, and the pervasiveness of female visual dependence is tested across measures.

Females are less precise (i.e., higher variable error) when setting a line to vertical than males (Witkin *et al.*, 1954; Gross, 1959; Groberg *et al.*, 1969; Bogo *et al.*, 1970; Hyde *et al.*, 1975). In these past studies a method of adjustment was employed which could have resulted in

Correspondence: Dr M. Barnett-Cowan, at *present address below.
E-mail: mbarnettcowan@gmail.com

**Present address*: MPI for Biological Cybernetics, Department of Human Perception, Cognition and Action, Spemannstraße 38, 72076 Tübingen, Germany.

Received 30 September 2009, revised 29 November 2009, accepted 30 November 2009

less reliable estimates of the precision with which participants set a line to vertical. Precision is another indication of how females and males perform perceptual tasks and provides another means of assessing whether the addition of conflicting sensory information differentially affects performance across the sexes. Because this information is of particular interest to the present study the method of constant stimuli is used in order to have more reliable estimates of the accuracy and precision with which participants make their judgments.

The following hypotheses were assessed

1. Males rely more on gravitational cues whereas females rely more on the internal representation of the body (hypothesis 1)
2. Females are less precise than males when performing orientation judgment tasks (hypothesis 2)
3. Males are less influenced by visual orientation cues in general in determining the direction of up (hypothesis 3).

Materials and methods

Participants

Fifty-three participants (29 female and 24 male) between 17 and 26 years of age (mean ± SD age, 19.6 ± 2.4 years) were recruited through the York University Undergraduate Research Participant Pool with participants receiving course credits. All observers had normal or corrected-to-normal vision, reported no history of vestibular dysfunction and provided informed consent as required by the Ethics Guidelines of York University which complies with the 1964 Declaration of Helsinki.

Convention

All orientations are reported with respect to the body midline of the participant; 0° refers to the orientation of the longitudinal body axis. Clockwise (CW) tilts from this orientation are assigned positive values and counter-clockwise (CCW) tilts as negative values.

Stimuli for determining the SVV

We measured the SVV using a variant of the 'luminous line' technique. A simple line probe (3 × 0.5°) was oriented about a central fixation point (0.45° of visual arc) and briefly presented. For testing the SVV when observers were upright the line was presented in one of 21 orientations (from −50° to +50° in 5° increments; Fig. 1c). For testing the SVV when right-side down the range of line orientations was from −140 to −20° in 6° increments; Fig. 1c). The range was adjusted to allow for the fact that the perception of gravity for most participants is biased between gravity and body orientation for tilts > 60° in the absence of visual cues (Aubert, 1861; Dyde *et al.*, 2006). The line probe was superimposed on a 35°-diameter circular background picture image which was either rich in visual cues for orientation (Fig. 1e), a neutral grey background of the same mean luminance (Fig. 1f), or contained a square white frame (29.7 × 29.7° of visual arc) against the same neutral grey background (Fig. 1g). The visual frame was oriented ±18° relative to the head. The polarized visual environment was displayed at ±18° and ±112.5°. All stimuli were displayed for 500 ms and then replaced with a screen of the same mean luminance. Participants responded by means of buttons on a gamepad using their left and right hands (buttons 1cm apart) as to whether the line appeared tilted CW or CCW with respect to gravitational vertical. There were 147 stimulus combinations: 21 (line orientations) × 7 (backgrounds: grey, frame ±18°, image ±18°, image ±112.5°) in each body orientation. Each stimulus combination was presented seven times using the method of constant stimuli. Sessions took about 20 min in each body orientation.

Stimuli for determining the PU

To determine the PU, we used the Oriented Character Recognition Test (OCHART; Dyde *et al.*, 2006). A 'p' symbol (3.1 × 1.9° of visual arc) was presented at the same position as the fixation point. The letter probe was presented in one of 24 orientations from 0 to 345° in increments of 15° (Fig. 1d). The character probe was superimposed on one of the 35°-diameter circular background pictures (Fig. 1e–g). Stimuli were displayed for 500 ms and then replaced with a screen of the same mean luminance. Participants responded as to whether the character appeared as a 'p' or a 'd'.

There were 168 combinations: 24 (letter orientations) × 7 (backgrounds: grey, frame ±18°, image ±18°, image ±112.5°) for each body orientation. Each stimulus combination was presented seven times using the method of constant stimuli. Sessions took ~25 min in each body orientation.

Procedure

Participants either sat on a padded chair (Fig. 1a) or lay on a bed on their right side on a foam mattress (Fig. 1b) with their head supported by foam blocks to ensure that their head was at 90° relative to gravity. Stimuli were presented in the frontoparallel plane on an Apple iBook laptop computer with a resolution of 48 pixels/cm (21 pixels/° at a viewing distance of 25 cm). Peripheral vision was masked to a circular screen of diameter 35° using a circular aperture shroud.

For the SVV, participants were asked to report whether the line probe was oriented CW or CCW relative to the 'direction in which a ball would fall if dropped'. For the PU participants reported whether the character that they saw on the screen looked more like the letter 'p' or the letter 'd'.

Data collection occurred over the course 2 h on the same day. Testing consisted of four blocks of trials: SVV upright, SVV right-side down, PU upright, PU right-side down. The order of test blocks was partially counterbalanced across all participants.

Analysis

For the SVV, a sigmoid function (eqn 1) was fitted to the percentage of times the line was judged CW relative to gravity as a function of line orientation. The orientation of the line probe at which it was equally likely to be judged tilted CW or CCW from gravitational vertical was taken as the SVV. For the PU, two sigmoids were fitted to the percentage of times the observers identified the character as a 'p' as a function of character orientation to determine each of the p-to-d and d-to-p transitions, i.e. when participants were equally likely to respond 'p' or 'd', for each visual background in each body orientation. The average of the two angles at which these transitions occurred was taken as the PU

$$y = \frac{100}{1 + e^{-\left(\frac{x - x_0}{b}\right)}}\% \tag{1}$$

where x_0 corresponds to the 50% point and b is the standard deviation (SD; so that b^2 is the variance).

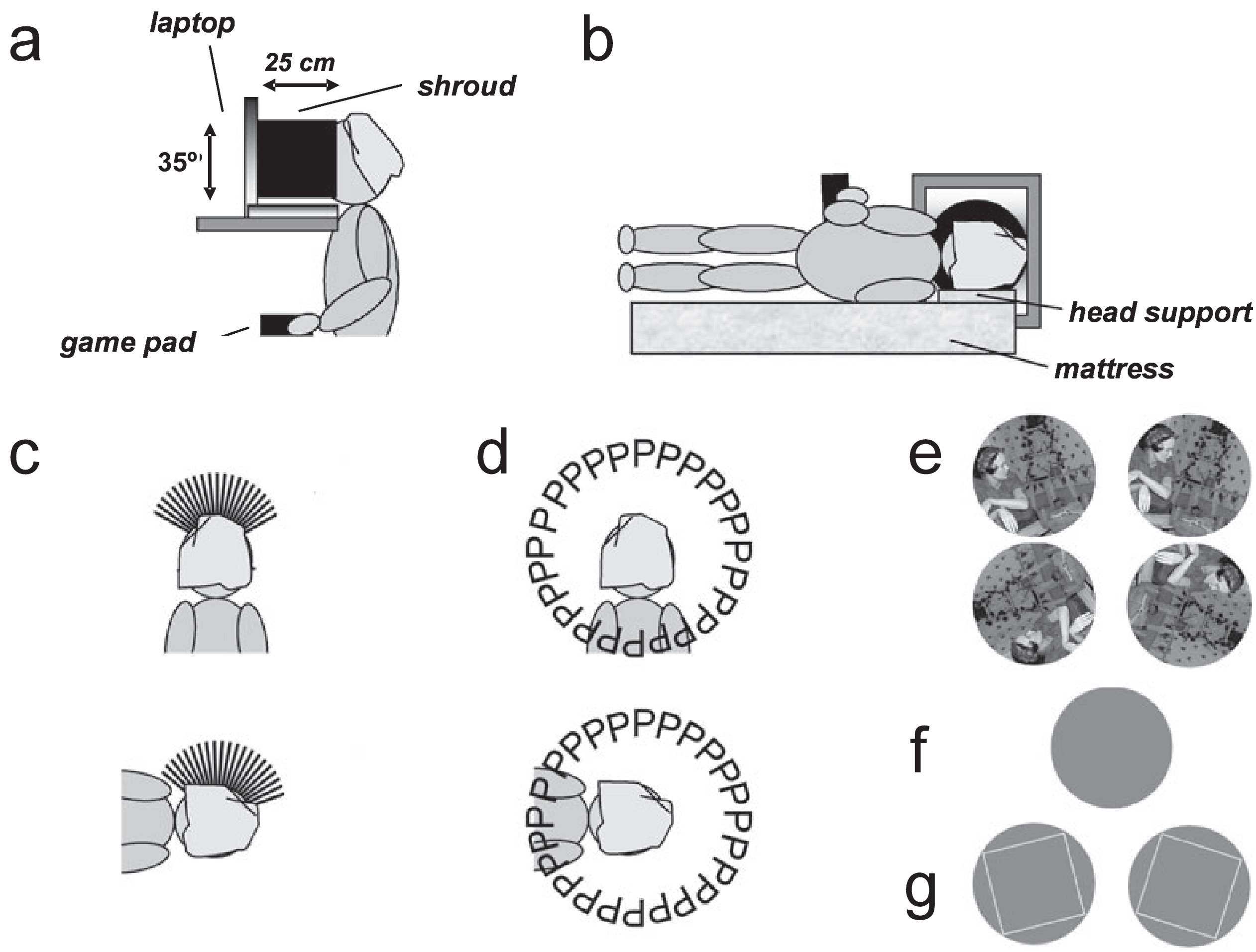

FIG. 1. The two body postures used in these experiments: (a) upright and (b) right-side down (RSD). Participants viewed the display through a shroud to obscure all peripheral vision. Viewed through the shroud, the screen subtended a 35° diameter circle at a distance of 25 cm. (c) Schematic depiction of line orientations used for the SVV task shown relative to the head when upright and RSD. Note the range for RSD is shifted CW by 10° relative to gravity. (d) Schematic depiction of letter character orientations used for the PU task when upright and RSD. Note that these are not shown to scale relative to the head and that all lines and characters were actually presented centrally relative to the observer. (e–g) The (e) highly polarized visual backgrounds, (f) grey background and (g) frame backgrounds used in these experiments.

Exclusion criteria

Exclusion of participant data was determined from the psychometric functions outlined in eqn 1 for the SVV and the PU. Participants were excluded from further analysis if their average SD in at least four (i.e., more than half) of the background conditions was > 3 SDs above the group mean. Based on this criterion, of the 29 female and 24 male participants, 27 female and 22 male participants were included for the SVV upright task, 22 female and 20 male participants were included for the SVV right-side down task, 28 female and 21 male participants were included for the PU upright task and 28 female and 22 male participants were included for the PU right-side down task.

Results

Visually shifting the SVV

For each individual participant we took their report of the SVV against the grey background when seated upright as their ‘baseline’ SVV value, and then calculated how far the SVV shifted from this baseline in the presence of a tilted background. Figure 2a shows the shift of the SVV caused by each of the tilted backgrounds (frame and background image). In each case the subjective visual vertical was shifted in the same direction as the background tilt. Figure 2b shows the total shift [abs(CCW – CW): frame effect or image effect] induced by each ‘pair’ of tilted backgrounds: frame ±18°; image ±18°; and image ±112.5°.

Three separate one-way ANOVAs showed that for all visual effects the difference in effect size was larger for females than males (18° frame: $F_{47} = 6.39$, $P = 0.015$; 18° image: $F_{47} = 6.06$, $P = 0.018$; 112.5° image: $F_{39} = 10.85$, $P = 0.002$). If a Bonferroni correction for multiple comparisons is applied (lowering the critical alpha to 0.0167) the results for the 18° frame and 112.5° image data are still reliably different across sexes, although the results for the 18° image data just fail to reach significance.

Visually shifting the PU

We calculated the shift in PU caused by the tilted background displays in the same way as for the SVV (i.e., by calculating the shift in PU from each individual’s baseline when seated upright: PU against the grey background). The results are shown in Fig. 2c and d. We conducted a series of three-one-way ANOVAs and found no reliable

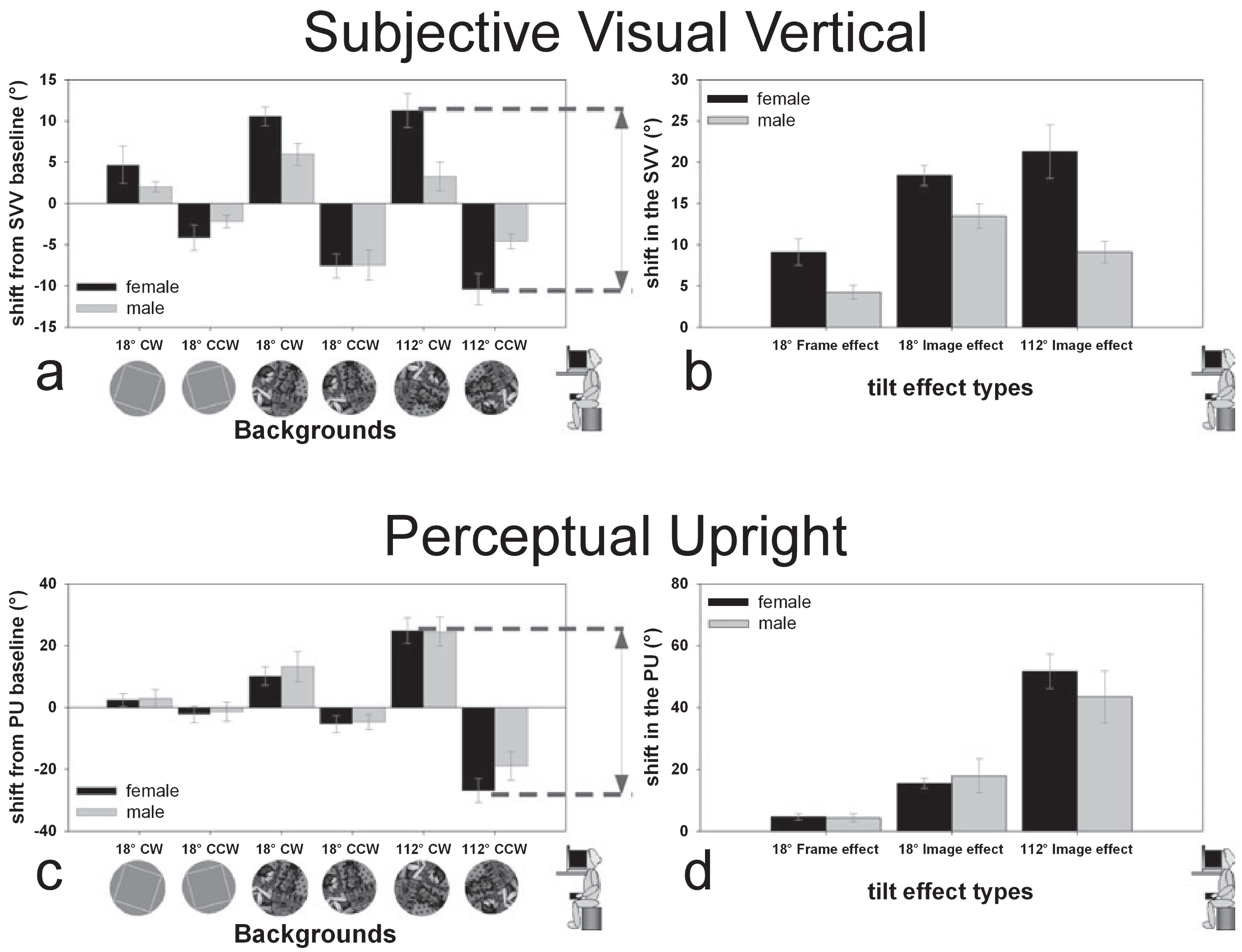

FIG. 2. The effect of a tilted visual background on (a and b) the SVV and on (c and d) the PU when seated upright. (a and c) the SVV and PU were measured against a series of tilted visual backgrounds. Results are grouped by sex and normalized to each observer's baseline SVV (see text). Positive values indicate a CW shift. (b and d) The total size of shift with a given background measured as shown by the arrows in (a) and (c), sorted by gender. Error bars indicate 1 SEM.

differences across sexes (18° frame effect: $F_{46} = 0.03$, n.s.; 18° image effect: $F_{47} = 0.21$, n.s.; 112.5° image effect: $F_{47} = 0.71$, n.s).

Variability

The SD of the psychometric function used to determine the PU and SVV (see eqn 1) is an indication of the precision with which the observers are making their judgments. Figure 3 illustrates the mean data across all backgrounds for this qualitative measure of SVV and PU when seated upright. For the SVV, but not for the PU, females were consistently less precise in their judgments than males. A one-way ANOVA for the SVV data showed a reliably higher SD for females: $F_{47} = 4.67$, $P < 0.05$. A one-way ANOVA on the mean SDs across all backgrounds for the PU data showed no reliable difference in SDs across sex: $F_{47} = 0.23$; n.s.

Right-side down

The more accurate and more reliable results for males' SVV (less influenced by visual cues and more precise in their judgments) might be as a result of an increased reliance on either their internal representation of their body orientation or on the vestibularly signaled direction of gravity. In the upright posture these cues are aligned and their relative contributions cannot be assessed. Therefore we separated these cues by having our observers lying right-side down and measured the SVV and the PU.

When the SVV was measured against a grey background (i.e. in the absence of visual cues) while in a right-side down posture, the SVV for males and females were found at an intermediate orientation between their long body axis (0°) and gravity (−90°): females had a mean ± SEM SVV of −64.4 ± 4.6 and males had a mean SVV of −69.8°± 4.0. A one-way ANOVA found no reliable difference in the SVV between sexes: $F_{40} = 0.78$; n.s. A similar pattern of results was found for the PU when right-side down: females had a mean PU of −29.2 ± 4.6 and males had a mean PU of −23.5 ± 4.5 with no reliable difference across the sexes: $F_{48} = 0.98$, n.s.

Figure 4a shows the shift of the SVV caused by the tilted background image relative to the baseline SVV value when right-side down. Figure 4b shows the total shift induced by the tilted scene background. Two separate one-way ANOVAs found no reliable difference in background image effect size between sexes (18° image:

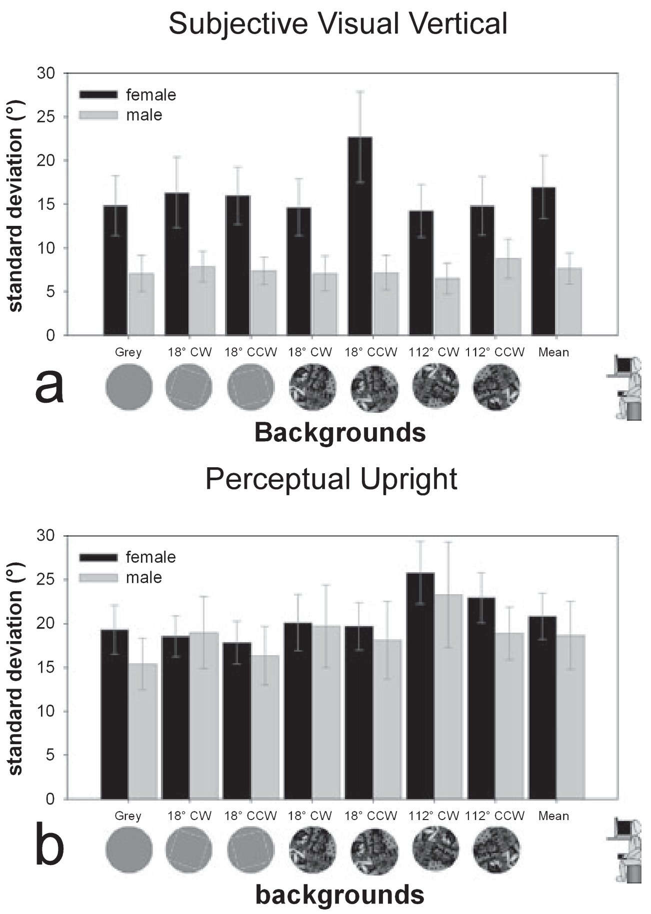

FIG. 3. The SD of the psychometric function used to derive each subject's (a) SVV and (b) PU when seated upright for each of the backgrounds, sorted by gender. The two right-most columns illustrate the mean SD across all backgrounds. Error bars show 1 SE of the group mean.

$F_{35} = 2.01$, $P = 0.165$; 112.5° image: $F_{36} = 0.0003$, n.s.). The same nonsignificant result was found for the PU (Fig. 4c and d: 18° image: $F_{47} = 0.05$, n.s.; 112.5° image: $F_{47} = 2.52$, $P = 0.119$).

Figure 5 illustrates a comparison between the SDs across sexes, across tasks (SVV and PU) and across body orientations (upright and right-side down). SVV SDs significantly increased when males were right-side down ($t_{18} = 3.48$, $P < 0.05$, two-tailed). This was not the case for females ($t_{21} = 0.64$, n.s.). A mixed-design ANOVA looking at the between-subjects factor (sex) and within-subjects factor (posture) failed to find an interaction between sex and posture for the SVV ($F_{1,39} = 0.66$, n.s) and for the PU ($F_{1,47} = 1.69$, n.s.).

Predicting the influence of the visual background from variability

If an individual has a low level of precision in their judgments then their percepts may be more easily influenced by other competing sensory information (Ernst & Banks, 2002), such as the orientation of the background. If this were the case, then the SD for an individual in the control condition (the grey background) may predict the amount the PU and SVV were influenced by vision.

For each observer we determined the 'normalized mean effect size' of the background for the SVV and PU when seated upright by calculating the average visual effect induced by each tilted background relative to baseline (grey background) and normalizing that to the maximum possible effect size (i.e., plus and minus the background tilt: frame, 36°; room, 225°).

A Fisher's Z-transformation of r found no differences between the correlations of male and female observers for the SVV or PU (both $P > 0.05$). Their data were therefore pooled. For each measure the size of the normalized visual effect could be predicted from the SD of the estimates (SVV: $r_{48} = 0.665$, $P < 0.001$, Fig. 6a; PU: $r_{48} = 0.301$, $P = 0.037$, Fig. 6b).

Discussion

Summary

For the SVV task, we found strong evidence for a difference between the sexes. Females were more influenced by the orientation of the ambient visual cues than males when judging the axis of gravity when upright. We found that the reliability with which individuals performed the SVV and PU tasks is positively correlated with the influence of tilted backgrounds. Further, females were also less precise in their judgments than males, showing reliably higher SDs. For the PU task we found no evidence for any difference between the performance of males and females either in the effect of the tilted background or on their SDs. Together these results suggest that increased visual dependence in females arises from females having significantly higher variance in the SVV task than males. As this was not found in the PU task, visual dependence in females would appear to be task-specific.

We found no evidence to support the suggestion that the performance advantage of males in the SVV task was related to changes in the relative emphasis placed on the internal representation of the body or of gravity. When right-side down the perceived axis of gravity was shifted slightly away from the direction of gravity in the direction of the body's orientation but the shift was equal for males and females in both the SVV and PU tasks and neither sex showed more reliable observations than the other.

Female visual dependency did not generalize: against the 'hardware hypothesis'

Reinking *et al.* (1974) found that the extent to which females were influenced by vision in the rod-and-frame test was reduced when subjects were instructed to attend to the internal representation of the body. In the same vein, Tremblay *et al.* (2004) found that the misperception of the morphological horizon, which is biased towards the feet in females when pitched backward by 45°, was reduced when given similar instructions. This observation, Tremblay *et al.* argued, supports a 'software hypothesis', which states that sex differences are attributable to neural strategies in performing spatial orientation tasks. However, despite this reduction in misperceiving the morphological horizon, sex differences were still found. Tremblay *et al.* speculated that sex differences in estimating the morphological horizon and the rod-and-frame test may stem from differences in the size of the otoliths between the sexes (Sato *et al.*, 1992). This they argued supports a 'hardware hypothesis', which states that sex differences are at least partially attributable to differences in the vestibular sensory organs. Tremblay *et al.* cited the work of Groberg *et al.* (1969) and Pitblado (1976) to support their hardware hypothesis. While Groberg *et al.* reported a significant effect of sex related to the starting orientation of a rod used to test the SVV when upright and with the head and body misaligned, differences between the sexes for the SVV when the body was tilted were not in

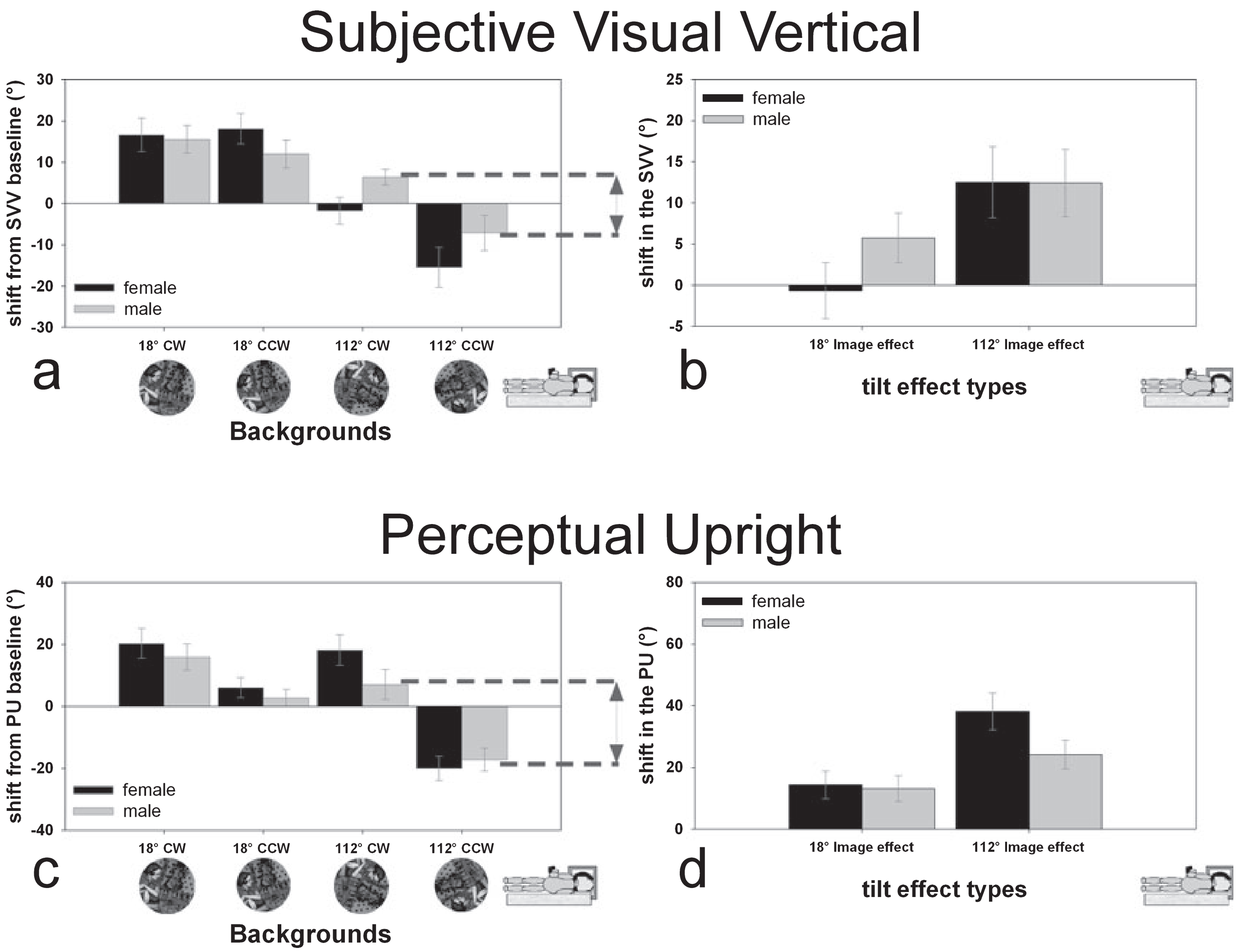

FIG. 4. The effect of the tilted background image on (a and b) the SVV and on (c and d) the PU when lying right-side down. Same conventions as Fig. 2.

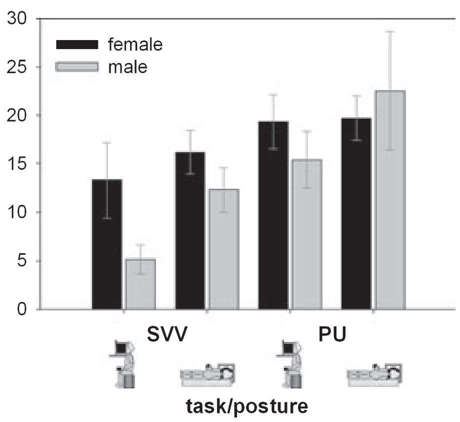

FIG. 5. The SD of the psychometric functions used to derive the SVV and PU are shown whilst observers were upright or right-side down against a grey background (no visual cues to orientation). Error bars show 1 SE of the group mean.

fact observed. Pitblado (1976) measured the SVV in females and males tilted on their side by 70° in roll and found that females set a rod near vertical while males set a rod towards their body and away from gravity by 7.5°. However, Pitblado unfortunately failed to compare male SVV responses to those of two females he later tested at 90° who set the rod towards their body and away from gravity, which is the typical response, and thus the results of Pitblado cannot be used to support the hardware hypothesis. Tremblay & Elliott (2007) more recently found that sex differences in misperceiving the morphological horizon seem to be unique to a 45° pitch orientation when blood distribution is least altered without prior whole-body rotation. More research is needed to explain this result.

In the present study the hardware hypothesis was tested using both the SVV and the PU against a grey background with the body lying right-side down. When lying right-side down the SVV and PU were judged as being between the direction of gravity and the orientation of the body. If females rely less on vestibular information because they have smaller otoliths then estimates of the SVV and PU should be shifted significantly closer to the body for females compared to males. We found no differences between females and males in these instances. It should be noted that while the PU is less influenced by vestibular input than the SVV task, and may be a less compelling test of the hardware hypothesis, the SVV task is highly influenced by vestibular input. For this reason we can with confidence reject the hardware hypothesis.

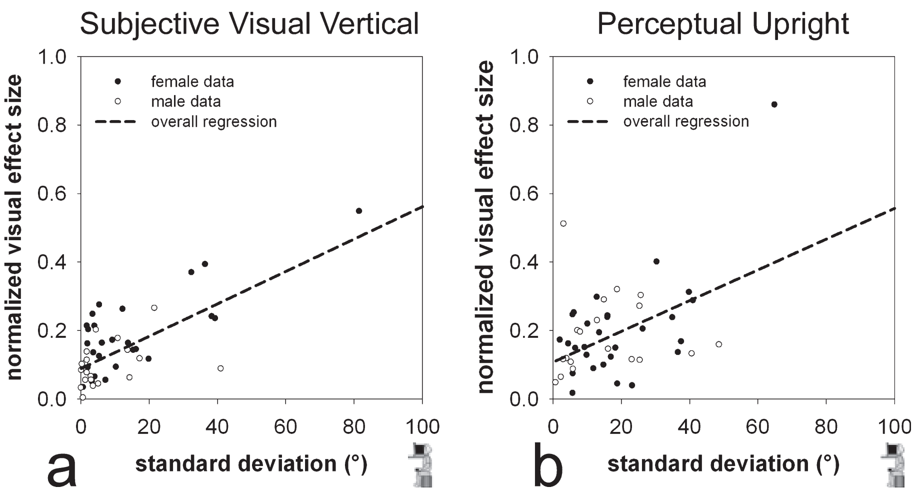

FIG. 6. The relationship between the mean effect size (see text) and the SD for the control (grey) background across sexes for (a) the SVV and (b) the PU when seated upright. The broken regression lines are fitted to all data. Black data points represent data for females and white data points for males.

'Which way is up' is different for females and males

If greater visual dependence in females is not attributable to anatomical differences in sensory end organs, this sex differences may lie in the integration of multisensory information. The perception of self-orientation is multisensory in nature (Howard, 1982; Mittelstaedt, 1988; Dyde *et al.*, 2006). Dramatic sex differences have been found in response to circular vection (Darlington & Smith, 1998), motion sickness (Lawther & Griffin, 1987), path integration (Fortenbaugh *et al.*, 2007) and recalibration of vestibular perception following sensory adaptation to conflicting visual–vestibular stimuli (Kennedy *et al.*, 1996; Viaud-Delmon *et al.*, 1998). Our results support the hypothesis of Berthoz & Viaud-Delmon (1999) who speculated that sex differences may exist in central processing of visual–vestibular interactions. Our different results for the PU and SVV imply that they use different mechanisms and that the sex differences that affect these mechanisms arise at the level of central neural interactions. These differences are most evident in the higher variability and lower accuracy found in females which only occurs when gravity and the long body axis align. Consequently, because females and males do not integrate visual, body sense and vestibular cues in similar fashions, 'which way is up' is different for females and males. This should be carefully considered when interpreting results from orientation perception studies. While we are unaware of studies indicating a sex difference in the weighting placed on visual cues in other multisensory combinations, such as ventriloquism (see Howard & Templeton, 1966; Alais & Burr, 2004), the results of this study suggest that sex differences in other multisensory tasks requires further investigation.

It should be noted that, while our participants were only tested while upright and when lying right-side down, we have no reason to suspect that different sex difference results would be obtained if participants were left-side down. The effect of posture on the SVV has been studied when lying to the left and right, where similar effects of posture are found (see Van Beuzekom & Van Gisbergen, 2000). The effect of posture on the PU is being specifically addressed in two separate forthcoming papers (see Jenkin *et al.*, 2007, 2008 for preliminary results). In general the effect of posture on the PU is similar when left-side down compared to right-side down when a significant general leftward bias of the PU is considered (Jenkin *et al.*, 2008). In addition, we do not suspect that factors affecting spatial attention such as pseudoneglect, where normal participants tend to bisect a horizontal line with a leftward bias, are directly related to sex differences in orientation perception. There has been no conclusive evidence indicating that females and males differ significantly in this respect (see Jewell & McCourt, 2000; but see Hausmann *et al.*, 2002).

Sex differences in spatial ability

There have been a number of explanations as to why females may be more visually dependent than males. Originally Witkin *et al.* (1954) speculated that field dependency in females was related to encultured dependence or passive–acceptance being encouraged in females while independence or active–analytical behavior was encouraged among males (see Witkin *et al.*, 1954, p. 487). More substantial explanations have attributed sex differences in perceived self-orientation to differences between females and males in other measures of spatial ability (Sherman, 1967; Hyde *et al.*, 1975; Shute *et al.*, 1983; Linn & Petersen, 1985; Voyer *et al.*, 1995; Parsons *et al.*, 2004).

The SVV (in the form of the rod-and-frame test) is a measure of spatial ability and is classified along with other tests such as the water level task (Inhelder & Piaget, 1999) as a measure of spatial perception (Linn & Petersen, 1985). Linn & Petersen (1985) defined spatial perception tests as those in which the observer determines spatial relationships with respect to their body despite distracting information. Can the PU be regarded as a spatial perception test? By this strict definition, probably not. The OCHART indirectly measures the PU defined by the orientation at which characters are most easily recognized. While the PU is certainly affected by multisensory orientation information as shown here, because it is an indirect measure it does not require the observer to determine or think about what the orientation of the letter character is in relation to the body; it is a letter recognition task requiring a different spatial ability than the SVV where a line is overtly judged relative to an internal representation of gravity's direction. This is what distinguishes the PU from the SVV and probably distinguishes it from other spatial ability measures. This may be why females and males did not perform differently in our PU task.

Within this framework we predict that the PU will not be affected by hormones (Resnick *et al.*, 1986; Gouchie & Kimura, 1991; Collaer

& Hines, 1995; Hampson, 1995; Moffat & Hampson, 1996), sex-linked genes (Stafford, 1961; Garron, 1970; Hartlage, 1970; Bock & Kolakowski, 1973; Yen, 1975) or academic performance (Peters *et al.*, 2006), in contrast to what has been found for other measures of spatial ability. We suggest that other measures of spatial ability (e.g., mental rotation) be measured along with the OCHART to confirm this hypothesis.

Variability and left-from-right confusion

That females perform more poorly than males in spatial ability tasks could be reflected in sex differences that we report in the variability of the SVV (see Fig. 3). Females are frequently reported as being less precise when setting a line to vertical than males using the method of adjustment (Witkin *et al.*, 1954; Gross, 1959; Groberg *et al.*, 1969; Bogo *et al.*, 1970; Hyde *et al.*, 1975) and this is confirmed in our results using the method of constant stimuli. Why is it that females have higher variability when setting a line to the apparent vertical than males? Linn & Petersen (1985) suggested that observers who analytically assess task features may perform worse than those who rely on more 'reflex' cues (such as gravitational and kinesthetic) when estimating the orientation of a line relative to gravitational vertical in the presence of conflicting visual cues. This could explain why the reinforcement of selecting the correct strategy in spatial perception tasks has been shown to partially reduce sex differences (Reinking *et al.*, 1974; Liben & Golbeck, 1980; Tremblay *et al.*, 2004).

Another possible explanation for the effects shown here is that of left-from-right confusion. Males are better able to discriminate left from right than females (Wolf, 1973; Harris & Gitterman, 1978; Hannay *et al.*, 1990; Ofte & Hugdahl, 2002; Gormley *et al.*, 2008). The SVV task requires participants to judge whether a visible line is oriented CW or CCW relative to the direction in which a ball would fall if dropped (i.e., gravity) and therefore requires participants to think about this direction and to distinguish CW from CCW. The PU task requires no such relative spatial judgment as the task demands are to simply identify the character 'p' or 'd'. As CW and CCW are easily substituted for right and left respectively, we speculate that sex differences in making left-from-right discriminations could explain why females are less precise than males when estimating the SVV compared to the PU, a lack of precision which our correlations demonstrate would in turn lead to a higher likelihood of being scored as visually dependent. More research is needed to assess this hypothesis.

Conclusion

Females rely more on vision for certain (e.g., SVV) but not all (e.g., PU) spatial tasks. As such, 'visual dependence' in females does not generalize to all aspects of spatial processing. Increased reliance on visual information does not come at a cost to the contributions of gravity and the internal representation of the body, and thus sex differences in sensory organ physiology seem an unlikely explanation for our pattern of results. We attribute sex differences in visual dependence to sensory processing differences in the brains of females and males unique to particular spatial tasks. We further suggest that well-known differences between the sexes in the selection of strategies to solve spatial tests (e.g., Linn & Petersen, 1985), and a greater tendency in females to confuse their left with their right, probably contribute to females' lower precision in setting a line to vertical.

Acknowledgements

This work was sponsored by the Natural Sciences Research Council of Canada (NSERC) to L.R.H. M.B.C. was an NSERC scholar.

Abbreviations

CCW, counter-clockwise; CW, clockwise; OCHART, Oriented Character Recognition Test; PU, perceptual upright; SD, standard deviation; SVV, subjective visual vertical.

References

Alais, D. & Burr, D. (2004) The ventriloquist effect results from near-optimal bimodal integration. *Curr. Biol.*, **14**, 257–262.

Aubert, H. (1861) Eine scheinbare bedeutende Drehung von Objecten bei Neigung des Kopfes nach rechts oder links. *Virchows Arch.*, **20**, 381–393.

Berthoz, A. & Viaud-Delmon, I. (1999) Multisensory integration in spatial orientation. *Curr. Op. Neurobiol.*, **9**, 708–712.

Bock, R.D. & Kolakowski, D. (1973) Further evidence of sex-linked major-gene influence on human spatial visualizing ability. *Am. J. Human Genet.*, **25**, 1.

Bogo, N., Winget, C. & Gleser, G.C. (1970) Ego defenses and perceptual styles. *Percept. Mot. Skills*, **30**, 599–605.

Collaer, M.L. & Hines, M. (1995) Human behavioral sex differences: a role for gonadal hormones during early development? *Psychol. Bull.*, **118**, 55–107.

Corballis, M.C., Zbrodoff, N.J., Shetzer, L.I. & Butler, P.B. (1978) Decisions about identity and orientation of rotated letters and digits. *Mem. Cognit.*, **6**, 98–107.

Darlington, C.L. & Smith, P.F. (1998) Further evidence for gender differences in circular vection. *J. Vestib. Res.*, **8**, 151–153.

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

Ernst, M.O. & Banks, M.S. (2002) Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, **415**, 429–433.

Fortenbaugh, F.C., Chaudhury, S., Hicks, J.C., Hao, L. & Turano, K.A. (2007) Gender differences in cue preference during path integration in virtual environments. *ACM Trans. App. Percept.*, **4**, 1–18.

Garron, D.C. (1970) Sex-linked, recessive inheritance of spatial and numerical abilities, and Turner's syndrome. *Psychol. Rev.*, **77**, 147–152.

Gorbet, D.J. & Sergio, L.E. (2007) Preliminary sex differences in human cortical BOLD fMRI activity during the preparation of increasingly complex visually guided movements. *Eur. J. Neurosci.*, **25**, 1228–1239.

Gormley, G.J., Dempster, M. & Best, R. (2008) Right-left discrimination among medical students: questionnaire and psychometric study. *Br. Med. J.*, **337**, a2826.

Gouchie, C. & Kimura, D. (1991) The relationship between testosterone levels and cognitive ability patterns. *Psychoneuroendocrinology*, **16**, 323–334.

Groberg, D.H., Dustman, R.E. & Beck, E.C. (1969) The effect of body and head tilt in the perception of vertical: comparison of body and head tilt with left and right handed, male and female subjects. *Neuropsychologia*, **7**, 89–100.

Gross, F. (1959) The role of set in perception of the upright. *J. Personality*, **27**, 95–103.

Hampson, E. (1995) Spatial cognition in humans: possible modulation by androgens and estrogens. *J. Psychiatry Neurosci.*, **20**, 397–404.

Hannay, H.J., Ciaccia, P.J., Kerr, J.W. & Barrett, D. (1990) Self-report of right-left confusion in college men and women. *Percept. Mot. Skills*, **70**, 451.

Harris, L.J. & Gitterman, S.R. (1978) University professors' self-descriptions of left-right confusability: sex and handedness Differences. *Percept. Mot. Skills*, **47**, 819–823.

Hartlage, L.C. (1970) Sex-linked inheritance of spatial ability. *Percept. Mot. Skills*, **31**, 610.

Hausmann, M., Ergun, G., Yazgan, Y. & Güntürkün, O. (2002) Sex differences in line bisection as a function of hand. *Neuropsychologia*, **40**, 235–240.

Hock, H.S. & Tromley, C.L. (1978) Mental rotation and perceptual uprightness. *Percept. Psychophys.*, **24**, 529–533.

Howard, I.P. (1982) *Human Visual Orientation*. J. Wiley, New York.

Howard, I.P. & Templeton, W.B. (1966) *Human Spatial Orientation*. J Wiley, London.

Hyde, J.S., Geiringer, E.R. & Yen, W.M. (1975) On the empirical relation between spatial ability and sex differences in other aspects of cognitive performance. *Multivariate Behav. Res.*, **10**, 289–309.

Inhelder, B. & Piaget, J.(1999). *The Growth of Logical Thinking from Childhood to Adolescence*. Routledge, London.

Jenkin, H., Barnett-Cowan, M., Islam, A., Mazour, E., Sanderson, J., Dyde, R.T., Jenkin, M.R. & Harris, L.R. (2007) The effect of tilt on the perceptual upright. *Perception*, **36**, S208.

Jenkin, H., Barnett-Cowan, M., Dyde, R.T., Sanderson, J., Jenkin, M.R. & Harris, L.R. (2008) Left ⁄ right asymmetries in the contribution of body orientation to the perceptual upright. *J Vis*, **8**, 1062, 1062a.

Jewell, G. & McCourt, M.E. (2000) Pseudoneglect: a review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia*, **38**, 93–110.

Jolicoeur, P. (1985) The time to name disoriented natural objects. *Mem. Cogn.*, **13**, 289–303.

Kennedy, R.S., Hettinger, L.J., Harm, D.L., Ordy, J.M. & Dunlap, W.P. (1996) Psychophysical scaling of circular vection (CV) produced by optokinetic (OKN) motion: individual differences and effects of practice. *J. Vestib. Res.*, **6**, 331–341.

Lawther, A. & Griffin, M.J. (1987) Prediction of the incidence of motion sickness from the magnitude, frequency, and duration of vertical oscillation. *J. Acoust. Soc. Am.*, **82**, 957–966.

Liben, L.S. & Golbeck, S.L. (1980) Sex differences in performance on Piagetian spatial tasks: differences in competence or Performance? *Child Dev.*, **51**, 594–597.

Linn, M.C. & Petersen, A.C. (1985) Emergence and characterization of sex differences in spatial ability: a meta-analysis. *Child Dev.*, **56**, 1479–1498.

Mittelstaedt, H. (1983) A new solution to the problem of the subjective vertical. *Naturwissenschaften*, **70**, 272–281.

Mittelstaedt, H. (1988) The information processing structure of the subjective vertical. A cybernetic bridge between its psychophysics and its neurobiology. In Marko, H., Hauske, G. & Struppler, A. (Eds), *Processing Structures for Perception and Action*. VCH Weinheim, Germany, pp. 217–263.

Moffat, S.D. & Hampson, E. (1996) A curvilinear relationship between testosterone and spatial cognition in humans: possible influence of hand preference. *Psychoneuroendocrinology*, **21**, 323–337.

Ofte, S.H. & Hugdahl, K. (2002) Right-left discrimination in male and female, young and old subjects. *J. Clin. Exp. Neuropsyc.*, **24**, 82–92.

Parsons, T.D., Larson, P., Kratz, K., Thiebaux, M., Bluestein, B., Buckwalter, J.G. & Rizzo, A.A. (2004) Sex differences in mental rotation and spatial rotation in a virtual environment. *Neuropsychologia*, **42**, 555–562.

Peters, M., Lehmann, W., Takahira, S., Takeuchi, Y. & Jordan, K. (2006) Mental rotation test performance in four cross-cultural samples ($N = 3367$): overall sex differences and the role of academic program in performance. *Cortex*, **42**, 1005–1014.

Pitblado, C. (1976) Superior performance by women in a visual orienting task: a limit on the concept of field dependence. *Percept. Mot. Skills*, **42**, 1195–1200.

Reinking, R., Goldstein, G. & Houston, B.K. (1974) Cognitive style, proprioceptive skills, task set, stress, and the rod-and-frame test of field orientation. *J. Pers. Soc. Psychol.*, **30**, 807–811.

Resnick, S.M., Berenbaum, S.A., Gottesman, I.I. & Bouchard, T.J.J.R. (1986) Early hormonal influences on cognitive functioning in congenital adrenal hyperplasia. *Dev. Psychol.*, **22**, 191–198.

Rock, I. (1973) *Orientation and Form*. Academic Press, New York.

Rock, I. & Heimer, W. (1957) The effect of retinal and phenomenal orientation on the perception of form. *Am. J. Psychol.*, **70**, 493–511.

Sato, H., Sando, I. & Takahashi, H. (1992) Computer-aided three-dimensional measurement of the human vestibular apparatus. *Otolaryng. Head Neck*, **107**, 405–409.

Sherman, J.A. (1967) Problem of sex differences in space perception and aspects of intellectual functioning. *Psychol. Rev.*, **74**, 290–299.

Shute, V.J., Pellegrino, J.W., Hubert, L. & Reynolds, R.W. (1983) The relationship between androgen levels and human spatial abilities. *B. Psychonomic Soc.*, **21**, 465–468.

Stafford, R.E. (1961) Sex differences in spatial visualization as evidence of sex-linked inheritance. *Percept. Mot. Skills*, **13**, 428.

Tremblay, L. & Elliott, D. (2007) Sex differences in judging self-orientation: the morphological horizon and body pitch. *BMC Neurosci.*, **8**, 6.

Tremblay, L., Elliott, D. & Starkes, J.L. (2004) Gender differences in perception of self-orientation: software or hardware? *Perception*, **33**, 329–338.

Van Beuzekom, A.D. & Van Gisbergen, J.A.M. (2000) Properties of the internal representation of gravity inferred from spatial-direction and body-tilt estimates. *J. Neurophysiol.*, **84**, 11–27.

Viaud-Delmon, I., Ivanenko, Y.P., Berthoz, A. & Jouvent, R. (1998) Sex lies and virtual reality. *Nat. Neurosci.*, **1**, 15–16.

Voyer, D., Voyer, S. & Bryden, M.P. (1995) Magnitude of sex differences in spatial abilities: a meta-analysis and consideration of critical variables. *Psychol. Bull.*, **117**, 250–270.

Witkin, H.A., Lewis, H.B., Hertzman, M., Machover, K., Meissner, P.B. & Wapner, S. (1954) *Personality Through Perception. An Experimental and Clinical Study.* Harper, New York.

Wolf, S.M. (1973) Difficulties in right-left discrimination in a normal population. *Arch. Neurol.*, **29**, 128–129.

Yen, W.M. (1975) Sex-linked major-gene influences on selected types of spatial performance. *Behav. Genet.*, **5**, 281–298.