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The effect of hand movements on numerical bisection judgments in early blind and sighted individuals

Luca Rinaldi¹, Tomaso Vecchi^{2,3}, Micaela Fantino³, Lotfi B. Merabet⁴, and Zaira Cattaneo^{1,2,*}

¹Department of Psychology, University of Milano-Bicocca, Milano, Italy

²Brain Connectivity Center, C. Mondino National Neurological Institute, Pavia, Italy

³Department of Brain and Behavioral Sciences, University of Pavia, Pavia, Italy

⁴The Laboratory for Visual Neuroplasticity. Department of Ophthalmology, Massachusetts Eye and Ear Infirmary, Harvard Medical School. Boston, USA

Abstract

Recent evidence suggests that in representing numbers blind individuals might be affected differently by proprioceptive cues (e.g., hand positions, head turns) than are sighted individuals. In this study, we asked a group of early blind and sighted individuals to perform a numerical bisection task while executing hand movements in left or right peripersonal space and with either hand. We found that in bisecting ascending numerical intervals, the hemi-space in which the hand was moved (but not the moved hand itself) influenced the bisection bias similarly in both early blind and sighted participants. However, when numerical intervals were presented in descending order, the moved hand (and not the hemi-space in which it was moved) affected the bisection bias in all participants. Overall, our data show that the operation to be performed on the mental number line affects the activated spatial reference frame, regardless of participants' previous visual experience. In particular, both sighted and early blind individuals' representation of numerical magnitude is mainly rooted in world-centered coordinates when numerical information is given in canonical orientation (i.e. from small to large), whereas hand-centered coordinates become more relevant when the scanning of the mental number line proceeds in non-canonical direction.

Keywords

Number bisection; Blindness; Pseudoneglect; Number line; Hand movements; Lateralization

Introduction

Consistent work has shown the existence of a tight and bidirectional coupling between the spatial representation of numbers (the so-called mental number line, Dehaene, 1992; for a review, de Hevia, Vallar & Girelli, 2008) and the representation of physical space. For instance, individuals tend to respond faster to smaller numerosities with the left hand and to

*Corresponding author: zaira.cattaneo@unimib.it.

larger numerosities with the right hand (at least in Western societies who read in the left-to-right direction), a phenomenon known as SNARC (Spatial Numerical Association of Response Codes) effect (Dehaene, Bossini & Giraux, 1993). Furthermore, processing numerical magnitude can orient attention to different portions of external space (small numbers biasing attention to the left, while large numbers bias to the right) (e.g., Cattaneo, Fantino, Tinti, Silvanto & Vecchi, 2010; Di Luca, Pesenti, Vallar & Girelli, 2013; Fischer, 2001; Goffaux, Martin, Dormal, Goebel & Schiltz, 2012; Schuller, Hoffmann, Goffaux & Schiltz, 2014). Accordingly, Loetscher, Bockisch, Nicholls and Brugger (2010) measured participants' eye position during a random number generation task and found that a leftward and downward change in eye position predicted that the next number would be smaller than the last. Conversely, a rightward and upward change in eye position predicted that the next number would be larger than the last. At the same time, moving the hand in the left space (Cattaneo, Fantino, Silvanto, Vallar & Vecchi, 2011) or turning the head leftwards (Loetscher, Schwarz, Schubiger & Brugger, 2008) biases attention to small numbers, with the reverse tendency for hand movements or head towards the right. Although it is important to stress that the mental number line can be evoked based on a purely attentional basis without any obvious motor component (Nicholls, Loftus, & Gevers, 2008), the analogies consistently reported between movements along the mental number line and physical space suggest that our mental representations may be grounded, at least to a certain extent, in sensorimotor experience (Fischer, 2012).

When sensory experience is altered such as in case of blindness, there is the potential that resulting mental representations are affected. In particular, converging evidence suggests that blind individuals' spatial representations rely more on body/hand centered coordinates compared to the sighted (Noordzij, Zuidhoek & Postma, 2006; Röder, Kusmierek, Spence & Schicke, 2007; for a review, see Cattaneo et al., 2008). The lack of prior visual experience has led to mixed reports in terms of its effect on the representation of external space and (at least to a certain extent) on the mental representation of numerical magnitude (Crollen, Dormal, Seron, Lepore & Collignon, 2013; Pasqualotto, Taya & Proulx, 2014). For example, prior evidence has found that blind individuals also tend to represent numbers in the form of a mental number line (Castronovo & Seron, 2007; Cattaneo et al., 2010; Szűcs & Csépe, 2005) showing attentional biases similar to those of sighted individuals when exploring it (Cattaneo, Fantino, Silvanto, Tinti & Vecchi, 2011). However, blind individuals may use different reference frames in representing numbers compared to sighted individuals, at least in certain experimental conditions. For instance, Crollen et al. (2013) recently reported that crossing the hands reversed the typical SNARC effect in early blind but not in sighted individuals while performing a numerical comparison task, suggesting that in comparing magnitudes blind participants mainly adopted a hand-based reference frame (see also Röder, Rösler & Spence, 2004, for similar findings in tactile temporal order judgments). However, in the same study, early blind participants' performance was unaffected by crossing the hands in a parity judgment task (i.e., judging whether a given numeral is odd or even) (Crollen et al., 2013). Other recent findings have questioned the canonical left-to-right orientation of the mental number line in blind individuals in light of their performance in a random number generation task. Specifically, while sighted individuals typically generate smaller numbers when turning the head left, and more large numbers when turning the head

right, early blind participants appear to show the opposite behavior (Pasqualotto et al., 2014).

Overall, prior evidence suggests that mental representation of numbers may be affected differently by proprioceptive cues (e.g., hand position, head turn) in blind than in sighted individuals, at least under specific task conditions (Crollen et al., 2013; Pasqualotto et al., 2014). In particular, the results by Crollen et al. (2013) suggest that blind individuals may anchor their mental representations more to the hands, and less to world-centered reference frame. The aim of this study was to shed further light on this issue. In a prior study by our group carried out in sighted participants, we found that hand movements performed in the left peripersonal space (irrespective of the hand used) accentuated underestimation (i.e., a leftward bias) in numerical bisection, whereas movements in the right peripersonal space (irrespective of hand used) had the opposite tendency (Cattaneo, Fantino, Silvanto, Vallar, & Vecchi, 2011). These results suggest that the correspondence between physical space and the mental number space in sighted individuals is anchored to a world-based reference frame centered on the participants' body (i.e., left in physical space and left on the mental number line). Such representation is not sensitive to which hand is actually moved, but rather to the hand's position in peripersonal space. However, following the results reported by Crollen et al. (2013), we hypothesized that in the case of early blindness, the effect of hand movement would be more evident given the reliance on egocentric frames of reference.

In order to investigate this issue, we asked a group of early blind and sighted individuals to perform a numerical bisection task while executing hand movements in left or right peripersonal space with either hand. If indeed early blind individuals rely more on hand-centered coordinates when representing numerical intervals, then the hand used (more than the space in which the hand is moved) should lead to biases in estimation along the mental number line.

Methods

Participants

Sixteen early-blind participants (8 males; mean age=42.3 ys, $SD=10.2$, range: 27–62 ys; mean education: 14.7 ys, $SD=2.5$) and sixteen sighted participants (8 males; mean age=42 ys, $SD=9.3$, range: 27–56 ys; mean education: 14.4 ys, $SD=2.3$) took part in the experiment. All participants were right-handed (Oldfield, 1971), did not have any neurological disorder apart from optic nerve damage (in case of some blind participants) and had normal motor function. Profound blindness occurred prior to the age of 24 months. Furthermore, all blind participants denied having any recollection of visual memories. All blind participants were proficient Braille readers (see Table 1 for further details on blind participants).

Procedure

Sighted participants were blindfolded throughout the entire experiment. The experimental task consisted of a numerical bisection paradigm that has been used in a number of prior studies to investigate spatial attentional biases in numerical representation (e.g., Cattaneo, Fantino, Silvanto, Tinti, & Vecchi, 2011; Göbel, Calabria, Farnè & Rossetti, 2006; Loftus,

Nicholls, Mattingley, Chapman & Bradshaw, 2009). Participants were verbally presented with a total of 80 different pairs of three-digit numbers; half in ascending (e.g., “117 166”) and half in descending order (e.g., “959 934”). The descending pairs were the reverse of the ascending pairs, so that ascending and descending pairs only differed in their order of presentation. Each pair of numbers was always in the same hundred value range and the numerical distance between each number pair was predetermined at 16, 25, 36, or 49 (Cattaneo, Fantino, Silvanto, Tinti, & Vecchi, 2011; Göebel et al., 2006). Note that the interval 64 (included in previous work) has been shown to generate opposite directional biases in previous studies and thus was not used in this study (Cattaneo, Fantino, Silvanto, Tinti, & Vecchi, 2011; Göebel et al., 2006). Numbers formed by pairs of a multiple of 10 were not used to avoid the possibility of easy computation. The different number pairs were recorded as a single sound file (3.5 seconds in duration) and presented in random order using E-prime2 (Psychology Software Tools, Pittsburgh, PA). Ascending and descending pairs were intermixed in the same block, in line with prior studies (Cattaneo, Fantino, Silvanto, Tinti & Vecchi, 2011; Loetscher, Bockisch, & Brugger, 2008; Longo & Lourenco, 2007, Experiment 2). Participants were instructed to quickly estimate and verbally report the number laying in the middle of the given number pair (for instance for the interval “352 368”, the correct answer is “360”) without making any arithmetic calculation. Responses had to be given within 3 seconds of the stimulus presentation (signalled by a “beep” sound) in order to limit the possibility that participants would answer based on an arithmetic calculation rather than an estimate. Responses given after 3 seconds were excluded from further statistical analyses. The experimenter typed the number provided by the participant on the computer keyboard, so that it was recorded by the software. Participants responses were also audio-recorded so that the values inserted by the experimenter were additionally verified offline.

The numerical bisection task was performed in blocks under 5 different conditions presented in a counterbalanced order across participants (see Cattaneo, Fantino, Silvanto, Vallar, & Vecchi, 2011, for similar procedure). In each condition, 16 different number pairs were presented with half in ascending, and half in descending order. We generated five different sets of number pairs, each containing two ascending pairs and two descending pairs for each considered interval (16, 25, 36 and 49). In no case was a descending pair presented with its corresponding ascending pair in the same set. Overall, the same number pairs were presented to each participant, but the order of the sets for condition was randomised across participants so as to avoid any carry over effect. In the baseline condition, participants completed the number bisection task without performing any concurrent task (i.e., a non-movement condition). In the other 4 conditions, participants performed a motor task in conjunction to the number bisection task. For the motor task, participants were required to use one hand and tap three radially oriented wooden blocks (5 cm² in area and 0.5 cm in height, separated approximately 1 cm apart). The motor sequence was performed in the radial rather than horizontal plane to avoid left/right movements that could possibly interfere with spatial processing mechanisms along the horizontally oriented mental number line. The center of the middle block was placed at a diagonal distance of approximately 50 cm with respect to the participant’s midsternum (see Figure 1). There were 4 movement conditions: 1) in the left hemispace with the left hand; 2) in the right hemispace with the right hand; 3)

in the right hemispace with the left hand; and 4) in the left hemispace with the right hand. Participants had to tap on the wooden blocks at a constant rate of approximately one tap per second from top to bottom and then from bottom to top, without interruption until the trial was completed. In the motion conditions, a trial started with participant performing the hand motion task alone for 2 seconds and then the numerical interval was presented and the participant was instructed to continue performing the motor sequence until they provided a verbal response to the numerical task. During the motor conditions, the other hand was resting comfortably on the table in front with the elbow bent at an angle of 90 deg towards the body midline and the forearm in a horizontal position. At the beginning of the experiment, two practice trials (one ascending and one descending interval) were performed for each condition in order to familiarise the participant with the task.

Deviations from the veridical midpoint (bias) were computed by subtracting half of the true size of the numerical interval from the interval between the first given number of the pair and the participant's estimated midpoint (see Cattaneo, Fantino, Silvanto, Tinti, & Vecchi, 2011; Göbel et al., 2006). This scoring method yielded a positive score if the participant's response was to the right of the objective mid-point and a negative score if the response was to the left of it.

Results

Fifty-three trials (corresponding to 2.1% of the total recorded) were excluded due to responses be given after the 3 seconds period. A first analysis was performed on the non-motion block to characterize each participant's baseline performance (see Figure 2). One sample *t*-tests against zero (i.e. absence of bias) revealed an overall significant underestimation of the numerical midpoint (i.e., a significant leftward bias on the putative mental number line) in both early blind, $t(15)=2.4$, $p=.03$, and sighted participants, $t(15)=6.4$, $p<.001$. A repeated measures ANOVA with numerical order (ascending vs. descending) as the within-subjects factor and group (blind vs. sighted) as the between-subjects factor revealed a significant effect of order, $F(1,30)=8.5$, $p=.007$, $\eta^2_p=.22$, with the leftward bias being larger for descending compared to ascending intervals. The main effect of group was also significant, $F(1,30)=8.1$, $p=.008$, $\eta^2_p=.21$ with sighted participants showing overall a stronger leftward bias than early blind participants. The interaction numerical order by group was not significant, $F(1,30)<1$, $p=.37$, $\eta^2_p=.03$.

A subsequent analysis was carried out to characterize the effect of moving the hand and hemispace in which the hand was moved on numerical bisection estimations. For this analysis, deviations in the motion conditions were normalised to the bias observed in the baseline condition (see also Cattaneo, Fantino, Silvanto, Vallar, & Vecchi, 2011, for a similar procedure). This was done by subtracting the bias measured from the baseline condition from the bias in each of the four movement conditions (see Figure 3). A repeated-measures ANOVA with numerical order (ascending vs. descending), hemispace (left vs. right), and moving hand (left vs. right) as within-subjects factors and with group (blind vs. sighted) as a between-subjects factor revealed a significant main effect of hemispace, $F(1,30)=10.5$, $p=.003$, $\eta^2_p=.26$, and a significant main effect of moving hand, $F(1,30)=7.9$, $p=.009$, $\eta^2_p=.21$. Neither the main effect of order ($p=.60$) nor the main effect of group ($p=.25$), reached

significance. Both the effects of hemispace and of moving hand were modulated by numerical order as indicated by the two significant interactions of hemispace by order, $F(1,30)=12.1$, $p=.002$, $\eta^2_p=.29$, and of hand by order, $F(1,30)=8.9$, $p=.005$, $\eta^2_p=.23$. All other interactions were not significant (all $ps>.05$).

The significant interaction of *hemispace by order* was further investigated by means of post-hoc t -tests (Bonferroni correction applied). The t -tests revealed that in bisecting ascending intervals, the hemispace in which the hand moved significantly affected the bisection bias, $t(31)=5.8$, $p=.001$: movements in the left hemispace increased the tendency of a leftward bias and movements in right hemispace increased the tendency of a rightward bias, irrespective of the hand used. In turn, with descending intervals, the hemispace in which movements were performed did not affect the bisection bias, $t(31)<1$, $p=.99$.

Post-hoc t -tests (Bonferroni correction applied) were carried out to further investigate the significant interaction of *hand by order* and revealed that in bisecting ascending intervals, the moved hand did not affect the bisection bias, $t(31)<1$, $p=.21$. In turn, the moved hand (irrespective of whether in left or right hemispace) significantly affected the bisection bias with descending intervals, $t(31)=4.1$, $p=.005$. Moving the left hand increased the participant's tendency towards a leftward bias whereas moving the right hand increased the tendency of a rightward bias.

Discussion

In this study, we observed that both early blind and sighted individuals showed an overall tendency to underestimate the true midpoint of a numerical interval (i.e., a leftward bias on the putative mental number line). In line with previous reports (Cattaneo, Fantino, Silvanto, Tinti, & Vecchi, 2011; Göbel et al. 2006; Loftus et al., 2009; Longo & Lourenco, 2007), this effect was particularly evident when numbers were presented in descending order. Moving one hand in space during bisection significantly affected participants' responses, and to a similar extent in both early blind and sighted individuals. When numbers were presented in ascending order (i.e., small number first, large number second) both early blind and sighted participants' estimates were affected by hand position (in left or right peripersonal space) irrespective of the hand used. Specifically, movements in the left peripersonal hemispace exaggerated the pre-existing underestimation, while those in right hemispace resulted in an opposite effect, replicating prior evidence in sighted individuals (Cattaneo, Fantino, Silvanto, Vallar, & Vecchi, 2011; in which only ascending intervals were used). In turn, when numbers were presented in descending order, the moving hand (and not its position), resulted in significant shifts in judgment biases, again to a similar extent in both early blind and sighted participants. More specifically, moving the left hand accentuated the underestimation of the numerical midpoint, whereas moving the right hand showed the opposite tendency.

Based on previous reports, we hypothesized that blind individuals would mainly depend on a hand-centered reference frame while sighted individuals would rely more on a world- or body-centered reference frame (across experimental settings, as suggested by Crollen et al., 2013). Our predictions were only partially confirmed by the results in this study. In fact, we

found that the order in which numbers were presented (i.e., ascending vs. descending) led to the adoption of a world-centered (for ascending intervals) vs. hand-centered (for descending intervals) reference frame in a similar fashion in both sighted and blind participants. For Western societies, individuals typically count objects in an external space following a left-to-right ascending order; that is, in the same direction as a reading task (Shaki, Fischer & Göbel, 2012). Accordingly, the mental number line is usually conceived as flowing from left (small numbers) to right (large numbers) and its mental exploration also goes from left to right (Dehaene, 1992; Dehaene et al., 1993; Zebian, 2005). When intervals were presented in ascending order (i.e., the canonical order with respect to typical reading direction and also the direction for which Braille text is read), a world-centered reference frame was likely activated, irrespective of the participant's visual status. This finding is also consistent with recent evidence suggesting that the "mental time line" is represented in external spatial coordinates in both the sighted and the blind (Bottini, Crepaldi, Casasanto, Crollen, & Collignon, 2015).

Prior studies have shown that the perceived space around the hand is prioritized in terms of the deployment of attention mechanisms. For instance, Reed et al. (2006) found that visual target detection near the hand was facilitated relative to detection away from the hand. Moreover, symptoms related to neglect syndrome (due to right-parietal lesions) have been shown to be reduced by left-hand movements in left space, but not by left hand-movements in right space (Gainotti, Perri & Cappa, 2002; Làdavas, Berti, Ruoizzi & Barboni, 1997; Robertson & North, 1992, 1993). This dichotomy illustrates the predominance of attentional orienting towards the hemispace where the hand is moved (in terms of body-centered coordinates) as opposed to the hand's anatomical location (i.e. on the left or right). Importantly, these effects do not seem to depend on visual feedback, but rather rely mainly on proprioceptive cues (Làdavas et al., 1997). In this view, we hypothesized that a judgment bias towards the hemispace in which the hand was moved would lead to a corresponding bias in the simultaneously activated spatial representation (i.e., the mental number line) (see Cattaneo, Fantino, Silvanto, Vallar, & Vecchi, 2011).

Interestingly, and contrary to our initial prediction, for both blind and sighted individuals it was the moving hand more than its position in space that affected performance in the case of descending intervals. The reason for this observation may not be intuitively obvious and thus deserves further consideration. In the baseline condition (where no concurrent hand movements were performed) the underestimation (i.e., leftward bias) was more pronounced for descending than ascending intervals, in line with prior studies using either auditory presentation (Cattaneo, Fantino, Silvanto, Tinti, & Vecchi, 2011) or visual presentation (Loftus et al., 2009; Longo & Lourenco 2007) of numbers. Longo and Lourenco (2007) suggested (on the basis of participants' debriefing) that the larger leftward bias observed with descending intervals possibly depended on participants reversing the smaller number (appearing visually to the right) to the left side of the larger number before bisection. This leftward mental movement would drive attention farther leftwards. As an alternative possibility, we suggest that when numbers were presented in descending order, participants engaged in a sort of "subtractive analysis". In this view, descending intervals would not be explored in the more typical canonical left-to-right direction, but rather, in the opposite direction (see Knops, Thirion, Hubbard, Michel & Dehaene, 2009; Pinhas & Fischer, 2008).

Along these lines, in tactile line bisection tasks, right-to-left scanning movements have been found to induce a more pronounced leftward bisection bias than left-to-right movements (Cattaneo, Fantino, Tinti et al., 2011; for a review, see Jewell & McCourt, 2000). In this more uncertain, non-canonical way to explore the mental number line, anatomical feedback from the hands may become more prominent, given that the hands typically represent the earliest embodied basis for apprehending magnitudes (see Crollen & Noël, 2015; Di Luca & Pesenti, 2011). Although early blind individuals may not rely on hand-based counting to the same extent as sighted individuals do (Crollen et al., 2014), the lack of visual input usually implies a higher reliance upon hand-reference coordinates (Crollen et al., 2013; Röder et al., 2004, 2007). Note that in the study of Crollen et al. (2014) more than one third of the early blind individuals tested did use finger counting strategy.

In the previous study by Crollen et al. (2013), the SNARC effect was reversed in blind but not in sighted participants when crossing the hands in a numerical comparison task. This suggests that blind subjects were relying on a hand-centered reference frame whereas sighted participants were relying on world-centered coordinates. No effect of the crossing-hand manipulation was observed on the SNARC effect in a control parity judgment task (Crollen et al., 2013). Our data converge with those by Crollen et al. (2013) by further suggesting that the adopted spatial reference frame may vary depending on the specific task demands at play. However, our findings suggest that this is the case for sighted individuals as well. Discrepancies between the two studies may derive not only by the different numerical tasks used (bisection vs. magnitude comparisons or parity judgment), but also by the fact that in the Crollen et al. (2013) study, participants were required to respond with their hands (the hands moving to make a response-key pressing, as typically carried out in SNARC paradigms). Responding with the hands compared to making task-related hand movements (unrelated to the response) may have influenced the adoption of hand-centered coordinates versus other spatial reference frames.

In this respect, it is also worth mentioning that blind individuals do not rely on an anatomically-anchored reference frame for all spatial mental tasks. For instance, blind individuals are able to successfully perform mental rotation tasks (although usually taking more time than sighted controls; e.g., Marmor & Zaback, 1976), and there is no evidence that these spatial representations in the blind during this task are more tied to the hands than to other external reference frames. In turn, other spatial mental tasks are more sensitive to different reference systems depending on how blind and sighted individuals interact with the physical world (Röder et al., 2004, 2007). For instance, mental navigation and memory for object position usually reflect a preference for egocentric coordinates in the blind, compared to allocentric coordinates in the sighted (e.g., Noordzij et al., 2006; Pasqualotto, Spiller, Jansari, & Proulx, 2013). Given the consistent evidence suggesting that blind and sighted individuals tend to rely on different reference frames in representing the external world, the question as to whether performance on a mental imagery task is directly affected by one's preferred spatial reference frame depends on the specific task being carried out (see also Crollen et al., 2013). Shifts of attention induced by hand movements are more likely to affect a concurrent spatial mental task if the latter requires one to operate on the same critical spatial dimension (in case of numbers bisection, left/right movements) that is tapped into by physical manipulation.

In the baseline condition (e.g., no concurrent hand movements), sighted individuals showed a larger leftward bias compared to blind individuals and this difference was not observed in our previous study (Cattaneo, Fantino, Silvanto, Tinti, & Vecchi, 2011). However, in our previous study, a larger numerical interval was also used (i.e. the distance between the numbers was as high as 64), which induced different direction biases in both blind and sighted participants (see also Göbel et al., 2006, for anomalous bisection bias with the interval of 64). Moreover, high inter-individual variability in attentional biases as measured in bisection tasks has been previously reported (e.g., Cowie & Hamill, 1998; Szczepanski & Kastner, 2013), which could also possibly account for differences among studies.

In a recent study, Pasqualotto et al. (2014) found that congenitally (but not late) blind participants were likely to produce more smaller rather than larger numbers when turning the head to the right. The reverse pattern was apparent when turning the head to the left, suggesting that the mental number line may be right-to-left oriented in congenitally blind individuals. In turn, our data suggest that early blind individuals are likely to represent numbers in a standard left-to-right orientation (resembling their natural reading habits), in line with prior evidence reporting a typical SNARC effect in this same group (Castronovo & Seron, 2007; Crollen et al., 2013; Szűcs & Csépe, 2005). Accordingly, the “mental time line” is likely to be left (i.e. past)-to-right (i.e. future) oriented in the early blind as in the case of sighted individuals (Bottini et al., 2015). Although differences in task design may partially account for inconsistent results across these studies, future research is needed to clarify whether the mental number line is differently oriented in blind as compared to sighted individuals.

In considering the orientation of the mental number line, it is important to stress that consistent evidence suggests that spatial-numerical associations are modulated by reading habits (e.g., Hung, Hung, Tzeng, Wu, 2008; Kazandjian, Cavézian, Zivotofsky, Chokron, 2010; Rashidi-Ranjbar, Goudarzvand, Jahangiri, Brugger, & Loetscher, 2014; Shaki, Fischer, & Petrusic, 2009; for a review, see Göbel, Shaki, & Fischer, 2011). In particular, data collected from cultures in which the reading direction of words and numbers differ suggest that opposite reading habits (i.e. reading from right to left) may weaken, or even cancel out, any preferred lateral association of numbers along the horizontal mental number line (e.g., Rashidi-Ranjbar et al., 2014; Shaki et al., 2009). A cross-cultural study in blind Braille readers would be interesting in this respect. As Braille is universally read from left-to-right, it would be expected that blind individuals should thus rely on a left to right oriented mental number line irrespective of the normal text reading direction of their native language. Further studies are needed to confirm this hypothesis.

The bisection bias observed in the baseline (i.e. no movement) condition with ascending and descending intervals might also provide new evidence for the concept of operational momentum (OM); that is, the systematic tendency to overestimate the resulting sum of an addition operation and to underestimate the resulting difference of a subtraction (Masson & Pesenti, 2014; McCrink, Dehaene, & Dehaene-Lambertz, 2007; Pinhas & Fischer, 2008; for a review, see Hubbard, 2014). The OM is believed to result from movement on the mental number line required by the operation; a left to right movement in case of addition, and a right to left movement in case of subtraction (see McCrink et al., 2007; Hubbard, 2014). In

the number bisection task used here, ascending intervals may induce a rightward movement (as in the case of addition) on the mental number line starting from the smaller number processed first to the larger number processed second. Similarly, descending pairs may induce a movement from the larger number (processed first) toward the smaller number, resulting in a leftward movement (as in the case of subtraction). Interestingly, the OM is larger in subtraction than in addition estimations (e.g., McCrinck et al., 2007; Pinhas & Fischer, 2008), possibly reflecting an OM and typical attentional (leftward) bias pushing in the same direction in the case of subtraction, and in opposite direction in the case of addition (see Hubbard, 2014). The larger leftward bias we observed in the case of descending compared to ascending intervals is consistent with this interpretation.

In interpreting our results a few limitations need to be considered. First, our conclusions are based on a relatively limited number of trials (16 in each experimental condition). Since the task used is very repetitive, we preferred to reduce the potential effects of fatigue (and thus maximize attention levels) in our study by keeping the experiment within approximately half an hour duration (including task explanations). However, despite this potential limitation, it is important to consider that bisection tasks are usually very sensitive in detecting attentional biases with relatively few trials. For instance, in the clinical setting, the line bisection task is very sensitive to the presence of unilateral neglect, although it is usually performed with only a few (i.e., 3–4) lines (e.g., Wilson, Cockburn, & Halligan, 1987). Second, we did not record the direction of the final tapping movement (i.e. towards the body vs. away from the body) when the verbal response was provided. Although the movement performed was not in the critical left-right dimension, the tapping direction may have influenced the final response since there seems to be a preference in associating small numbers with spatial positions close to the body, and large numbers with positions far away from it (e.g., Gevers, Lammertyn, Notebaert, Verguts, & Fias, 2006; Shaki, & Fischer, 2012). However, it is important to stress here that opposite directional movements were intermixed in each trial. Although the final verbal response may have occurred during a towards-the-body movement, the response may have been mentally processed during an away-from-the body movement. Hence, in order to specifically consider the influence of tapping direction, movement directions should be investigated using a blockwise design in future studies.

In summary, our data show that the order in which numbers are presented in a number bisection task (i.e. ascending vs. descending) affects the spatial reference frame individuals rely on in performing this task. In particular, when performing a concurrent hand movement, the position of the moving hand in the left vs. right hemispace affects the bisection bias for numbers presented in ascending order, regardless of which hand is moved. When bisecting in the descending order, it is the moving hand (left or right), irrespective of whether it is moved in the left or right hemispace, that affects the bisection bias. This occurs regardless of the visual status of the participant. Overall, our data suggest that both sighted and early blind individuals' representation of numerical magnitude is mainly rooted in world-centered coordinates when numerical information is given in canonical orientation (i.e. from small to large). In contrast, hand-centered coordinates become more relevant when the scanning of the mental number line proceeds in a non-canonical direction.

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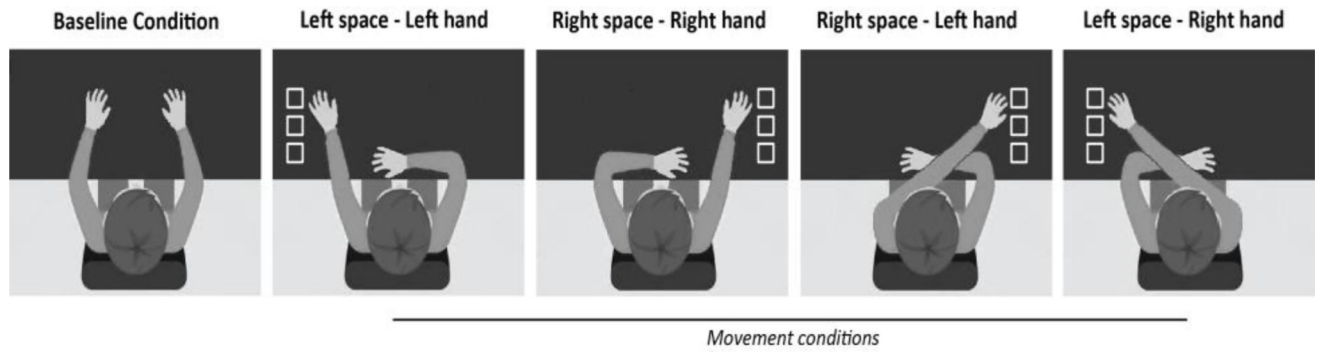


Figure 1.

Experimental setting. Participants were seated in front of a table and were required to perform the numerical bisection task in 5 different conditions. In the baseline condition, no movement was required. In the movement conditions, participants tapped on the three wooden blocks that were radially-aligned on a panel: 1) in the left hemispace with the left hand; 2) in the right hemispace with the right hand; 3) in the right hemispace with the left hand; and 4) in the left hemispace with the right hand. Sighted participants were blindfolded throughout the entire experimental session.

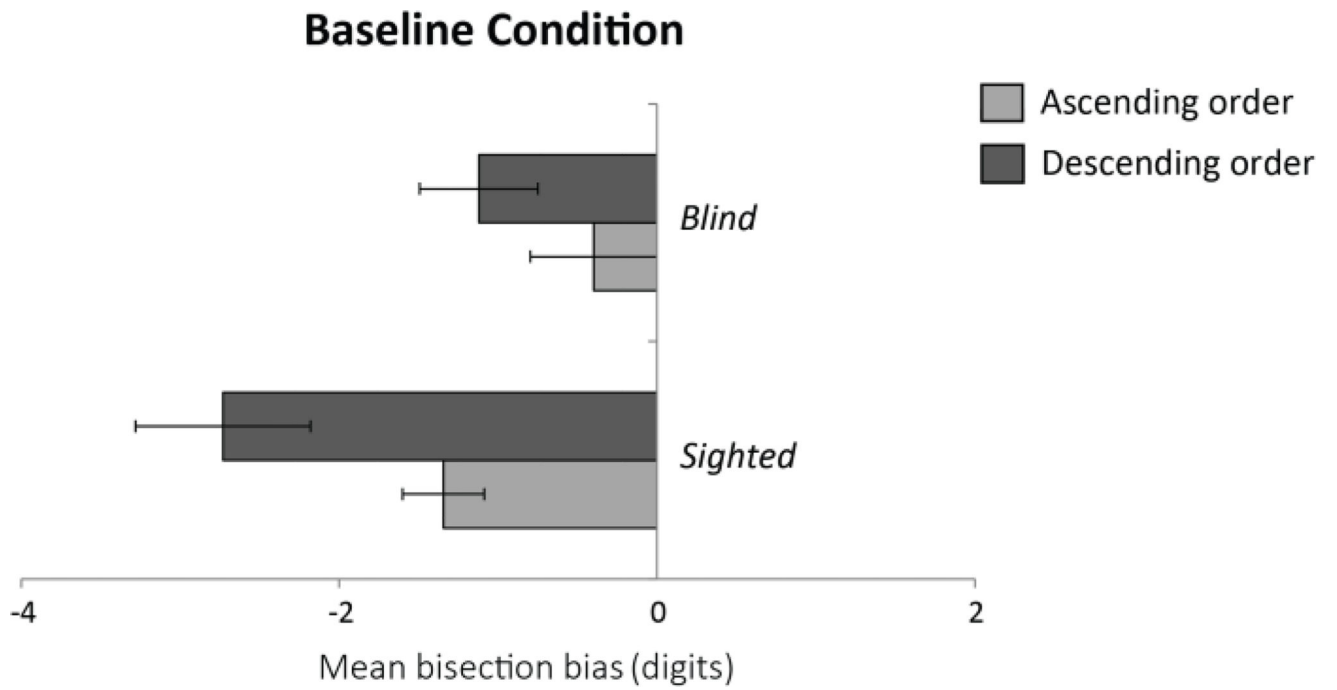


Figure 2. Mean numerical bisection bias (in digits) in early blind and sighted participants in the baseline (non-movement) condition for ascending and descending intervals. Error bars indicate ± 1 SEM.

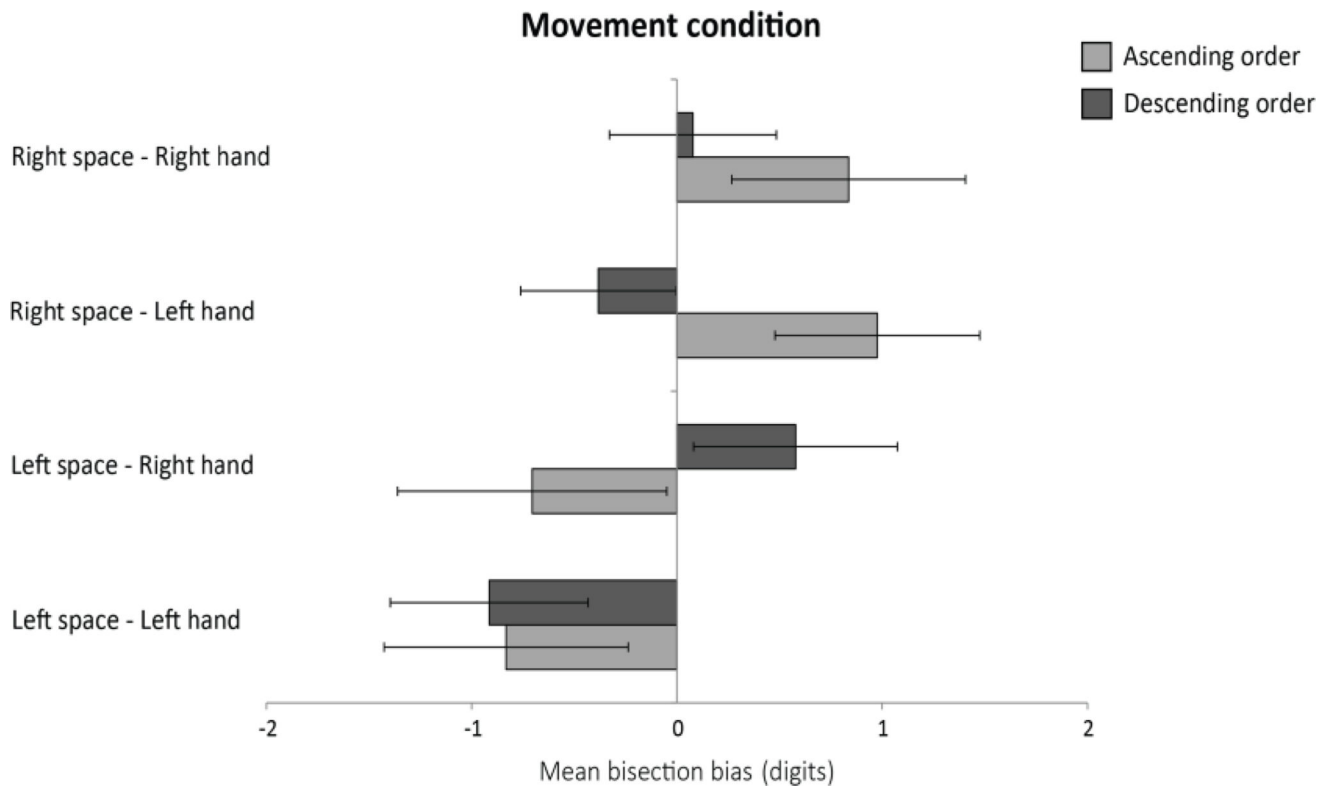


Figure 3. Mean numerical bisection bias in the hand movement conditions, normalized to the bias in the no-movement condition for ascending and descending order. There were no significant differences between blind and sighted participants, hence data are presented collapsed across the two groups. Error bars indicate ± 1 SEM.

Table 1

Characteristics of early blind participants in this study.

Gender	Age	Education (years)	Cause of Blindness	Light perception present
M	33	16	Trauma	–
M	48	16	Optic nerve damage	–
M	51	13	Retinopathy of prematurity	–
F	31	17	Retinopathy of prematurity	–
M	38	17	Optic nerve damage	–
F	55	17	Panophtalmia	+ (until 16 years)
F	59	10	Optic nerve damage	+
M	27	16	Retinopathy of prematurity	–
F	40	13	Optic nerve damage	–
F	37	15	Congenital glaucoma	–
M	40	10	Optic nerve damage	+
M	34	17	Retinal degeneration	+
F	45	17	Optic nerve damage	–
M	40	12	Congenital glaucoma	–
F	62	13	Retinitis pigmentosa	+
F	36	16	Optic nerve damage	–