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Research Report

Spatial bias induced by a non-conflictual task reveals the nature of space perception

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ABSTRACT

The aim of the present study was to show that space perception depends on sensori-motor experience. We induced spatial biases by a non-conflictual lateralized sensori-motor task on twenty seven right-handed healthy volunteers (left-to-right readers). After a pre-test and before a post-test, which assessed visuo-motor and perceptual subjective midpoint in line bisection, participants performed a short lateralized pointing task (towards the left or right hemispace). Results indicated that this lateralized pointing task induced deviations towards the stimulated hemispace in both the visuo-motor and the perceptual estimations of the subjective line centre. These spatial biases varied as a function of pointing direction (left or right pointing), spatial location and line lengths. These findings suggest that a preceding non-conflictual lateralized sensori-motor experience influences subsequent space perception. Accordingly, ecological sensori-motor experience could be involved in asymmetric perception exhibited by normal individuals and neglect patients.

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1. Introduction

Convergent evidence from normal individuals and human lesion studies support the view that space perception differs from physical space. The use of bisection protocols has indeed demonstrated an asymmetric perception of space, when the participant is asked to estimate the centre of a line or a rod. If pseudoneglect refers to the small leftward error in line bisection exhibited by right-handed normal individuals (Bowers and Heilman, 1980; Jewell and McCourt, 2000), right-brain damaged neglect patients typically bisect horizontal lines with a dramatic bias to the right of their veridical midpoint. Unilateral neglect is a syndrome in which patients fail to respond or orient towards stimuli located in the space contralateral to a brain lesion (Halligan et al., 2003; Heilman et al., 1987). Re-

cently, a meta-analytic study showed that both neglect and pseudoneglect biases were similarly influenced by a variety of modulating variables (McCourt and Jewell, 1999). Among all these factors, the literature reported for example that the amplitude of these biases varies as a function of spatial location and line length. This assessment supported the view that both neglect and pseudoneglect phenomena share a fundamental relationship to one another. Investigation of the core mechanisms of asymmetric perception among normal individuals should therefore be appropriate for understanding the underlying cognitive functions in typical development as well as in space disorders.

Different theories have been offered to explain asymmetric perception among healthy individuals. Contrary to the hypothesis related to the innate preferential activation of the right

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Abbreviation: PSE, point of subjective equiprobability

hemisphere (Bradshaw et al., 1987), Chokron and Imbert (1993) have demonstrated the influence of individuals' cultural background on spatial biases: French participants (left-to-right readers) transected the line to the left of centre while Israeli participants (right-to-left readers) erred to the right of centre. Early observations indicated that an imposed scanning direction influences line bisection among normal individuals as well as among unilateral neglect patients (Chokron et al., 1998; Reuter-Lorenz and Posner, 1990). Thus, Chokron and Imbert (1993), Chokron and De Agostini (1995), Chokron et al. (1997) and Chokron et al. (1998) proposed that reading habits determine specific scanning directional trends, even in non-directional spatial tasks (Abed, 1991), which may influence the orientation of attention during line bisection. Other authors suggested that the attentional direction of approach to the midpoint is the determining factor in directional scanning (Halligan et al., 1991; Mattingley et al., 1993). In favour of this explanation, Riddoch and Humphreys (1983) have shown that cueing to the left end of lines reduces the massive rightward bias of left neglect patients. As a whole, these explanations assume that pseudoneglect could be due to lateralized sensori-motor habits, like scanning directional trends or attention orientation (via lateralized oculomotor activity). Recently, Maass and Russo (2003) found a reliable negative correlation between right directionally bias of Arab students and the number of years students had spent in countries where the dominant language is written from left to right. This study suggests that the magnitude of spatial bias evolves with language exposure and raises the question of the degree in which space perception is culturally determined and can be biased by lateralized sensori-motor experience, like reading and writing activities.

It is well established that sensori-motor experience of most neglect patients is asymmetric as a consequence of their neglect behaviour. For instance, many neglect patients suffer from directional hypokinesia, exhibiting abnormalities in motor performance with the non-paretic ipsilesional arm: They are reluctant and slow to initiate a hand movement in the direction contralateral to their brain lesions (Heilman et al., 1985). According to Mesulam (1981, 1999), neglect is the result of a disturbance in the "attentional network" which integrates sensory, motor and motivational processing: A lesion to any of these three components or to their interconnections should result in lateralized distribution of spatial attention towards the contralateral side of space. Given the lateralized sensori-motor experience of neglect patients, certain visuo-spatial behavioural manifestations of neglect might be related to their biased sensori-motor preference. Taken together, literature of unilateral neglect and normal individuals may suggest that spatial biases depend on on-going as well as previous sensori-motor activities.

The link between on-going action and perception of space has been demonstrated in multiple studies, showing for instance, the influence of the arm movement during the task on neglect signs (Robertson and North, 1992) or the influence of the starting position of the hand on straight-ahead estimation among healthy and neglect adults (Chokron and Bartolomeo, 1997; Chokron and Imbert, 1995). It has also been shown that evocation of action afforded by a target influences spatial detection of this target in neglect patients (Humphreys and Riddoch, 2001) or perceived egocentric distance (i.e. the distance between the target and the observer) in healthy participants

(Proffitt et al., 2003; Witt et al., 2004). The link between space perception and previous sensori-motor activities has been demonstrated with paradigms always involving sensori-motor conflict and/or adaptation, e.g. prism adaptation. Actually, spatial biases can be dramatically improved in neglect patients following a short exposure to a 10° right prismatic shift of the visual field (Angeli et al., 2004; for a review see Chokron et al., 2007; Rossetti et al., 1998) or induced in normal adults following an exposure to a 15° leftward visual shift (Berberovic and Mattingley, 2003; Colent et al., 2000; Ferber and Murray, 2005; Girardi et al., 2004; Michel et al., 2003; Rossetti et al., 1998). According to the authors, these researches suggested that processes involved in sensori-motor adaptation would affect the cognitive processes involved in spatial representation affecting in turn subsequent spatial perception (Colent et al., 2000; Michel et al., 2003; Rossetti et al., 1998). Applying similar procedures in virtual reality, Glover and Castiello (2006) hypothesized that recovery of space perception resulted from the requirement to make movements in the left neglected side of space. If asymmetric sensori-motor activity is involved in the spatial biases exhibited by both neglect and normal individuals, then a brief lateralized sensori-motor experience without conflict should induce spatial biases. To our knowledge, the induction of a lateralized perceptual spatial after-effect following non-conflictual sensori-motor task has never been demonstrated.

The purpose of the present study was therefore to investigate the influence of lateralized sensori-motor experience on spatial processing. To be more precise, we wanted to show, among healthy participants, that pointing towards the left or the right hemispace induces a subsequent spatial bias in bisection towards the stimulated hemispace. In addition, trying to induce a spatial bias by way of a motor pointing task offers the opportunity to test the hypothesis proposed by Rossetti and collaborators (1998) that sensori-motor experience could induce a supramodal change in the cognitive system involved in spatial processing. Accordingly, both the perceptual (landmark test, Milner et al., 1992, 1993) and visuo-motor versions of the line bisection protocol were administered to disentangle the perceptual and motor components of the expected spatial bias. If the observed spatial bias was not induced by the unique influence of low-level sensori-motor processes but rather by higher-level spatial processes involved in space perception, then it should be observed on both the perceptual and visuo-motor bisection tasks. Moreover, it is well established that the bias observed among healthy and neglect adults increases with lines length and depend on lines location (Azouvi et al., 2006; Cubelli et al., 1994; Jewell and McCourt, 2000; McCourt and Jewell, 1999; Michel et al., 2003). Given that we wanted to induce biases closed to those exhibited by neglect patients, we expected that the observed spatial bias due to our lateralized pointing task should be modulated by the stimulus characteristics (i.e. line length) and/or the sector of space in process (i.e. horizontal location of the lines). Thus, we wanted to show that the bias induced by pointing towards the left or the right hemispace differs according to the line characteristics (length and/or location of the lines). In other words, we expected an interaction between group and condition of line display (length and location of the lines).

These predictions have been assessed by submitting twenty seven right-handed healthy volunteers (left-to-right readers)

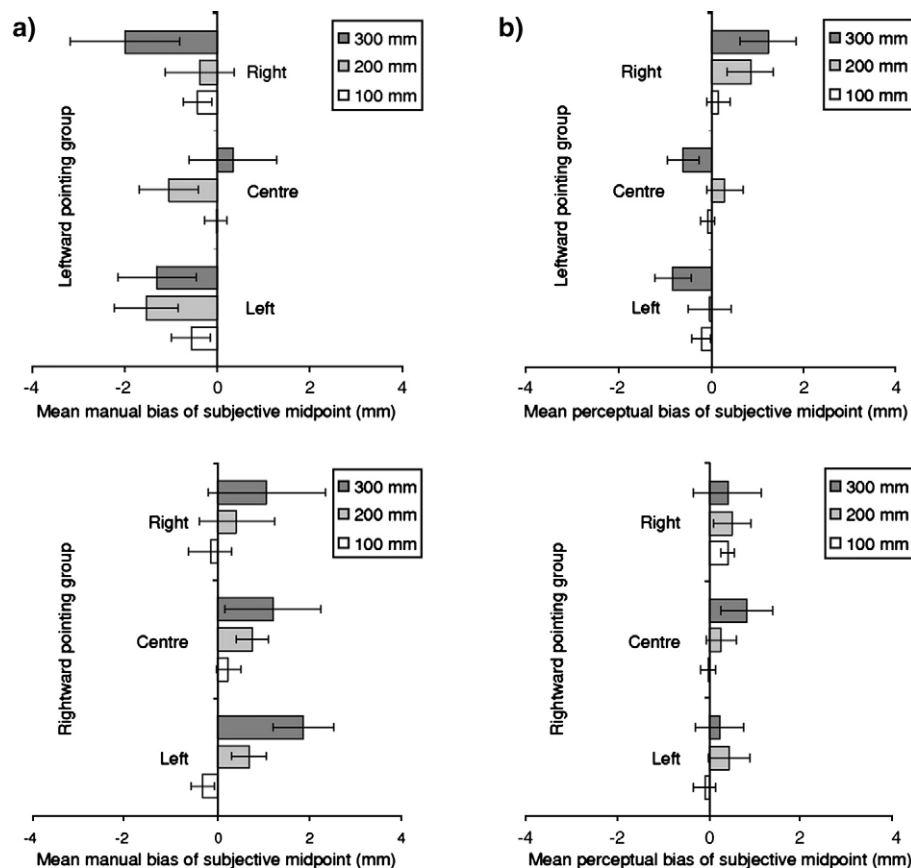


Fig. 1 – Uncorrected, mean bias of subjective midpoint (\pm uncorrected¹ SE) as a function of Location (left, centre, right), Length (100, 200, 300 mm) of visual horizontal lines and pointing Group (leftward, rightward) for (a) manual and (b) perceptual bisection tasks.

to the following three stages experimental procedure: (1) pre-test baseline measurement of performance on both the visuo-motor and perceptual versions of the line bisection task, (2) asymmetric pointing task (towards targets randomly displayed in the left hemispace for half of the participants and in the right hemispace for the remaining half), and (3) post-test measurement (identical to pre-test). In the visuo-motor bisection tasks performed during both the pre-test and post-test measurements, participants were asked to place, with their right hand, a short cross-mark at the centre of each of the lines successively displayed. In the perceptual version, participants had to judge whether transected lines were to the left or to the right of their centre. The lines successively displayed were either accurately bisected or transected to the left or to the right of their true centre. For both the perceptual and visuo-motor bisection tasks, lines of various lengths (100, 200 or 300 mm long) were randomly displayed either leftward, rightward or centred to the participant. Accuracy and verbal responses were recorded for the visuo-motor bisection task and the perceptual task respectively.

¹ Although the ANOVA was performed on arctangent data, we present original means and standard errors for ease of interpretation and comparison with existing literature.

2. Results

For the visuo-motor bisection task, the subjective midpoint was estimated in each condition as the average algebraic distance between the mark placed by the participant and the true centre of the lines. For the perceptual bisection task, subjective midpoint was obtained as the Point of Subjective Equiprobability (PSE) of the individual best-fit sigmoid curves of leftward and rightward responses. Thus, this PSE corresponds to the transition offset (an extracted parameter from the best-fit sigmoid function) at which the frequency of left responses was equal to right ones (i.e., 50%). All the analyses were performed on arctangent data because of unequal error variances of the distributions.

2.1. Bisection performances in Pre-test

In pre-test, since no significant effect of the group was found in preliminary analyses ($p > .10$), group equivalence could be established and this factor was not considered in pre-test analyses. ANOVAs with Length (100, 200, 300 mm) and Location (centre, left, right) as within factors were separately performed on subjective perceptual midpoint (PSE) and subjective visuo-motor midpoint (mean algebraic errors).

The visuo-motor subjective midpoint was significantly deviated leftward ($M = -1$ mm, $SD = 2.05$, $t(26) = -2.54$, $p < .05$). The

main Length effect was marginally significant ($F(2, 52)=2.97$, $p=.060$) showing a tendency for leftward bias to increase with line Length ($F(1, 26)=4.16$, $p=.052$). In addition, there was a significant Location by Length interaction ($F(4, 104)=3.02$, $p<.05$). Post-hoc Tukey test revealed that for 300-mm lines, leftward deviation of the subjective middle significantly increased when lines were located in central space compared to the condition in which they were located in the right hemispace.

In the perceptual bisection, the mean position of the subjective middle did not significantly differ from the objective one ($M=+0.39$ mm, $SD=2.5$, $t(26)<1$). The repeated measures ANOVAs only revealed an effect of Length on the position of the subjective middle ($F(2, 52)=5.65$, $p<.05$). The linear trend analysis was significant ($F(1, 26)=9.87$, $p<.05$).

2.2. Effect of the lateralized pointing task on bisection performance

ANOVAs with Group (leftward pointing, rightward pointing) as a between-subject factor, Length (100, 200, 300 mm) and Location (centre, left, right) as within-subject factors were separately performed for the visuo-motor and perceptual bisection tasks. The treatment variable was the additional bias recorded at post-test, i.e. the mean error difference (or PSE difference) between post-test and pre-test. A negative difference was interpreted as a leftward deviation as compared to pre-test, a positive difference as revealing a rightward deviation.

Figs. 1a and b show the bias obtained in each group (as a function of the pointing hemispace) for each condition of line Location and Length for both the visuo-motor and perceptual bisection tasks.

For the visuo-motor bisection task, the main Group effect was significant ($F(1, 25)=7.69$, $p<.05$). Pointing towards the right hemispace induced a significant rightward bias in subsequent bisection tasks ($M=0.65$ mm, $SD=1.38$, $t(13)=1.96$, $p<.05$) whereas a significant leftward bias ($M=-0.78$ mm, $SD=1.50$, $t(12)=-1.96$, $p<.05$) was observed for the leftward pointing group. As expected, the Group by Length interaction was significant ($F(2, 50)=4.46$, $p<.05$) showing that bias differences between the leftward and rightward pointing groups were larger for the longest lines (i.e. 200 and 300 mm) than for the shortest one (100 mm) ($F(1, 25)=7.24$, $p<.05$). As shown in Fig. 1, conservative tests (Scheffe test) revealed that the bias gradually increased with Length ($F(1, 25)=8.72$, $p<.05$) for the rightward pointing group, but not for leftward pointing group ($F(2, 50)<1$, even with an *a-priori* test).

In the perceptual bisection, the ANOVA failed to show a significant main Group effect ($F(1, 25)<1$). Interestingly, as expected, the two-way Group by Location by Length interaction was significant ($F(4, 100)=2.52$, $p<.05$). The decomposition of this interaction into its one degree of freedom components showed that the bias difference between the leftward and rightward pointing more strongly increased with Length (300 mm compared to 200 and 100 mm) at the centre as compared to the left or right lines ($F(1, 25)=10.73$, $p<.01$). For 300-mm lines at the centre, the difference between groups was significant ($F(1, 25)=7.58$; $p<.05$) in the expected direction since the leftward pointing group showed a leftward bias ($M=-0.60$ mm, $SE=0.34$) and the rightward pointing group a rightward bias ($M=0.82$ mm, $SE=0.57$).

As shown in Fig. 1, Tukey analyses revealed that the bias induced on 300-mm lines by leftward pointing differed according to their left or right hemispace Location ($p<.01$): Significant leftward biases were found for lines located in the left hemispace ($M=-0.84$ mm, $SD=1.42$, $t(12)=-2.51$, $p<.05$) and significant rightward biases for those located in the right hemispace ($M=1.23$ mm, $SD=2.17$, $t(12)=2.43$, $p<.05$).

3. Discussion

The purpose of this study was to examine whether previous lateralized pointing would influence subsequent visuo-motor and/or perceptual bisection. In the pre-test condition (baseline condition), results from the visuo-motor bisection task showed a leftward spatial bias which varied as a function of line Length and Location. This finding is consistent with the literature (for a review, see Jewell and McCourt, 2000). The leftward bias did not extend to the perceptual estimation (perceptual bisection) even if an effect of Length on deviation of subjective middle was observed in this later task.

As expected, our short lateralized pointing task induced spatial biases in both the perceptual and visuo-motor bisection tasks. In the visuo-motor bisection of post-test phase, an additional bias was observed towards the right following rightward pointing and towards the left following leftward pointing. With respect to the perceptual bisection, a significant influence of the previous pointing task was observed on bisection judgements in some conditions of line display, namely longest lines displayed at centre, showing biases in the direction of the previous pointing hemispace, as for the visuo-motor bisection. Moreover, we showed that the influence of the previous lateralized pointing task in both the perceptual and visuo-motor bisections was modulated by the characteristics of the stimulus (Length and Location). In visuo-motor bisection, results indeed indicated that the spatial bias induced by the pointing task increases for the longest lines. In the perceptual bisection, as shown by the significant two-way Group by Length by Location interaction, results indicated that the bias difference between the leftward and rightward pointing more strongly increased with Length at the centre as compared to the left or the right Location of lines. In the leftward pointing group, results also showed biases towards the left for 300-mm lines displayed on the left hemispace and towards the right for the 300-mm rightward lines. This opposite perceptual biases induced by leftward pointing did not confirm our hypothesis. Actually, for the 300-mm lines, the difference between the leftward and rightward pointing groups is significant neither for the lines displayed in the left ($F(1, 25)=2.28$; $p=.14$) nor right ($F(1, 25)=0.96$; $p=.35$) side of the screen. Thus, the opposite perceptual biases induced by leftward pointing for 300-mm lines cannot be explained by the difference between groups, i.e. by the direction of the pointing task.

These findings demonstrate that a low-order lateralized sensori-motor task with no perceptual or motor conflict can affect high-level spatial processing, and in turn, can induce subsequent biases on space perception. We indeed showed that a simple lateralized pointing, performed for only 5 min, was able to generate a subsequent significant spatial bias in visuo-motor and

perceptual bisection task. Given that the visual judgements of transected lines in the perceptual bisection task were deprived of any motor component, the induced deviation on bisection cannot be attributed to simple motor biases. Previous lateralized pointing rather seems to affect higher-level processes, namely those involved in space perception. Thus, preceding sensori-motor activity may influence how space is subsequently organized in normal adults. Accordingly, these results would support a dynamic conception of spatial perception. Along those lines, subjective space should not be regarded as a stable and definitive construction, but should be considered directly dependent upon sensori-motor interactions with the environment. Spatial processing is probably directly affected not only by online sensori-motor information (such as attentional or spatio-motor cueing, as mentioned in the introduction) but also by spatial location and direction of sensori-motor habits.

As it was found previously using prismatic adaptation (Michel et al., 2003), the biases induced by our lateralized pointing in both the perceptual and visuo-motor bisections may share some characteristics with pseudoneglect and neglect phenomena (see Jewell and McCourt, 2000). The post-test biases were indeed modulated by the line Length and Location. The greatest bias observed for longest lines is not surprising since longest lines are more sensitive to unilateral neglect (Azouvi et al., 2006; Bisiach et al., 1983). Similarly, pseudoneglect phenomenon is well known to be influenced by line Length, such that significant bias was only induced for longest lines (McCourt and Olafson, 1997). If lateralized sensori-motor activity performed for only 5 min is able to affect space perception in the same way as pseudoneglect and neglect phenomena, we may hypothesize that lateralized sensori-motor habits determine spatial biases exhibited by normal individuals and neglect patients. This explanation of pseudoneglect phenomenon is compatible with previous research showing that learned, cultural factors, such as reading and writing habits, influence the perception of space (Chokron et al., 1998; Chokron et al., 1997; Chokron and De Agostini, 1995; Chokron and Imbert, 1993). For instance, the results reported by Maass and Russo (2003), showing that spatial biases evolves with language exposure in Italian and Arab students, may be explain by the lateralized sensori-motor activity of the participants daily involved in their reading and writing experience.

According to this explanation of spatial biases, we might also hypothesize that poor recovery after neglect is due, at least in part, to the asymmetric pattern of activity of left neglect patients. The attentional deficit observed in left neglect patients is often interpreted as a difficulty in orienting towards the left hemispace together with an over-attractability towards the rightward hemispace (see Bartolomeo and Chokron, 2002 for review; Chokron et al., 2004). This attentional deficit, as well as the directional hypokinesia (Heilman et al., 1985) observed in left neglect patients, may be responsible for an asymmetric spatial exploration favouring the right hemispace. The present results suggest that the rightward preference for perception and action of neglect patients probably in turn reinforces left neglect behaviour. Recently, it has been suggested that non-spatially lateralized deficits combined with lateralized impairments could be responsible for the acute neglect disorders (Husain and Rorden, 2003; Robertson, 2001). The non-later-

alized deficits might affect several processes such as sustained attention (Robertson et al., 1997), selective attention at central fixation (Husain et al., 1997) or in both visual fields (Battelli et al., 2001), analysis of local features in the visual scene (Doricchi and Incoccia, 1998), as well as spatial working memory (Husain et al., 2001) or spatial remapping (Pisella and Mattingley, 2004). Along those lines, left neglect patients could suffer from a complex interaction between the consequence of the right parietal lesion (lateralized and non-lateralized spatial deficits) and their rightward behavioural bias.

Our findings look like to those reported by studies inducing spatial biases in healthy adults with prism adaptation. First, the amplitude of the present induced spatial biases was comparable to those induced by prism. For instance, applying prism among healthy adults, the greatest bias in perceptual bisection reported by Michel and collaborators (2003) was observed for 375-mm lines displayed at centre and averaged 1.9 mm. In the same study, the spatial bias averaged 0.65 mm for 250-mm lines. In the perceptual bisection of the present study, the bias observed for 300-mm lines at centre averaged -0.60 mm and 0.82 mm for the leftward and rightward pointing group respectively. Secondly, the modulations of the spatial biases by the characteristics of the lines mirror the results reported by Michel and collaborators (2003) who found significant bisection bias in some conditions of line length and location (e.g. 375-mm lines and centre lines) but not in others (e.g. 125-mm lines and right lines). The similarity of the present findings and those observed among healthy adults following exposure to prism goggle (Colent et al., 2000; Michel et al., 2003) encourages us to investigate more precisely these effects. First, further studies will record ocular movements in order to determine the role of ocular responses in the present findings. In addition, long-term spatial after-effect following prismatic adaptation have been reported among neglect patients (Frassinetti et al., 2002; Pisella et al., 2002) and recently, in healthy adults (Hatada et al., 2006). Thus, further studies are needed to address the long-term duration of the current effect on healthy adults as well as on brain-damaged patients. Finally, it would be interesting to test the transfer of the effect of the lateralized pointing task to other modalities such as haptics with the task reported by Girardi and collaborators (Girardi et al., 2004).

4. Conclusion

In conclusion, the present study revealed that the way we act on space may influence space perception. The present findings suggest that lateralized sensori-motor experience may bias space organization. These findings might explain the large inter-individual variability observed in visuo-spatial tasks. Accordingly, pseudoneglect bias could be related to lateralized sensori-motor activity which characterizes normal individuals. More studies are needed, but if we extend these results beyond the pseudoneglect phenomenon, we may hypothesize that the large rightward lateralized sensori-motor experience combined with the non-lateralized spatially deficits exhibited by right-brain damaged patients may reinforce left neglect behaviour, thus limiting recovery processes.

5. Experimental procedure

5.1. Participants

Twenty seven healthy adults (nineteen females and eight males) volunteered to participate in the study. All participants, ranging from 20 to 43 years of age (mean age: 25.5 years, S.D: 5.8 years), had normal or corrected-to-normal vision and were naive with regard to the purpose of the study. All participants were right-handed and left-to-right readers. They gave informed written consent prior to participating.

5.2. Apparatus and stimuli

The experiment was conducted in a room lit by desk lamps hanging from the ceiling above the apparatus. A computer screen with a display area 376.5 mm wide and 300 mm high (1280×1024 pixels, 75 Hz) was disposed in the fronto-parallel plane in front of the individual's head and centred with respect to the sagittal body middle. Vision of this display area was restricted by an elliptical window (365 mm×270 mm) with 160 mm wide white borders. The elliptical window was oriented horizontally and centred on the computer screen so that it blocked the black screen border as well as the equipment around. Behind this elliptical window, black stimuli were aligned with the horizontal axis of the elliptical window on a white background.

For the visuo-motor bisection task, stimuli consisted of 45 horizontal lines. They were drawn on separate A4 white sheets of paper (297×420 mm) which were horizontally introduced one by one, on a support between the elliptical window and the computer screen. Stimuli were 1 mm wide and 100, 200 or 300 mm long drawn at various positions: For each line length, the objective midpoint of the line was either centred, or 31 mm left, or 31 mm right with respect to the mid-sagittal plane of the individual's body. The order of presentation of the sheets was randomized for each participant. An extra fine-point pen was provided for marking the subjective centre of the lines.

In the perceptual bisection task, four hundred and eighty six lines were presented. They were identical to those of the visuo-motor bisection task with the exception that each line, generated on a Pentium III PC, was displayed on the white background of the computer screen, and that the line stimuli were already transected with a 6-mm vertical mark. For each line length (100, 200 and 300 mm) and each spatial location (centre of the screen, 31 mm left or right of the centre of the screen), the lines were accurately bisected or transected at 4, 8, 16 or 24 pixels (approximately 1.2, 2.3, 4.7 and 7 mm) to the right or left of the true centre. Pre-transected lines were randomly displayed by blocks of 162 stimuli including 2 lines for each cross-marked position, each spatial location and each line length. Participants performed three blocks yielding a total of 486 trials. Moreover, a mask (376×9.4 mm), built by random juxtaposition of black and white pixels, was used in order to prevent retinal persistence of the line. The mask was displayed along the whole horizontal axis of the elliptical window, so that lines were occluded whatever their length or horizontal location.

For the pointing task, targets consisted of black dots of approximately 6 mm in diameter. They were randomly displayed

one by one between 182 mm to the left and 182 mm to the right of the screen centre and distributed across thirty-two spatial locations spaced out by 11.8 mm. A mask was used in this task in order to erase the previous target. The mask was the same as the one used for the perceptual bisection task except that its width was 14.7 mm. Furthermore, a miniature device was used in order to prompt the participant to perform the task correctly. This miniature patch-like device was placed upon the right index finger tip to let the participant believe that the movement parameters were recorded together with pointing accuracy.

5.3. Procedure

Participants were tested individually and underwent a similar procedure composed of two 1 h sessions, from two days to 2 weeks spaced. In the first session, participants performed two bisection tasks (visuo-motor and perceptual) counterbalanced across participants. A break was managed between the 3 blocks of trials of the perceptual bisection task. The second session was identical to the first one, except that the visuo-motor bisection task and each of the three blocks of the perceptual bisection task were preceded by the lateralized pointing task. In the second session as in the first, the order of the bisection tasks was counterbalanced across participants. Half the participants performed the visuo-motor and perceptual bisection tasks in the same order in both sessions, and the remaining half performed the tasks in the opposite order. During all the tasks, participants sat at a 600-mm distance from the computer screen.

5.3.1. Visuo-motor bisection task

During the visuo-motor bisection task, the experimenter was standing behind the screen in front of the participant so that he could introduce a sheet of paper between the computer screen and the elliptical window between each trial. Since the introduction of the paper sheet was somewhat time demanding, participants were instructed to keep their eyes closed between each trial². This instruction was given during both the pre-test and post-test sessions, so that the same conditions were applied in both sessions. For each trial, the stimulus was displayed until the response was made. Participants were asked to place a short cross-mark at the exact centre of the line using their right hand. They were given the pencil and asked to place their hand on the table in front of them after each bisection. The task duration was approximately 15 min. After each experimental session, the subjective centre of each line was measured to the nearest millimetre. Leftward deviation from centre was coded as a negative value and rightward error as a positive value.

5.3.2. Perceptual bisection task

For each trial of the perceptual bisection task, the line disappeared after the response was given and was immediately followed by the mask presented for 300 ms. Participants were told that each line was marked to the left or to the right from centre. They were asked to judge whether the transected lines

² If the lateralized pointing task of this study biased spatial perception, it is uncertain what may influence the disappearance of these biases. As their disappearance may be influenced by visual cues, it is preferable to minimize the subject's exposure to the visual scene.

were transected rightward or leftward of the true centre (forced-choice task). They indicated their response (left or right deviation) by responding on a numerical keyboard with their right finger. They pressed (left) button 1 to indicate their response “to the left” and (right) button 3 to indicate “to the right”. After each response, they placed their forefinger on the centre button 2. Each block of the perceptual bisection task lasted at least 10 min, ranging from 5 to 15 min depending on the participants response time.

5.3.3. Pointing task

The lateralized pointing task was performed 4 times in the post-test session, i.e. before the visuo-motor bisection task and each block of the perceptual bisection task because of the time needed to perform this later task. For each trial of the pointing task, the target was presented for 1500 ms and immediately followed by the target's mask for 300 ms, with a total of one hundred and fifty-three trials. Targets were displayed on the left or on the right side of the screen, depending on the group in which participant was assigned. The seventeen possible spatial locations of the target were comprised between 182 mm to the left and 6 mm to the right from the screen centre for the left pointing group, and between 6 mm to the left and 182 mm to the right for the right pointing group. Fourteen participants were randomly assigned to the right pointing group and the remaining ones were included in the left pointing group. Independent of group, participants were to point as quickly and as accurately as possible to each target with their right index finger. Before beginning the task, the miniature device was placed upon the right index finger tip and participants were asked to replace their hand on the table in front of them after each pointing movement. Although participants were told that the pointing parameters were analyzed, no measure was actually recorded during this task. As a matter of fact, we were interested in the subsequent effect of the pointing task on the bisection performances but not pointing performances *per se*. The task duration was 5 min.

5.4. Data analysis

For the visuo-motor bisection task, algebraic errors across the six trials of each condition were averaged for each subject. For the perceptual bisection task, subjective midpoint was obtained as the point of subjective equiprobability (PSE) of leftward and rightward responses corresponding to the transition offset at which the frequency of left responses was equal to rightward ones (i.e., 50%). In this task, the dependant measure was the number (or percent) of trials (out of a total of six trials) on which participants indicated that the cross-mark was located to the left of perceived line midpoint. The method of constant stimuli was used to derive individual psychometric functions in each condition so that the percentage of left choices was plotted as a function of the position of the line cross-mark. Regressions were then performed to fit a sigmoid distribution to each of these psychometric functions by method of non linear least squares approximation. This computation was done on Matlab® using lsqcurvefit. Sigmoid function was described by the equation:

$$f(x, \delta, \beta) = 0.5 [1 + \tanh((\delta - x)/\beta)]$$

Where x is the cross-mark location, β is the slope of the sigmoid, and δ is the x -axis location solution corresponding to $y=0.5$ (i.e., the mark location at which left-right responses would occur with equal frequency). Based on these best-fit sigmoid curves, individual PSE, corresponding to the parameter δ , were extracted for all experimental conditions.

Effect of lateralized pointing on bisection performance was examined by performing ANOVAs comparing pre- and post-test biases. Separate analyses were conducted in both the visuo-motor and perceptual bisection tasks, i.e. on mean pre-post differences in the visuo-motor bisection task, and on PSE pre-post differences in the perceptual version of the task. In each condition, pre-post differences were calculated for each participant as the difference of mean errors (or PSE) in post-test minus mean errors (or PSE) in pre-test. So, bias carried a negative sign if the bias recorded at post-test was to the left compared to the pre-test and a positive value in the case of an induced rightward bias compared to pre-test.

In addition, an arctangent transformation of all data was used to adjust for unequal error variances of the distributions. Actually, in both the visuo-motor and perceptual bisection tasks, the most important variances (inter-individual variability) were obtained with the longest lines, independent of line Location, Group or treatment (mean error, PSE or induced bias). This phenomenon was neither marginal nor surprising, as reported in numerous articles. To test our hypothesis, trend analyses (the decomposition of the effect in its one degree of freedom components) were performed only when main effects or interactions were significant. For each significant trend analysis presented, the test of residual treatment (the not explicated variance) was not significant ($F < 1$).

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REFERENCES

- Abed, F., 1991. Cultural influences on visual scanning patterns. *J. Cross-Cult. Psychol.* 22, 525–534.
- Angeli, V., Benassi, M.G., Làdavas, E., 2004. Recovery of oculo-motor bias in neglect patients after prism adaptation. *Neuropsychologia* 42 (9), 1223–1234.
- Azouvi, P., Bartolomeo, P., Beis, J.M., Perennou, D., Pradat-Diehl, P., Rousseaux, M., 2006. A battery of tests for the quantitative assessment of unilateral neglect. *Restor. Neurol. Neurosci.* 24 (4–6), 273–285.
- Bartolomeo, P., Chokron, S., 2002. Orienting of attention in left unilateral neglect. *Neurosci. Biobehav. Rev.* 26 (2), 217–234.
- Battelli, L., Cavanagh, P., Intriligator, J., Tramo, M.J., Henaff, M.A., Michel, F., et al., 2001. Unilateral right parietal damage leads to bilateral deficit for high-level motion. *Neuron* 32 (6), 985–995.

- Berberovic, N., Mattingley, J.B., 2003. Effects of prismatic adaptation on judgements of spatial extent in peripersonal and extrapersonal space. *Neuropsychologia* 41 (4), 493–503.
- Bisiach, E., Bulgarelli, C., Sterzi, R., Vallar, G., 1983. Line bisection and cognitive plasticity of unilateral neglect of space. *Brain Cogn.* 2 (1), 32–38.
- Bowers, D., Heilman, K.M., 1980. Pseudoneglect: effects of hemispace on a tactile line bisection task. *Neuropsychologia* 18 (4–5), 491–498.
- Bradshaw, J.L., Nathan, G., Nettleton, N.C., Wilson, L., Pierson, J., 1987. Why is there a left side underestimation in rod bisection? *Neuropsychologia* 25 (4), 735–738.
- Chokron, S., Imbert, M., 1993. Influence of reading habits on line bisection. *Brain Res Cogn Brain Res* 1 (4), 219–222.
- Chokron, S., Imbert, M., 1995. Variations of the egocentric reference among normal subjects and a patient with unilateral neglect. *Neuropsychologia* 33 (6), 703–711.
- Chokron, S., De Agostini, M., 1995. Reading habits and line bisection: a developmental approach. *Brain Res Cogn Brain Res* 3 (1), 51–58.
- Chokron, S., Bartolomeo, P., 1997. Patterns of dissociation between left hemineglect and deviation of the egocentric reference. *Neuropsychologia* 35 (11), 1503–1508.
- Chokron, S., Bernard, J.M., Imbert, M., 1997. Length representation in normal and neglect subjects with opposite reading habits studied through a line extension task. *Cortex* 33 (1), 47–64.
- Chokron, S., Bartolomeo, P., Perenin, M.T., Helft, G., Imbert, M., 1998. Scanning direction and line bisection: a study of normal subjects and unilateral neglect patients with opposite reading habits. *Brain Res. Cogn. Brain Res.* 7 (2), 173–178.
- Chokron, S., Colliot, P., Bartolomeo, P., 2004. The role of vision in spatial representation. *Cortex* 40 (2), 281–290.
- Chokron, S., Dupierri, E., Tabert, M., Bartolomeo, P., 2007. Experimental remission of unilateral spatial neglect. *Neuropsychologia* 45 (14), 3127–3148.
- Colent, C., Pisella, L., Bernieri, C., Rode, G., Rossetti, Y., 2000. Cognitive bias induced by visuo-motor adaptation to prisms: A simulation of unilateral neglect in normal individuals? *NeuroReport* 11 (9), 1899–1902.
- Cubelli, R., Pugliese, M., Gabellini, A.S., 1994. The effect of space location on neglect depends on the nature of the task. *J Neurol* 241 (10), 611–614.
- Doricchi, F., Incoccia, C., 1998. Seeing only the right half of the forest but cutting down all the trees? *Nature* 394 (6688), 75–78.
- Ferber, S., Murray, L.J., 2005. Are perceptual judgments dissociated from motor processes?—A prism adaptation study. *Brain Res. Cogn. Brain Res.* 23 (2–3), 453–456.
- Frassinetti, F., Angeli, V., Meneghello, F., Avanzi, S., Làdavas, E., 2002. Long-lasting amelioration of visuospatial neglect by prism adaptation. *Brain* 125 (Pt 3), 608–623.
- Girardi, M., McIntosh, R.D., Michel, C., Vallar, G., Rossetti, Y., 2004. Sensorimotor effects on central space representation: prism adaptation influences haptic and visual representations in normal subjects. *Neuropsychologia* 42 (11), 1477–1487.
- Glover, S., Castiello, U., 2006. Recovering space in unilateral neglect: a neurological dissociation revealed by virtual reality. *J. Cogn. Neurosci.* 18 (5), 833–843.
- Halligan, P.W., Manning, L., Marshall, J.C., 1991. Hemispheric activation vs spatio-motor cueing in visual neglect: a case study. *Neuropsychologia* 29 (2), 165–176.
- Halligan, P.W., Fink, G.R., Marshall, J.C., Vallar, G., 2003. Spatial cognition: evidence from visual neglect. *Trends Cogn. Sci.* 7 (3), 125–133.
- Hatada, Y., Miall, R.C., Rossetti, Y., 2006. Two waves of a long-lasting aftereffect of prism adaptation measured over 7 days. *Exp. Brain Res.* 169 (3), 417–426.
- Heilman, K.M., Bowers, D., Coslett, H.B., Whelan, H., Watson, R.T., 1985. Directional hypokinesia: prolonged reaction times for leftward movements in patients with right hemisphere lesions and neglect. *Neurology* 35 (6), 855–859.
- Heilman, K.M., Bowers, D., Valenstein, E., Watson, R.D., 1987. Hemispace and hemispatial neglect. In: Jeannerod, M. (Ed.), *Neurophysiological and neuropsychological aspects of spatial neglect*. Elsevier Science Publishers B.V., North-Holland, pp. 115–150.
- Humphreys, G.W., Riddoch, M.J., 2001. Knowing what you need but not what you want: affordances and action-defined templates in neglect. *Behav. Neurol.* 13 (1–2), 75–87.
- Husain, M., Rorden, C., 2003. Non-spatially lateralized mechanisms in hemispatial neglect. *Nat. Rev., Neurosci.* 4 (1), 26–36.
- Husain, M., Shapiro, K., Martin, J., Kennard, C., 1997. Abnormal temporal dynamics of visual attention in spatial neglect patients. *Nature* 385 (6612), 154–156.
- Husain, M., Mannan, S., Hodgson, T., Wojciulik, E., Driver, J., Kennard, C., 2001. Impaired spatial working memory across saccades contributes to abnormal search in parietal neglect. *Brain* 124 (Pt 5), 941–952.
- Jewell, G., McCourt, M.E., 2000. Pseudoneglect: a review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia* 38 (1), 93–110.
- Maass, A., Russo, A., 2003. Directional bias in the mental representation of spatial events: nature or culture? *Psychol. Sci.* 14 (4), 296–301.
- Mattingley, J.B., Pierson, J.M., Bradshaw, J.L., Phillips, J.G., Bradshaw, J.A., 1993. To see or not to see: the effects of visible and invisible cues on line bisection judgements in unilateral neglect. *Neuropsychologia* 31 (11), 1201–1215.
- McCourt, M.E., Olafson, C., 1997. Cognitive and perceptual influences on visual line bisection: psychophysical and chronometric analyses of pseudoneglect. *Neuropsychologia* 35 (3), 369–380.
- McCourt, M.E., Jewell, G., 1999. Visuospatial attention in line bisection: stimulus modulation of pseudoneglect. *Neuropsychologia* 37 (7), 843–855.
- Mesulam, M.M., 1981. A cortical network for directed attention and unilateral neglect. *Ann. Neurol.* 10 (4), 309–325.
- Mesulam, M.M., 1999. Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philos. Trans. R. Soc. Lond., B Biol. Sci.* 354 (1387), 1325–1346.
- Michel, C., Pisella, L., Halligan, P.W., Luaute, J., Rode, G., Boisson, D., et al., 2003. Simulating unilateral neglect in normals using prism adaptation: implications for theory. *Neuropsychologia* 41 (1), 25–39.
- Milner, A.D., Brechmann, M., Pagliarini, L., 1992. To halve and to halve not: an analysis of line bisection judgements in normal subjects. *Neuropsychologia* 30 (6), 515–526.
- Milner, A.D., Harvey, M., Roberts, R.C., Forster, S.V., 1993. Line bisection errors in visual neglect: misguided action or size distortion? *Neuropsychologia* 31 (1), 39–49.
- Pisella, L., Mattingley, J.B., 2004. The contribution of spatial remapping impairments to unilateral visual neglect. *Neurosci. Biobehav. Rev.* 28 (2), 181–200.
- Pisella, L., Rode, G., Farne, A., Boisson, D., Rossetti, Y., 2002. Dissociated long lasting improvements of straight-ahead pointing and line bisection tasks in two hemineglect patients. *Neuropsychologia* 40 (3), 327–334.
- Proffitt, D.R., Stefanucci, J., Banton, T., Epstein, W., 2003. The role of effort in perceiving distance. *Psychol. Sci.* 14 (2), 106–112.
- Reuter-Lorenz, P.A., Posner, M.I., 1990. Components of neglect from right-hemisphere damage: an analysis of line bisection. *Neuropsychologia* 28 (4), 327–333.
- Riddoch, M.J., Humphreys, G.W., 1983. The effect of cueing on unilateral neglect. *Neuropsychologia* 21 (6), 589–599.
- Robertson, I.H., 2001. Do we need the “lateral” in unilateral neglect? Spatially nonselective attention deficits in unilateral

- neglect and their implications for rehabilitation. *NeuroImage* 14 (1 Pt 2), S85–S90.
- Robertson, I.H., North, N., 1992. Spatio-motor cueing in unilateral left neglect: the role of hemispace, hand and motor activation. *Neuropsychologia* 30 (6), 553–563.
- Robertson, I.H., Manly, T., Beschin, N., Daini, R., Haeske-Dewick, H., Homberg, V., et al., 1997. Auditory sustained attention is a marker of unilateral spatial neglect. *Neuropsychologia* 35 (12), 1527–1532.
- Rossetti, Y., Rode, G., Pisella, L., Farne, A., Li, L., Boisson, D., et al., 1998. Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect. *Nature* 395 (6698), 166–169.
- Witt, J.K., Proffitt, D.R., Epstein, W., 2004. Perceiving distance: a role of effort and intent. *Perception* 33 (5), 577–590.