**Spatial biases in peripersonal space in sighted and blind individuals revealed by a haptic line bisection paradigm**



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**Spatial Biases in Peripersonal Space in Sighted and Blind Individuals Revealed by a Haptic Line Bisection Paradigm**

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There is ample evidence that neurologically normal individuals tend to represent spatial extents in a slightly distorted way, as demonstrated by the existence, in both the visual and haptic modality, of illusionary phenomena such as the horizontal–vertical illusion (e.g., Finger & Spelt, 1947; Millar & Al-Attar, 2000) or the tendency to overrepresent the left portion of space, known as pseudoneglect (see Bowers & Heilman, 1980; Jewell & McCourt, 2000, for reviews). The latter refers to a phenomenon in which neurologically normal individuals bisect lines slightly to the left of their physical midpoint. This tendency is opposite to the rightward bisection bias usually found in neglect patients where neglect refers to a syndrome (usually after right parietal damage) that makes it difficult for the patients to orient toward stimuli in the contralesional hemispace, or toward the contralesional side of the stimuli themselves (see Vallar, 2001). As shown by an extensive meta-analysis conducted by Jewell and McCourt (2000), the leftward bias shown by neurologically normal individuals in line bisection tasks is consistent across studies and occurs in both the visual and haptic modality. However, the bias is subtle and appears to be affected by several factors related to both individual variables (e.g., age, gender, and handedness) and experimental manipulations, such modality (visual or haptic), line length, cueing, and the location of space where the lines appear (see Jewell & McCourt, 2000). As a consequence, a high intra- and intersubject variability has been found in bisection paradigms, a factor that should be taken into account in studies involving small groups of participants (see Manning, Halligan, & Marshall, 1990).

It has been suggested that pseudoneglect in line bisection may depend on differences in the role of the right and left hemisphere in the control of spatial attention ( Jewell & McCourt, 2000). In this view, the right hemisphere plays a dominant role in attentional control, which may make lines appearing in the contralateral left hemifield seem longer than they physically are. This view is supported by the finding that attended parts of stimuli have an enhanced perceived magnitude in comparison with unattended ones (e.g., Masin, 2003, 2008). Nonetheless, the relationship between attention and perceived line length is not entirely clear, with some studies reporting an increase in the perceived length of unattended lines (see Tsal & Shalev, 1996; for a review, see Tsal, Shalev, & Zakay, 2005) and others showing attentional effects on the variability in line judgments but not on perceived length ( Prinzmetal & Wilson, 1997).

Consistent biases in line bisection have also been observed in the vertical and radial planes. With visually presented lines, neurologically normal participants tend to err away from their body in the radial axis (e.g., Halligan & Marshall, 1993; Shelton, Bowers, & Heilman, 1990), and in the upward direction in the vertical axis (e.g., Drain & Reuter-Lorenz, 1996; Halligan & Marshall, 1993; Jeerakathil & Kirk, 1994; Post, O'Malley, Yeh, & Bethel, 2006; Shelton et al., 1990). These biases have been interpreted as being either retinotopic, body centered, or object centered ( Chewning, Adair, Heilman, & Heilman, 1998; Geldmacher & Heilman, 1994; Jeerakathil & Kirk, 1994; Previc, 1990). According to the retinotopic account ( Previc, 1990), stimuli falling in the lower hemiretina (upper visual field) are processed preferentially because the lower hemiretina is specialized for visual search and recognition mechanisms directed toward far space (

Geldmacher & Heilman, 1994; Previc, 1990). With vertical lines and radial lines presented below eye level, the upper and distal parts of the line will be projected to the lower hemiretina, resulting in the upward and distal bias. Body-centered factors may also give rise to the observed bias: during visual exploration, attention is likely to be preferentially distributed away from the body because the visual system is tuned to detect distant stimuli ( Shelton et al., 1990), leading to a distal bias in bisecting radial lines. In support of both the retinotopic and body-centered hypotheses, Geldmacher and Heilman (1994) found that when radial lines were presented above eye level, so that the proximal portion of the line appeared in the upper visual field/lower hemiretina, the bisection error did not significantly differ from zero, possibly because, in this condition, the head-centered and retinal factors were in conflict ( Geldmacher & Heilman, 1994; see also Chewning et al., 1998). Finally, object-centered biases may also play a role: In particular, visual attention may preferentially be biased toward the upper part of objects ( Jeerakathil & Kirk, 1994).

Whether hemispheric asymmetry in the control of spatial attention plays a role in determining the bisection biases in the vertical and radial planes is not fully clear (see Drain & Reuter-Lorenz, 1996). Behavioral studies have not always found a correlation between bisection performance in different spatial planes (e.g., McCourt & Olafson, 1997; Post et al., 2006; see also Nicholls, Mattingly, Berberovic, Smith, & Bradshaw, 2004), as one may expect if the same cortical mechanisms lead to the observed biases in the three dimensions. In fact, neglect in the radial and vertical dimensions has been observed in patients with damage to the occipitoparietal and occipitotemporal regions in either hemisphere, with the direction of the bias depending on the specific site of the lesion (cf. Kageyama, Imagase, Okubo, & Takayama, 1994; Kori & Geldmacher, 1999; Mennemeier, Wertman, & Heilman, 1992; Rapcsak, Cimino, & Heilman, 1988; Shelton et al., 1990). Still, the right hemisphere may be more critical, as suggested by the finding that patients with right hemisphere damage usually show the stronger symptoms (see Halligan & Marshall, 1989). Accordingly, neuroimaging studies have found activations in the right inferior parietal cortex in neurologically normal individuals during line bisection judgments regardless of whether horizontal or vertical lines were presented ( Fink, Marshall, Weiss, & Zilles, 2001).

As briefly mentioned earlier, the modality (visual vs. haptic) in which the bisection task is performed has been found to influence the extent of pseudoneglect. There are a number of differences between the two domains that may explain this. Intuitively, haptic bisection (in which both kinaesthetic and proprioceptive factors are involved) requires active manual motor exploration, whereas visual bisection does not. Moreover, although participants usually move their eyes to scan the visual line (typically making an initial leftward eye movement to the end of the line, followed by a rightward scan, after which they again move leftward to the center of the line; see Kim, Anderson, & Heilman, 1997), the length estimation in visual bisection can also be obtained through parallel processing. Conversely, haptic exploration is inherently sequential, with participants having to maintain in memory both the start and end positions of the scan (whereas, in vision, the two extremities of the line are simultaneously available). Despite these differences, the direction of the horizontal bias in the visual and haptic modality tends to be similar, with neurologically normal individuals bisecting to the left of the veridical midpoint ( Jewell & McCourt, 2000; see also Gallace, Auvray, & Spence, 2007, on the possible involvement of higher order multisensory/amodal processes in bisection tasks). It is important to note, however, that the extent of pseudoneglect in the haptic modality depends on numerous modality-specific factors, such as the way the rod is explored (one search vs. multiple searches; see Baek et al., 2002), whether the left or right hand is used for scanning (e.g., Brodie & Pettigrew, 1995), tactile versus kinesthetic scanning ( Sampaio & Philip, 1991), participants' handedness (e.g., Sampaio & Chokron, 1992), and the spatial position of the line with respect to the head–body axis ( Bradshaw, Nettleton, Nathan, & Wilson, 1983). Conversely, the bias reported in the haptic modality for rods presented in the vertical and radial planes is the opposite of that observed with visually presented lines; that is, toward the body in the radial plane and in the downward direction in the vertical plane ( Baek et al., 2002; Chewning et al., 1998; Shelton et al., 1990). This has been explained in terms of kinesthetic–motor mechanisms, which are inherent to haptic exploration and which are relatively body centered, thus inducing a toward-the-participant bias ( Chewning et al., 1998; Shelton et al., 1990).

The haptic line bisection task has also been conducted with visually impaired individuals, offering an insight into hemispheric specialization in blind individuals ( Bradshaw, Nettleton, Nathan, & Wilson, 1986; Coudereau, Gueguen, Pratte & Sampaio, 2006; Sampaio, Gouarir, & Mvondo Mvondo, 1995). Studies using auditory localization paradigms suggest that the right hemisphere is specialized in spatial processing in blind individuals as well ( Gougoux, Zatorre, Lassonde, Voss, & Lepore, 2005; Voss et al., 2004; Weeks et al., 2000). The available evidence indicates that blind participants show pseudoneglect in line bisection, but the results are not entirely consistent. For instance, in their study, Sampaio and colleagues (1995) reported that blind children bisected horizontal lines significantly to the left of their veridical midpoint with both right and left hands, whereas sighted children bisected to the right of the midpoint with their left hand and did not show any significant directional bias when using the right hand. Partially sighted children did not show any directional bias; overall, no differences in the accuracy of the three groups were reported ( Sampaio et al., 1995). More recently, Coudereau et al. (2006) investigated pseudoneglect by means of a haptic bisection task in a group of blind individuals, some of whom were archery experts. Overall, the blind archery experts showed a significant pseudoneglect effect, whereas no particular deviations were observed in blind individuals who did not practice archery. However, the hand used for exploration and the direction of the final exploration played a critical role in the latter study. When the right hand was used for exploration, all blind participants showed a leftward bias, which was strongest when the final movement was performed from right to left. In an earlier study by Bradshaw and colleagues (1986), a group of early blind adults were asked to adjust the extremities of a rod protruding from a copper tube. Six of the 10 participants erred in protruding the rod rightward from the tube, thus overestimating the left side of space (that was perceived to be as long as the right side, although it was physically shorter), resembling the pattern of performance in sighted individuals (cf. Bradshaw et al., 1983). In one condition, participants performed the task with their hands crossed. In this condition, the blind participants were found to err in protruding the rod leftward from the tube, whereas the sighted participants' bias was unaffected ( Bradshaw et al., 1986).The opposite directional bias in the crossed-hands condition (as compared with the uncrossed-hands condition) suggests that the blind participants tended to rely on body-centered coordinates more than the sighted controls. In particular, what was coded as left side of space by the blind participants depended on the position of their left hand, whereas sighted participants relied on eye-centered spatial codes, regardless of hand position ( Bradshaw et al., 1986). Indeed, converging evidence suggests that blind individuals tend to code the locations of items in the outside world with respect to a part of their body, such as the hands, the midsagittal plane, or their body as a whole ( Gaunet & Rossetti, 2006; Postma, Zuidhoek, Noordzij, & Kappers, 2008a, 2008b; Röder, Focker, Hotting, & Spence, 2008; Röder, Rösler, & Spence, 2004; for reviews, see Cattaneo et al., 2008; Thinus-Blanc & Gaunet, 1997).

The existing evidence is thus not completely consistent on whether pseudoneglect develops in the absence of vision or whether leftward biases in blind individuals only depend on specific experimental or individual variables (see Coudereau et al., 2006). Moreover, how blind individuals perform in a haptic bisection task when rods are presented in the radial or vertical plane is not known. The present study addressed these issues by investigating the performance of early blind participants in a haptic bisection task in the horizontal, vertical, and radial dimensions. Specifically, we used a haptic bisection task very similar to that previously used by Baek et al. (2002). Baek et al. required blindfolded sighted participants to explore (with their right index finger) rods of different lengths presented in the horizontal, vertical, or radial plane. In the single-search condition, only one search movement was allowed; in the multisearch condition, participants could scan the rod as many times as they wanted, with no time limits. In both conditions, the initial search direction was controlled by the experimenter, by positioning the participant's index finger over either one of the rod's two extremities. Our paradigm was similar to the multisearch condition of Baek et al.'s study, but we gave a time limit of 10 s to reduce interparticipant variability. Moreover, as we were interested in possible biases in the choice of the first movement direction, our participants were free to choose the direction in which they began the exploration. Both sighted and early blind participants were tested.

We expected sighted participants to show leftward, downward, and proximal biases, as reported by Baek et al. (2002). In light of the evidence suggesting a right hemisphere dominance in spatial tasks in blind individuals ( Gougoux et al., 2005; Voss et al., 2004; Weeks et al., 2000) and in light of previous studies using a bisection task with blind individuals ( Coudereau et al., 2006; Sampaio et al., 1995), we expected blind participants to display a significant leftward bias when bisecting horizontal rods. Predictions for the vertical and radial planes were less straightforward. As mentioned earlier, individuals lacking any visual experience tend to rely mainly on body-centered or hand-centered coordinates (and less on object-centered/allocentric codes) when representing the external space ( Bradshaw et al., 1986; Röder et al., 2004; for reviews, see Cattaneo et al., 2008; Thinus-Blanc & Gaunet, 1997). Accordingly, if the adoption of a body-centered reference frame (as compared with a more allocentric type of spatial representation) plays a major role in causing the unidirectional bias in haptic bisection of vertical and radial lines in the sighted, then blind participants should show a similar consistent downward/proximal bias ( Chewning et al., 1998; Shelton et al., 1990). Moreover, assuming that they adopt a hand-centered code, blind participants' directional errors may also be particularly affected by the specific hand movement direction (in particular, by a tendency to err toward the direction of the final movement; see Baek et al., 2002; Coudereau et al., 2006). In this regard, it is also worth considering that, when relying on proprioceptive position information only (with no available visual information), individuals are usually better at localizing hand positions closer to the shoulder (see van Beers, Sittig, & Denier van der Gon, 1998). This might be relevant when bisecting rods in the radial and vertical planes, as larger response uncertainty may be associated with increased hand–shoulder distance. Finally, some preliminary data discussed by Cornoldi and Vecchi (2003, pp. 105–106) suggested that blind individuals may encounter specific difficulties in mentally visualizing the vertical dimension: in particular, it was found that blind participants made significantly more errors when required to imagine a mental pathway on a vertical haptic matrix compared with a matrix placed in the horizontal plane. This might be due to a limited familiarity with the vertical dimension: If locomotion allows one to explore objects that are distant in depth (i.e., in the radial plane), the vertical dimension cannot be easily explored by blind individuals. Hence, we might hypothesize blind participants' intra- and interparticipant variability to be particularly high when exploring along the vertical axis (with which blind individuals are little familiar), thus preventing or reducing the emergence of a unidirectional bias.

**Method**

**Participants**

Eighteen sighted participants (9 male, 9 female; mean age = 30.22 years, SD = 4.33; age range = 25–40; mean education = 18.39 years, SD = 2.40) and 17 blind participants (10 male, 7 female; mean age = 35.94 years, SD = 7.10; age range = 23–48; mean education = 14.59 years, SD = 2.96) took part in the experiment (see Table 1 for details). All of the participants were free of neurological or psychiatric illness and were right-handed as assessed by the Edinburgh Handedness Inventory ( Oldfield, 1971). The cause of blindness in the blind participants was peripheral, with a congenital or early (<6 months of age) onset. It is important to note that all blind participants had normal hand function, and in no case was blindness due to diabetic retinopathy (which may result in peripheral neuropathies in the hands; see Travieso & Lederman, 2007). A local ethics committee approved the experiment.

**Details of the Blind Participants Tested in This Experiment**

**Materials**

Figure 1 depicts the experimental setting. Wooden rods of five different lengths (300, 350, 400, 450, and 500 mm) with a diameter of 14 mm were used as stimuli. Units of measurement (millimeters) were marked on each of the rods with a pen and could not be haptically perceived. The rods were presented in the horizontal, vertical, or radial plane and were fixed with Velcro on a wooden panel along the three spatial dimensions. Participants were seated at a table. In the horizontal plane, the midpoint of the rod was aligned with the midsagittal plane of the participant's body and head, and the distance between the participant's midsternum and the midpoint of the rod was 380 mm. In this way, the object-centered spatial representation and the body-centered spatial representation of the midline coincided. In the vertical axis, the rods were placed vertically along the midsagittal plane of the participant's body, and the distance between the participant's midsternum and the midpoint of the rod was about 350 mm. The midpoints of the rods were leveled with the participant's shoulder, so that the upper end of the longest rod was at the level of the participant's forehead. In this way, assuming that the elbow was kept aligned in front of the shoulder, the same amount of arm movement was needed to reach the top and the bottom extremity of the rod (so that, again, body-centered and object-centered representation of the midpoint approximately coincided). In the radial condition, the rods were placed on the table along the participant's midsagittal plane, with the distance between the participant's midsternum and the midpoint of the rod being about 380 mm (see Baek et al., 2002, for a similar paradigm). In this way, the radial rod fell along the projection of the midsagittal line of participants on the plane of the table, and distance was such that the midpoint of the rod fell approximately at half extension of the arm.

Table 1
*Details of the Blind Participants Tested in This Experiment*

| Participant | Gender | Age | Job activity | Education (years) | Blindness etiology | Blindness onset | Residual vision | Mobility tools |
|---|---|---|---|---|---|---|---|---|
| 1 | Male | 39 | Call operator | 10 | Optic nerve damage | Birth | None | Cane |
| 2 | Female | 39 | Physiotherapist | 13 | Optic nerve damage | Birth | None | Cane |
| 3 | Female | 34 | Call operator | 16 | Optic nerve damage | Birth | None | Cane |
| 4 | Male | 26 | Employee | 18 | Oxygen therapy | Birth | None | Cane |
| 5 | Female | 36 | Call operator and university student | 16 | Congenital glaucoma | Birth | None | Cane |
| 6 | Male | 37 | Call operator | 18 | Optic nerve damage | Birth | None | Cane |
| 7 | Male | 33 | Physiotherapist | 13 | Trauma | 4 months | None | Cane |
| 8 | Male | 40 | Physiotherapist | 11 | Oxygen therapy | Birth | None | Cane |
| 9 | Male | 46 | Call operator | 10 | Optic nerve damage | Birth | None | Cane |
| 10 | Female | 29 | English teacher | 18 | Retrolental fibroplasias | Birth | None | Cane |
| 11 | Male | 48 | Call operator | 13 | Optic nerve damage | Birth | None | Dog |
| 12 | Male | 46 | Call operator | 16 | Optic nerve damage | Birth | None | Cane |
| 13 | Male | 32 | Employee | 16 | Trauma | Birth | None | Cane |
| 14 | Male | 23 | University student | 16 | Optic nerve damage | Birth | None | Cane |
| 15 | Female | 40 | Teacher | 17 | Trauma | 6 months | None | Cane |
| 16 | Female | 28 | English teacher | 17 | Trauma | 8 months | None | Cane |
| 17 | Female | 35 | Call operator | 10 | Optic nerve damage | Birth | None | Cane |

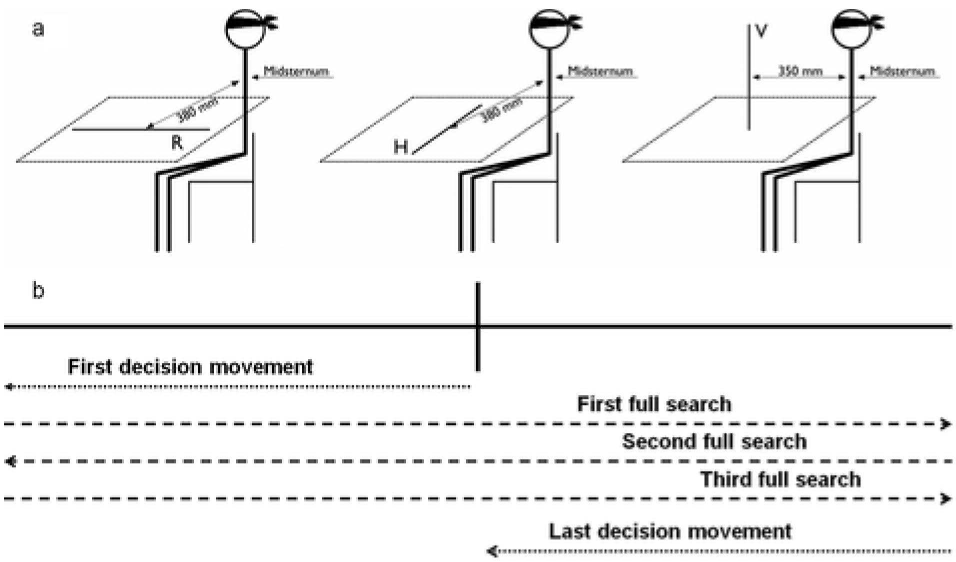


Figure 1. (a) The experimental setting showing the bisection task in the horizontal, vertical, and radial axes. (b) An example of a horizontal trial in which participants started exploration to the left end of the rod (initial decision movement); performed three full searches; and, at the end of the 10 seconds, ended exploration by performing a right-to-left movement (final decision movement).

**Procedure**

Sighted participants were blindfolded throughout the entire experiment. Blind participants were not blindfolded (none of them could count on any residual light perception; therefore a blindfold was not necessary). At the beginning of each trial, the experimenter placed the palm of the participant's right hand on the rod so that it covered the midpoint of the rod, but the middle of the palm could be either slightly to the left or right of the rod's midpoint in the horizontal axis, slightly above or below the rod's midpoint in the vertical axis, and slightly nearer the body or farther away from the body compared with the true rod's midpoint in the radial axis. We used this starting point for haptic exploration to look at the spontaneous scanning strategies adopted by participants, whereas in most previous studies, the starting search direction was predetermined (but see Barrett, Crosson, Crucian, & Heilman, 2002) as participants had to start exploration from either one or the other end of the rod. It is important to note that this palm-based starting position could not be used as an accurate estimate of the rod's midpoint because of its approximate nature and because, at the start of each trial, participants were asked to lift their palm off the rod and to begin to explore it with their right index finger.

Participants were instructed to explore the length of the rod using their right index finger only and in their preferred direction: left to right (L-R) or right to left (R-L) in the horizontal axis; up to down (U-D) or down to up (D-U) in the vertical axis, and near the body (F-N) or far from the body (N-F) in the radial axis. Participants were given 10 s to scan the rod, and they could do so as many times as they wanted. After 10 s, a sound indicated the end of the trial. Participants were instructed that, after hearing the sound, they had to complete the search they were performing and then perform another half-search to the estimated midpoint (see Figure 1b). The experimenter gave neither information about the length of the rod before the experiment nor feedback about the participant's bisection performance during the experiment. The speed of movement of the index finger during the bisection was not specified.

Each of the five rods was presented three times in each spatial axis (horizontal, vertical, and radial); hence, each participant performed a total of 45 trials. The 15 trials of each spatial axis (horizontal, vertical, and radial) were presented in blocks. The different lengths of rods were presented in a random order in each block. The order of presentation of the 3 blocks was counterbalanced across participants. Two practice trials were presented before each block; data from the practice trials were not included in the analysis. In each trial, the direction of the initial half-search and of the final half-search were recorded by the experimenter. The entire experiment lasted for approximately 1 hr.

**Results**

To measure the participant's performance, we marked the middle of the participant's right index fingernail with a pen. Deviations from the objective midpoint were recorded to the nearest millimeter. A negative score was assigned to errors to the left (horizontal axis), to the bottom (vertical axis), and toward the body (radial axis) relative to the actual midpoint. A positive score was assigned to errors to the right (horizontal axis), to the top (vertical axis), and away from the body (radial axis). The mean line bisection errors in millimeters (corresponding to the so-called constant error [CE]; see Guth, 1990) and their standard deviations (variable bisection error [VE]) were then analyzed.

**Line Bisection CE**

Figure 2 shows sighted and blind participants' mean bisection bias in millimeters in the horizontal ( Figure 2a), vertical ( Figure 2b), and radial ( Figure 2c) axes for each rod's length (see also Table 2 and Table 3). One-sample t tests were first conducted by comparing the mean CE with the null set (zero, that is the true midpoint). The five different rod lengths were collapsed together in this analysis. Sighted individuals showed a significant leftward bias in the horizontal axis, $t(17) = 3.48$, $p = .003$; a significant downward bias in the vertical axis, $t(17) = 4.17$, $p = .001$; and a significant proximal bias in the radial axis, $t(17) = 2.39$, $p = .029$. Blind individuals showed a significant leftward bias in the horizontal axis, $t(16) = 7.18$, $p < .001$; however, they did not show any significant bisection bias in the vertical ( $p = .99$) and radial ( $p = .72$) axes (see Table 2 for blind participants' individual biases).

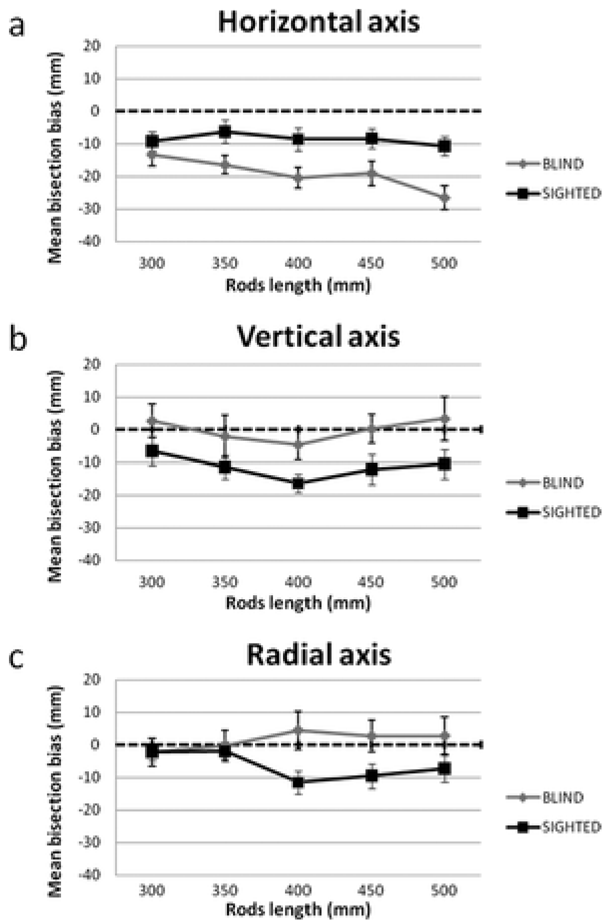


Figure 2. Mean line bisection error (constant error [CE]; in millimeters) in blind ( n = 17) and sighted ( n = 18) participants in bisecting rods in the (a) horizontal, (b) vertical, and (c) radial dimensions. A mean bisection bias equal to zero (dotted line in the graph) corresponds to the absence of a consistent directional bias. A positive value in the horizontal plane indicates a rightward bias; a negative value indicates a leftward bias. A positive value in the vertical plane indicates an upward bias; a negative value indicates a downward bias. A positive value in the radial plane indicates a distal bias; a negative value indicates a proximal bias. Error bars indicate ±1 standard error of the mean.

Table 2 Bisection Bias in Millimeters (and Standard Deviations) Averaged Across the Five Different Lengths for Each Blind Participant in Each Spatial Plane

| Participant | Horizontal axis | Vertical axis | Radial axis |
|---|---|---|---|
| 1 | −29.3 (9.5) | 9.7 (27.2) | 25.5 (16.9) |
| 2 | −13.2 (8.4) | −17.2 (21.5) | 19.5 (15.3) |
| 3 | −20.4 (16.9) | 8.5 (22.4) | 9.7 (11.4) |
| 4 | −21.3 (17.3) | −9.5 (22.9) | −7.7 (11.5) |
| 5 | −13.2 (14.3) | 3.5 (14.8) | 8.7 (16.2) |
| 6 | −24.5 (10.4) | 27.4 (16.2) | 16.4 (13.6) |
| 7 | −27.9 (6.2) | 6.2 (19.2) | −18.3 (13.4) |
| 8 | −17.3 (13.6) | 44.1 (25.5) | 24.9 (19.4) |
| 9 | −11.7 (22.5) | −9.3 (17.8) | −29.5 (21.4) |
| 10 | −20 (13) | 21.7 (10.9) | 6.1 (18.4) |
| 11 | −33.9 (30) | 3.9 (17) | 4.1 (12.4) |
| 12 | −12.9 (12.6) | −21.5 (10.7) | −17.8 (6.4) |
| 13 | 8.5 (17.9) | −15 (9.7) | 10.7 (16) |
| 14 | −7.9 (13.4) | −16.1 (13.8) | 5.5 (11.4) |
| 15 | −19.3 (6.9) | −24.5 (11.6) | −18.5 (9.1) |
| 16 | −20.8 (15.8) | −17.7 (19.4) | 11.9 (19) |
| 17 | −40 (7.4) | 4.8 (26.9) | −25 (17.8) |

| Participant | Horizontal axis | Vertical axis | Radial axis |
|---|---|---|---|
| Sighted | −8.6 (15.6) | −11.4 (17.3) | −6.5 (13.9) |
| Blind | −19.2 (13.8) | −0.06 (18.1) | 1.54 (14.7) |

Bisection Bias in Millimeters Averaged Across the Five Different Lengths for Sighted and Blind Participants in Each Spatial Plane

A repeated-measures analysis of variance (ANOVA) was conducted for each group of participants on the mean CE (in millimeters) with spatial axis (horizontal, vertical, and radial) and length (300, 350, 400, 450, and 500 mm) as within-participants variables. In sighted participants, axis was not significant, $F(2, 34) = 0.79$, $p = .46$; the effect of length almost approached significance, $F(4, 68) = 2.33$, $p = .065$; and the Length × Axis interaction was not significant, $F(8, 136) = 0.97$, $p = .46$. The almost significant effect of length reflected a tendency of the sighted participants to show larger biases with longer rods (see Figure 2). In the blind participants, the analysis revealed a significant effect of axis, $F(2, 32) = 9.68$, $p = .001$, $\eta^2 = 0.38$; no significant effect of length, ( $p = .82$); and a significant Axis × Length interaction, $F(8, 128) = 2.20$, $p = .032$, $\eta^2 = .12$ (see Figure 2). Pairwise comparisons showed that the effect of axis was due to the bisection bias being overall larger in the horizontal axis than in the radial axis, $t(16) = 4.45$, $p < .001$; and in the horizontal axis compared with the vertical axis, $t(16) = 3.12$, $p = .007$. No difference was reported between the bisection bias in the vertical and radial axes ( $p = .74$). To analyze the significant Axis × Length interaction, we looked at the main effect of length in each axis: Length did not influence CE in either the vertical axis, $F(4, 64) = 0.94$, $p = .45$, $\eta^2 = .06$; or the radial axis, $F(4, 64) = 0.75$, $p = .56$, $\eta^2 = .05$. Conversely, length significantly affected the CE in the horizontal axis, $F(4, 64) = .4.38$, $p = .003$, $\eta^2 = .22$; with the CE being overall larger for the longer lines (although only the difference between the longest and the shortest line survived Bonferroni correction for multiple comparisons, $p = .041$).

Independent-samples t tests revealed that blind participants' leftward bias was significantly larger than that of the sighted participants when bisecting horizontal rods, $t(33) = 2.90$, $p = .007$ (see Figure 2a). The two groups also significantly differed in bisecting vertical rods, $t(33) = 2.14$, $p = .039$; with the sighted showing a downward bias and blind participants not showing any specific directional bias (see Figure 2b). Finally, in the radial plane, the bisection error was comparable in blind and sighted participants, $t(33) = 1.61$, $p = .12$ (see Figure 2c).

**VE**

Figure 3 shows sighted and blind participants' mean VE in millimeters in the horizontal ( Figure 3a), vertical ( Figure 3b), and radial ( Figure 3c) axes for each rod's length (see also Table 2 and Table 3). To get a measure of the individuals' bisection variability, we conducted a repeated measures ANOVA in each group of participants on the VE (i.e., the mean standard deviations associated with the mean bisection biases), with spatial axis (horizontal, vertical, and radial) and length (300, 350, 400, 450, and 500 mm) as within-participants variables. In the sighted group, the analysis showed a significant effect of length, $F(4, 68) = 3.55$, $p = .011$, $\eta^2 = .17$. Axis was not significant ( $p = .15$), nor was the Axis × Length interaction ( $p = .26$). The effect of length was due to variability increasing as the length of the rod increased, although only the difference between the shortest 30-cm rod and the longest 45-cm and 50-cm rods reached significance when corrected for multiple comparisons (Bonferroni correction applied), ps = .019 and .003, respectively.

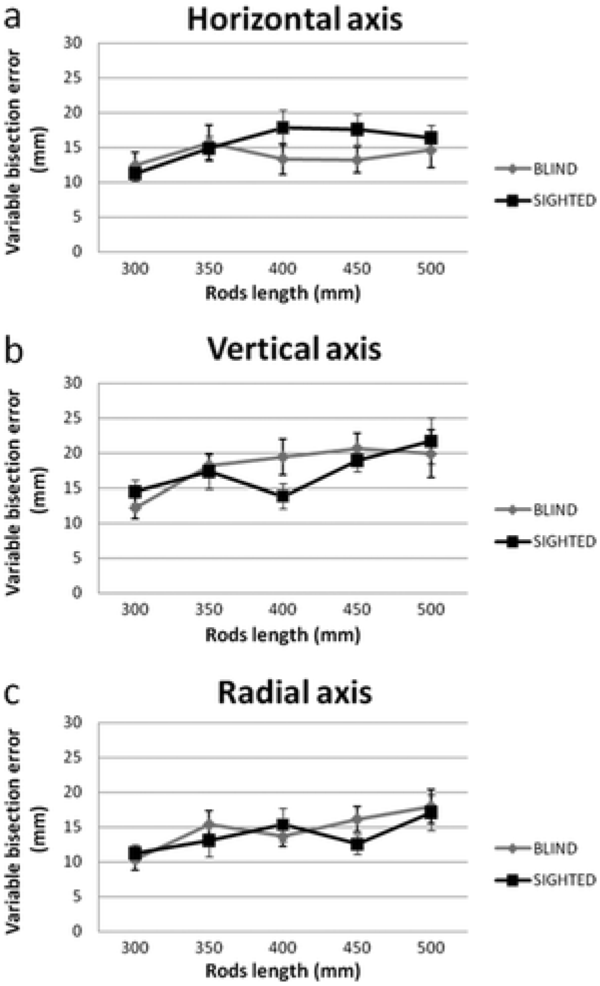


Figure 3. Mean variable bisection error (VE; in millimeters) as a function of length of rods in blind ( n = 17) and sighted ( n = 18) participants in bisecting rods in the (a) horizontal, (b) vertical, and (c) radial dimensions. Error bars indicate ±1 standard error of the mean.

In the blind group, an ANOVA revealed a significant effect of length, $F(4, 64) = 3.72$, $p = .009$, $\eta^2 = .19$; and an almost significant effect of axis, $F(2, 32) = 3.18$, $p = .055$, $\eta^2 = .17$. The Axis × Length interaction was not significant. Pairwise comparisons revealed that blind individuals' variability was higher in the vertical axis compared with the radial axis, $t(16) = 2.46$, $p = .026$; and tended to be higher in the vertical axis compared with the horizontal axis, $t(16) = 1.94$, $p = .07$ (see Figure 3). No difference was reported in variability between the horizontal and radial axes ( $p = .64$). The effect of length was due to individual variability increasing at the increase of the rod length, although when Bonferroni correction for multiple comparisons was applied, the VE was significantly different only between the 30-cm and the 35-cm rods ( $p = .048$).

Independent-samples t tests were conducted to compare sighted and blind participants' VEs in the three different axes. The analysis revealed that blind participants did not differ significantly from sighted participants in either axis; $t(33) = 0.97$, $p = .34$, for the horizontal axis (see Figure 3a), $t(33) = 0.42$, $p = .68$, for the vertical axis (see Figure 3b); and $t(33) = 0.52$, $p = .61$, for the radial axis (see Figure 3c).

Proportion of Trials in Each Initial Movement Direction

In sighted participants, R-L initial movements ( $n = 195$) were significantly more frequent than L-R initial movements ( $n = 75$) in the horizontal axis, $\chi^2 = 53.33$, $p < .001$. In the vertical and radial axes, no differences were reported between initial D-U ( $n = 132$) and U-D movements ( $n = 138$), $\chi^2 = 0.13$, $p = .72$; and between initial F-N ( $n = 148$) and N-F movements ( $n = 122$), $\chi^2 = 2.5$, $p = .11$.

In the blind group, R-L initial movements ( $n = 157$) in the horizontal axis were significantly more frequent than L-R initial movements ( $n = 98$), $\chi^2 = 13.65$, $p < .001$. In the vertical axis, D-U initial movements ( $n = 188$) were more frequent than U-D initial movements ( $n = 67$), $\chi^2 = 57.42$, $p < .001$. In the radial axis, no significant difference was reported between initial F-N movements ( $n = 128$) and N-F movements ( $n = 127$), $\chi^2 = .004$, $p = .95$.

**Bisection Error According to the Final Movement Direction**

A further analysis was conducted in each group of participants to verify whether the bisection bias was affected by the final movement direction (see Baek et al., 2002, for a similar analysis ). Figure 4 shows blind and sighted participants' mean bisection error, in millimeters, in the horizontal ( Figure 4a), vertical ( Figure 4b) and radial ( Figure 4c) axes according to the final movement direction (collapsed across rod's length). In the sighted group, we found a significant effect of the final movement direction in all the three axes: For the horizontal axis, $F(1, 269) = 5.92$, $p = .016$, $\eta^2 = .02$; for the vertical axis, $F(1, 269) = 9.16$, $p = .003$, $\eta^2 = .03$; and for the radial axis, $F(1, 269) = 18.12$, $p < .001$, $\eta^2 = .06$. As tactile bisection errors were affected by the final movement direction, we sorted the bisection results according to final movement direction and performed one-sample t tests to examine whether each result deviated significantly from the true midpoint. In the horizontal axis, sighted participants showed a significant leftward bias compared with the true midpoint both in the R-L condition, $t(156) = 7.14$, $p < .001$; and in the L-R condition, $t(112) = 2.63$, $p = .010$; but the bias was larger in the R-L direction compared with the L-R direction. In the vertical axis, sighted participants showed a significant downward bias both in the U-D direction, $t(143) = 7.74$, $p < .001$; and in the D-U condition, $t(125) = 3.45$, $p = .001$; but the bias was larger in the U-D condition than in the D-U condition. In the radial axis, sighted participants showed a significant proximal bias in the F-N condition, $t(164) = 6.78$, $p < .001$; conversely, the proximal bias in the N-F condition was not significant, $t(104) = 0.10$, $p = .92$.

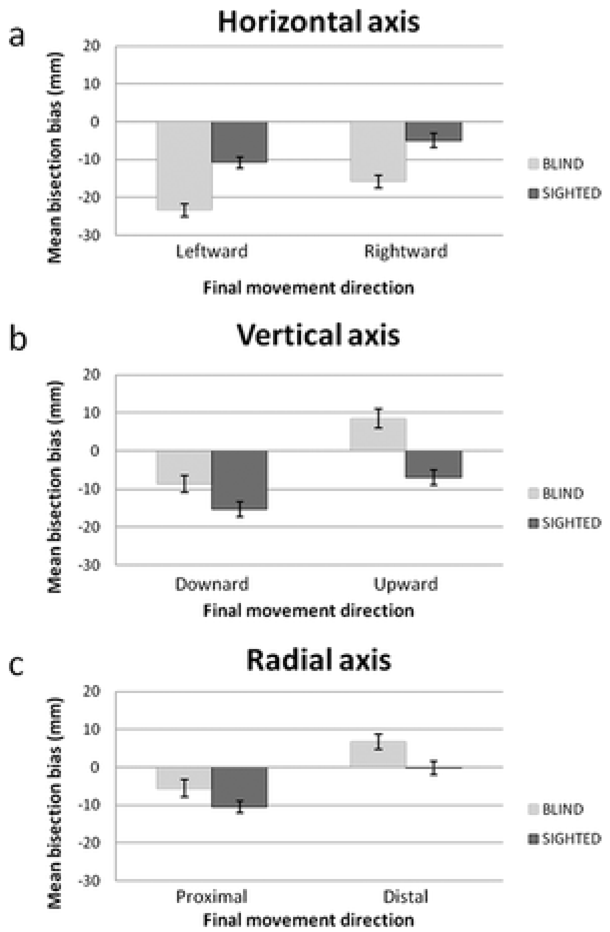


Figure 4. Mean line bisection error (constant error [CE]; in millimeters) in blind ( $n = 17$) and sighted ( $n = 18$) participants in bisecting rods in the (a) horizontal, (b) vertical, and (c) radial dimensions according to the final movement direction. A positive value in the horizontal plane indicates a rightward bias; a negative value indicates a leftward bias. A positive value in the vertical plane indicates an upward bias; a negative value indicates a downward bias. A positive value in the radial plane indicates a distal bias; a negative value indicates a proximal bias. Error bars indicate ±1 standard error of the mean.

In the blind group, we found a significant effect of the final movement direction in all the three axes: For the horizontal axis, $F(1, 254) = 9.59$, $p = .002$, $\eta^2 = .04$; for the vertical axis, $F(1, 254) = 26.00$, $p < .001$, $\eta^2 = .09$; and for the radial axis, $F(1, 254) = 16.19$, $p < .001$, $\eta^2 = .06$. In the horizontal axis, blind participants showed a significant leftward bias compared with the true midpoint both in the R-L condition, $t(110) = 13.83$, $p < .001$; and in the L-R condition, $t(143) = 9.26$, $p < .001$; but the bias was larger in the R-L direction compared with the L-R direction. In the vertical axis, blind participants showed a significant downward bias compared with the true midpoint in the U-D condition, $t(129) = 3.78$, $p < .001$; and a significant upward bias in the D-U condition, $t(124) = 3.45$, $p = .001$. In the radial axis, blind participants showed a significant proximal bias compared with the true midpoint in the F-N condition, $t(101) = 2.46$, $p = .016$; and a significant distal bias in the N-F condition, $t(152) = 3.38$, $p = .001$.

Independent-samples t tests were conducted to compare the two groups' line bisection CE in each axis according to the final search direction. In the horizontal axis, the leftward bias showed by the blind participants was larger than that shown by the sighted participants both in the R-L condition, $t(266) = 5.48$, $p < .001$; and in the L-R condition, $t(255) = 4.25$, $p < .001$ (see Figure 4a). In the vertical axis (see Figure 4b), sighted participants' downward bias in the U-D condition was significantly larger than the downward bias showed by the blind participants, $t(272) = 2.27$, $p = .024$. The two groups were also significantly different in the D-U condition, $t(249) = 4.85$, $p < .001$; this time reflecting an opposite directional bias: downward for the sighted participants and upward for the blind participants. In the radial axis (see Figure 4c), the proximal bias in the F-N condition was similar in the two groups (although it tended to be larger in the sighted group), $t(265) = 1.84$, $p = .066$; conversely, the two groups significantly differed in the N-F condition, $t(256) = 2.44$, $p = .016$; with the blind group showing a distal bias and the sighted group showing an almost null proximal bias.

**Number of Full Searches**

A further analysis was conducted to investigate whether the number of full searches varied according to the rods' length and to the spatial plane in which rods were presented. On this purpose, a repeated measures ANOVA was conducted in each group on the total number of searches, with axis (horizontal, vertical and radial) and rods' length (300, 350, 400, 450, and 500 mm) as within-participants variables. In sighted participants, the analysis revealed a significant main effect of length, $F(4, 68) = 12.93$, $p < .001$, $\eta^2 = .43$. Axis was not significant ( $p = .78$; mean number of searches in the horizontal plane = 3.99, SD = 1.70; mean number of searches in the vertical plane = 3.91, SD = 1.81; mean number of searches in the radial plane = 3.87, SD = 1.41); nor was the Axis × Length interaction ( $p = .46$). The effect of length was due to the number of searches decreasing at the increase of the rod length: in particular, pairwise comparisons (Bonferroni correction applied) showed that the number of searches performed on the 300-mm rod was significantly larger than that performed on all the other rods ( $p < .05$) and that the number of searches performed on the 350-mm rod was significantly larger than that performed on the 500-mm rod ( $p = .04$).

The same analysis conducted for the blind group revealed a significant effect of length $F(4, 64) = 4.54$, $p = .003$, $\eta^2 = .22$, with the number of searches overall decreasing at the increase of the rod length. Axis was not significant ( $p = .29$; mean number of searches in the horizontal plane = 2.14, SD = 0.69; mean number of searches in the vertical plane = 2.14, SD = 0.70; mean number of searches in the radial plane = 2.02, SD = 0.55). The Axis × Length interaction was significant, $F(8, 128) = 2.68$, $p = .009$, $\eta^2 = .14$. In fact, further analysis clarified that the decrease in the number of searches at the increase of the line length was significant in the horizontal axis, $F(4, 64) = 4.89$, $p = .002$, $\eta^2 = .23$; and radial axis, $F(4, 64) = 6.17$, $p < .001$, $\eta^2 = 0.28$; but not in the vertical axis ( $p = .74$).

We conducted independent-samples t tests to compare the number of full searches in each axis between the two groups. The analysis revealed that, overall, sighted participants performed a higher number of searches compared with the blind participants in all spatial axes: For the horizontal axis, $t(33) = 4.19$, $p < .001$; for the vertical axis, $t(33) = 3.77$, $p = .001$; and for the radial axis, $t(33) = 5.10$, $p < .001$.

**Discussion**

Our results show that, when bisecting horizontal rods, both blindfolded sighted and blind participants displayed a significant tendency to bisect to the left of the veridical midpoint (pseudoneglect). Pseudoneglect is often interpreted as reflecting a right-hemisphere dominance in the control of spatial attention (see Jewell & McCourt, 2000), which results in lines in the left hemifield appearing to seem longer than they physically are. In our study, such a bias was also found in the choice of the starting direction of the manual exploration, which was toward the left end of the rod in the majority of the trials in both blind and sighted participants. A leftward bias in the representation of spatial extents has been previously reported in blind individuals ( Bradshaw et al., 1986; Coudereau et al., 2006; Sampaio et al., 1995), although the results are not entirely consistent. For instance, Coudereau et al. (2006) found a consistent leftward bias only in spatially skilled (e.g., archery experts) blind participants, whereas nonskilled blind participants showed pseudoneglect only in certain conditions (e.g., when the right hand was used and the final exploration was from right to left). Nevertheless, the existence of pseudoneglect in blind individuals is in line with other evidence suggesting that the right-hemisphere dominance for spatial processing develops even in the absence of vision ( Gougoux et al., 2005; Voss et al., 2004; Weeks et al., 2000). It is important to note, however, that factors other than hemispheric asymmetry in attentional control may contribute to the leftward bias shown by both sighted and blind participants. For example, it has been suggested that the leftward bias in visuospatial tasks may be related to the L-R reading direction used in Western languages, including Braille (e.g., Chokron, Bernard, & Imbert, 1997; Chokron & Imbert, 1993). Our findings are consistent with this explanation, as all our blind participants were Braille readers.

It is interesting that the leftward bias was significantly larger in the blind participants than in the blindfolded sighted participants, regardless of the direction of the final movement (discussed later). This difference cannot be due to response variability, as this was comparable in the two groups. One possibility is that the intense spatial training experienced by our blind participants, all of whom had been trained to orient themselves independently in large-scale environments, may have resulted in a larger hemispheric imbalance in the control of spatial attention (see Jewell & McCourt, 2000) than found in sighted controls. This would be in line with the evidence of an overall stronger leftward bias in blind individuals who were highly trained in spatial skills such as archery ( Coudereau et al., 2006). However, this explanation is at this point speculative.

Consistent with previous studies ( Baek et al., 2002; Coudereau et al., 2006), the magnitude of the leftward bias found in our study was affected by the final scanning direction. In the study by Baek et al. (2002), a significant leftward bias in horizontal rod bisection was evident when the final scanning direction was R-L, whereas a nonsignificant rightward bias (reflecting the so-called “overshoot” phenomenon) was found when the final scanning direction was the opposite (cf. Manning et al., 1990; see also Coudereau et al., 2006). In our study, the bias was significantly to the left of the physical midline in both L-R and R-L searches in both groups of participants, but the leftward bias was significantly larger when the final scan was R-L. This shows that, in both the blind and the sighted participants, the tendency to err to the left was diminished (although not reversed) when the movement was in the opposite direction. The mechanisms mediating the overshoot phenomenon (cf. Baek et al., 2002) are not completely clear. The tendency to bisect in the direction of the final movement may reflect an “inertial” motor phenomenon ( Baek et al., 2002), or an expansion of either the spatial representation of the line or of the motor–kinaesthetic computation based on this representation, so that when individuals attempt to move half of the length of this representation, the movement overestimates the actual midline ( Baek et al., 2002). It is interesting that Manning et al. (1990) suggested that the influence of the final movement direction may be explained in terms of the middle of the line representing an “indifference zone,” which segments the original stimulus into two subjectively equal lines. If the individual's predominant strategy is to continue the movement through the indifference zone and terminate at a point where subjective equality turns to inequality, the same systematic bias would be observed. Such overshoot would be proportional to stimulus length by virtue of the constraints imposed by Weber's law ( Manning et al., 1990). According to Weber's law, a stimulus has to be increased by a constant fraction of its value to be noticeably different: It thus follows that the standard deviations of the transsection displacements should be (linearly) related to the stimulus length ( Manning et al., 1990). In line with this prediction, we found that both blind and sighted participants' variability in bisecting the rods linearly increased at the increase of the rod length, consistent with previous evidence (e.g., Manning et al., 1990).

In the radial plane, blindfolded sighted participants showed a significant proximal bias, in line with previous evidence (see Baek et al., 2002, Experiment 2; Chewning et al., 1998; Shelton et al., 1990). In contrast, this bias was not present in blind participants. However, the lack of a consistent directional bias in the blind was due to the strong influence of the final movement on their responses. In fact, blind participants showed a significant proximal bias when the final movement direction was toward the body and a significant distal bias when the final movement direction was away from the body (overshoot phenomenon). It is interesting that neither the blind participants nor the sighted participants consistently started exploration in a preferred direction, suggesting that the preferential direction of exploration in the horizontal axis may be related to reading habits (e.g., Chokron et al., 1997; Chokron & Imbert, 1993). Responses' variability was also comparable in blind and sighted participants.

It has been suggested that the proximal bias in radial haptic bisection mainly depends on the use of a body-centered reference frame (e.g., Chewning et al., 1998; Shelton et al., 1990). Although blind participants tend to rely more on body-centered (egocentric) and less on allocentric codes in spatial tasks (for a review, see Thinus-Blanc & Gaunet, 1997), other evidence suggests that blind individuals may also encode space in hand-centered coordinates (see Bradshaw et al., 1986; Röder et al., 2004). Indeed, egocentric representations may be body centered, eye centered, or hand centered ( Kappers, 2007). One may thus speculate that, in blind individuals, the representation of the arm direction prevailed over that of the body, thus cancelling out the proximal bias. In other words, blind participants may have been more susceptible to a motor bias causing the hand to overshoot the target (see Manning et al., 1990). In this regard, it is interesting to note that, in proprioceptive pointing tasks, in which participants have to point with their hand toward targets presented in the sagittal plane, movement direction and amplitude are overvalued in early blind participants (overshoot) and undervalued in blindfolded sighted participants (undershoot; Gaunet & Rossetti, 2006).

When bisecting in the vertical plane, sighted participants showed a consistent downward bias, supporting previous evidence ( Baek et al., 2002). Conversely, the blind participants did not show any consistent unidirectional bias, even though they tended to start the exploration by moving downward, whereas no significant preferential direction of exploration was reported in the sighted participants. However, as in the radial plane, the final movement direction significantly affected participants' responses. In the sighted group, the downward bias was greater for U-D final searches than for D-U final searches (see Baek et al., 2002). In the blind group, a significant downward bias was reported for U-D search movements. This bias was significantly smaller than that reported by the sighted participants in the same condition, possibly depending on a haptic object-centered bias toward the bottom of the object also modulating performance in sighted individuals (as suggested by Chewning et al., 1998). Conversely, a significant upward bias in blind participants was reported after D-U search movement (overshoot phenomenon). As in the case of radial lines, a possible greater influence of kinesthetic motor factors (arm centered) in blind participants, compared with sighted participants, may be responsible for the lack of an overall significant unidirectional bias in the former. However, in case of vertical lines' bisection, response variability may be a critical factor. Although response variability was comparable between blind and sighted participants in the vertical condition, an intragroup effect was found in blind participants because of their responses in the vertical plane being more variable (reflecting higher uncertainty) than in the other two planes. Also, blind participants' total number of searches in this condition was not influenced by the length of the rods as was the case in the other conditions. This may reflect higher uncertainty in this condition. In light of this, the lack of a consistent unidirectional bias in the vertical domain could also (at least partially) reflect higher uncertainty in the representation of the vertical dimension, a finding in line with previous evidence ( Cornoldi & Vecchi, 2003).

Overall, the variability of participants' responses tended to increase with the rod length, consistent with previous findings ( Chieffi et al., 2008; Manning et al., 1990). This may also reflect, at least in the vertical and radial planes, the fact that hand positions closer to the shoulder are localized more precisely than positions further away (see van Beers et al., 1998). The effect of length on the bisection bias was less consistent; previous literature is also unclear about this effect, which may depend on the specific measure adopted (i.e., absolute bias in millimeters versus percentage bias; see Baek et al., 2002; Manning et al., 1990). Overall response variability was similar for blind and sighted participants in the three axes, suggesting that performance in the two groups was consistent. A similar level of variability in blind and sighted participants has also been reported in other studies investigating proprioceptive spatial encoding in blind individuals; for instance, in a pointing task ( Gaunet & Rossetti, 2006). However, early blind participants were found to perform more variably than sighted participants in a parallel setting task, suggesting that early visual experience may provide structure to the representations derived from haptic inputs ( Postma et al., 2008a). Although all are based on proprioceptive information, haptic line bisection tasks, parallel setting tasks, and pointing tasks also involve different spatial–attentional and motor mechanisms; this may explain why response variability is not consistent across different tasks.

Finally, blind participants performed a smaller number of full explorations in all spatial axes compared with the sighted participants. This may reflect slower exploration rather than faster responses, because participants were instructed to continue the exploration until the end of the available scanning time was signaled. In the haptic modality, a mental representation of the rod's extent has to be reconstructed from sensations perceived in series: The slower exploration of blind participants may reflect their higher difficulty in generating the corresponding mental representation. This would be consistent with previous evidence on spatial mental imagery limitations in blind individuals (see Thinus-Blanc & Gaunet, 1997, for a review).

In conclusion, our results on sighted individuals are mostly consistent with previous findings obtained with a similar task ( Baek et al., 2002), by revealing significant biases in the horizontal, vertical, and radial planes. Our research extends these results by showing that blind individuals also tend to overrepresent the left portion of space (i.e., they exhibit pseudoneglect), whereas they do not exhibit any significant spatial bias in the vertical and radial dimensions. The lack of consistent directional biases in the vertical and radial planes in blind individuals is likely to reflect the higher tendency of these individuals to rely on hand-centered codes when exploring the rods and thus be more susceptible to motor inertial phenomena (overshoot phenomena). Accordingly, previous evidence suggests that, when encoding peripersonal space, blind and sighted individuals adopt different reference frames, with sighted individuals' spatial representations being highly affected by their dominant visual experience (see Millar, 1994).

Footnotes

1 Note that Baek et al. (2002) performed a similar analysis, although considering the initial or final search direction (the direction of the first of latest complete scan) rather then the direction of the initial or final (half search) movement. Hence, what we consider as a final L-R movement, for instance, corresponds to what Baek et al. (2002) considered a final R-L search: indeed, in both our study and Baek et al.'s study, a final L-R half-search movement was always preceded by a R-L complete search.

2 The first half-search movement and the final half-search movement were not included in this analysis, which only considered the number of the rod full searches as in Baek et al. (2002).

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