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Attention biases the perceived midpoint of horizontal lines

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ABSTRACT

In patients with right brain damage and left visual neglect, attention tends to be captured by right-sided objects and cannot easily disengage from them. While these phenomena can account for several clinical and experimental patterns of performance such as biased visual search, its role is more controversial for other neglect-related signs, such as the typical rightward shifts in horizontal line bisection. It is thus important to see whether and how attentional orienting can bias line bisection in normal participants using standard clinical bisection stimuli. In 3 experiments, we explored the Attentional Repulsion Effect (ARE, Suzuki & Cavanagh, 1997) on pre-bisected lines. Normal observers saw horizontal lines with a vertical bisection mark near the center, preceded by a cue to the left or right of the line, or by no cue. On each trial, observers indicated whether they saw the bisection mark to the left or at the right of the midpoint. We plotted the proportion of 'seen-at-right' responses as a function of the mark's actual position. For uncued lines, the point of subjective equality was slightly at the left of the true center, consistent with the pseudoneglect phenomenon. Right-sided cues shifted the apparent bisection point to the left (and vice versa), as predicted by the ARE. Similar results occurred with different task instructions (compare the length of the left-sided line segment to the right-sided segment) and in the presence or absence of central fixation marks. These results obtained in normal participants support attentional accounts of biased line bisection in neglect patients.

1. Introduction

Patients with right brain lesions and left neglect demonstrate a directional bias towards the right side of space when perceiving and acting in their environment (Bartolomeo & Chokron, 2002); their attention tends to be captured by right-sided objects and cannot easily disengage from them (Posner, Walker, Friedrich, & Rafal, 1984; Rastelli, Funes, Lupiáñez, Duret, & Bartolomeo, 2006). These deficits often provoke clinical signs such as "magnetic attraction" of gaze to right-sided stimuli (Gainotti, D'Erme, & Bartolomeo, 1991) and neglect of left-sided items on visual search (Mark, Kooistra, & Heilman, 1988). When asked to bisect a horizontal line, neglect patients typically err rightwards (Schenkenberg, Bradford, & Ajax, 1980). Even when no manual action is required, as in the landmark task (Harvey, Milner, & Roberts, 1995), patients consider the right segment as being longer than the left one (Milner, Harvey, Roberts, & Forster, 1993), consistent with their bisection behavior.

Neurologically healthy subjects, on the other hand, may make (much smaller) errors in the opposite direction, and bisect lines to the left of the veridical center, a phenomenon dubbed "pseudoneglect" (Bowers & Heilman, 1980; see Jewell & McCourt, 2000 for a review). On the landmark task, when judging lines pre-bisected to the left of their true center, normal participants consider the left segment as being longer than the right one (Milner, Brechmann, & Pagliarini, 1992). This asymmetry likely results from the specialization of networks in the right hemisphere for the deployment of spatial attention (Heilman & Van Den Abell, 1980; McCourt & Jewell, 1999; McCourt & Olafson, 1997; Mesulam, 1999), although reading habits could also contribute by biasing left-to-right readers to explore the line from its left endpoint (Chokron & Imbert, 1993).

This evidence from normal and brain-damaged patients suggests that spatial attention influences the perceptual estimation of horizontal lengths, leading to over-estimation of the portion of the line where attention is focused on. For example, Marshall and Halligan (1990) proposed that during line bisection neglect patients search the line for its midpoint from the right to the left, and subsequently place the bisection point where the two hemi-segments

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appear to be of equal length. A rightward attentional bias might thus increase the perceptual salience of the right portion relative to the left portion of the line (Anderson, 1996), with consequent overestimation of the right portion of the line (Urbanski & Bartolomeo, 2008).

Alternatively, however, deviations on bisection-like tasks in neglect could result from an acquired anisometry of a mental representation of space that is progressively compressed from the right to the left (Bisiach, Pizzamiglio, Nico, & Antonucci, 1996; Bisiach, Ricci, & Neppi Modona, 1998; Savazzi, Posteraro, Veronesi, & Mancini, 2007, but see Doricchi et al., 2008). According to this view, rightward shifts in neglect would be the consequence of a progressive right-to-left relaxation of spatial coordinates, so that the left half of the line would be subjectively perceived as shorter than the right half. This hypothesis originated from the finding that, when neglect patients were asked to place the endpoints of an imaginary line around a given centre, the left-sided imaginary segment was longer than the right-sided one. Importantly, Bisiach, Rusconi, Peretti, and Vallar (1994) claimed that such a pattern of performance was inconsistent with current accounts of neglect, including attentional hypotheses.

In view of this debate, it is important to see whether length estimation can actually be linked to relatively uncontroversial attentional mechanisms. Such a demonstration would provide a proof of principle that biased attentional orienting can at least partially determine neglect patients' perceptual estimation of horizontal lengths.

In the present study, we investigated these issues by taking advantage of the Attentional Repulsion Effect (ARE), whereby briefly presented visual stimuli appear displaced away from the focus of attention (Suzuki & Cavanagh, 1997). In the original study, a central cross was presented for 1800 ms, attention was then focused at a given location by a transient peripheral cue lasting 30 ms. After an SOA of 180 ms, two vertical lines aligned across a wide gap (a vernier) were flashed for 60 ms and followed by a mask presented for 255 ms. In a two-alternative forced choice procedure, subjects had to decide whether the vernier offset was directed clockwise or counterclockwise. Results showed that the line closer to the attentional focus was seen further away. The effect disappeared rapidly as the vernier was exposed for a longer duration (more than 200 ms), which suggested the involvement of a transient component of spatial attention (Nakayama & Mackeben, 1989). The attentional nature of the ARE has been convincingly demonstrated, and several candidate nonattentional mechanisms (figural after effects, perception of apparent motion from the cue to the nearer vernier line) have been excluded (Suzuki & Cavanagh, 1997). Subsequently, Pratt and Arnott (2008) examined whether the AREs are analogous to effects obtained in temporal attentional tasks. They used onset cues (i.e., cues appearing suddenly and remaining present), offset cues (cues disappearing suddenly and never reappearing) and onset–offset cues (cues suddenly appearing and disappearing), all of which produced attentional repulsion effects that were equivalent in magnitude. However, when simultaneous onset and offset cues always appeared or disappeared on the same side of the display, the magnitude of the repulsion was greater for onset cues than for offset cues. This result is consistent with the response time literature on spatial attention, where onsets have priority for the exogenous allocation of attention in situations when two objects both appear and disappear at the same time. Thus, these experiments confirmed the evidence obtained by Suzuki and Cavanagh (1997), by demonstrating that the repulsion effect can be modulated by attentional manipulations, and proposed that the repulsion effect could be a spatial analogue of temporal effects in response times typical of exogenous spatial cueing.

Although the perceptual consequence of the cue is a repulsion in the test position away from the cue, Suzuki and Cavanagh (1997) attributed the result to the effect of attention on receptive fields activated by the cue. Specifically, the physiological literature has reported that attention leads to a shifting of the effective centers of receptive fields toward the cue and a spatial narrowing of the receptive fields (Connor, Preddie, Gallant, & Van Essen, 1997; Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006). According to the labeled line view of location perception (e.g. Barlow, 1972) where the activity of each neuron signals a specific feature or location value, this would lead to a magnification of space around the cue, and a resulting shift in the centroid of responses to the subsequent test. These intermediate effects would lead to the perceived offset of a subsequent test away from the initial cue: the Attentional Repulsion Effect. An attentional magnification should also lead to the expansion in the linear extent of the portion of any test that is closer to the cue. For example, with the horizontal lines used in the present experiments, attention would "stretch" the portion of the line that is closer to the cue. In the original Suzuki and Cavanagh (1997) study, there was only blank space between the cue and the test so that study could not directly examine any other effects.

The present study consists of three experiments carried out to assess whether the repulsive effect of an exogenous cue is able to bias the location of perception. The effect of cueing on the perception of a midline has been studied in pseudoneglect (McCourt, Garlinghouse, & Reuter-Lorenz, 2005) and we now extend this work to landmark stimuli similar to those employed with neglect patients and by asking judgments not only of the midpoint but also of horizontal extent. The occurrence of an ARE in these conditions in normal subjects would obviously support accounts of neglect patients' biased performance on line bisection as resulting, at least in part, from asymmetrical orienting of exogenous attention.

2. Experiment 1

In Experiment 1, observers judged the position of the transector in pre-bisected lines. Exogenous cues were briefly presented adjacent to the left or right extremity of the line. If an ARE occurs in this setting, then observers should perceive the cued segment as longer, and therefore subjectively displace the transector towards the uncued extremity.

2.1. Observers

Eight students (three males and five females, aged 20–33 years), all strongly right-handed as assessed by using the Edinburgh laterality inventory (Oldfield, 1971) (mean score, 96.28; SD, 9.10), participated in Experiment 1. All observers were naïve as to the purpose of the study and had normal or corrected-to-normal vision.

2.2. Stimuli

All stimuli were displayed on a 1280 × 1024 pixels resolution, 85 Hz refresh rate Compaq P1220 colour monitor at a viewing distance of 57.3 cm, such that each pixel subtended 2.34′ (minutes of arc) of visual angle. The experiments were programmed and executed using Matlab 7.5 and the Psychophysics Toolbox extension (Brainard, 1997; Pelli, 1997), controlled by a laptop Dell Latitude D620. Experiments were conducted in a dimly lighted room. Stimuli were all black drawn against a white background. During the whole trial, a fixation cross (1.4° × 1.04°) was presented in the middle of the screen. In the second experiment the fixation cross was present only at the beginning of each trial for 700 ms before the sequence started. Cues were black circles of 1.17° in diameter, presented at 0.4° from the right or left endpoint of the bisected line. The stimulus consisted of a horizontal line 19.5° long and 0.1° thick, centered on the screen, situated 4.9° above the fixation cross. The line was bisected by a vertical transector 1.04° long, 0.1° thick, situated either centrally or to the right or to the left of the true midpoint. Observers viewed the transector displaced at 1, 2, 3, 5, 7 pixels (respectively, 2.34′, 4.68′, 7.02′, 11.7′ and 16.38′) to the right or to the left from the real center of the line. Each value was presented 20 times. At the end of the trial a mask consisting of mixed black lines on a white background, subtending a 20.59° × 2.58° area, was presented.

2.3. Procedure

Before administering the experimental trials, the experimenter ensured that all participants had understood the task instructions. To this end, each participant had 33 practice trials or more as needed. There was no time limit. Fig. 1 illustrates the sequence of events in one trial. At the beginning of the trial the fixation cross

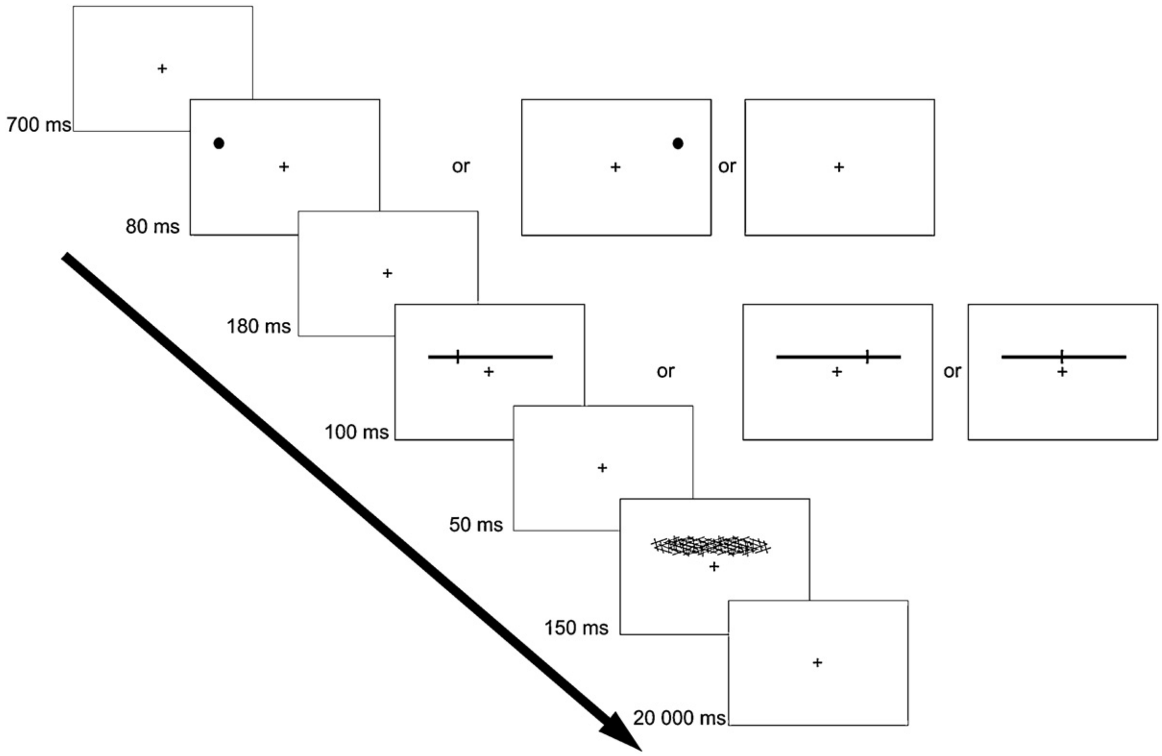

Fig. 1. Sequence of events in one trial.

appeared at the center of the screen. Observers fixated the cross for 700 ms before the trial events started. Observers were asked to maintain fixation throughout the trial, including the response scene. The trial sequence consisted of (a) a flash for 80 ms of the cue circle presented randomly at the left or at the right of the display (or no cue for the neutral condition); (b) a blank interval for 180 ms; (c) the bisected line was then briefly presented (100 ms); (d) another blank interval (50 ms); (e) the mask (for 150 ms); (f) a blank interval for the response (20 s maximum). The observer could answer from the onset of the bisected line and indicated whether the transector appeared to the right or to the left of the true center of the line. The observer responded by pressing the appropriate keys ('m' for right and 'q' for left) on a French keyboard. Subjects were falsely informed that the transector was always deviated. Thus, even in the case of a transector presented at the true center of the line, subjects were forced to choose between right and left.

For each of three cue conditions (left, right and no-cue), 11 transector locations were randomly presented. Each participant performed all 33 experimental conditions. Stimuli were presented in two blocks of 330 trials each one, which resulted in a total of 10 trials per condition in one block. Participants received one block per session. In all, each observer passed 660 trials. In total, the whole task took 30–40 min divided in two test sessions, separated by a 10 min interval break.

2.4. Results

The percentage of 'seen-at-right' responses (i.e., when observers judged the transector as being to the right of the true center) was calculated for each of the 11 transector positions. For each observer and condition, we plotted the proportion of the responses to the different positions of the transector and fit a sigmoidal function to the data.

Despite some variability in the absolute magnitude of the effects, a repulsion effect was obtained for all observers. Right-sided cues shifted the apparent bisection point more to the left than did left-sided cues, as predicted by the ARE phenomenon. Fig. 2A (one observer) and B (means) show that the curve in the left-cue condition is shifted furthest to the left (pattern observed in individual performances of six out of eight subjects), whereas the curve with right-sided cues is shifted furthest to the right (as observed in individual performances of all but one observer). The curve for the no-cue condition is in the middle, between the left-cue curve at the left, and the right-cue curve at the right (pattern observed in individual performances of six observers).

By calculating the points of subjective equality (PSE) for each curve, we obtained the amount of offset necessary for subjects to see the bisection marker as being at the horizontal line's midpoint (Fig. 3). For left-sided cues, the mean displacement necessary to see the line as being symmetrically bisected was 8.41′ to the left of the midpoint; for right-sided cues, the perceived midpoint was slightly (0.63′) to the right of the true midpoint. For the no-cue condition, the bisector was shifted 3.22′ to the left of the midpoint in order to appear centered. A repeated measures ANOVA revealed a significant main effect of the cue position $F(2,7) = 8.01$, $p = 0.005$. Post-hoc comparisons (Tukey HSD) revealed a significant difference between the mean obtained in the left-cue and right-cue conditions ($p = 0.003$). There was no significant difference between the mean obtained in the no-cue condition and either the right-cue or left-cue conditions. Thus, to appear as located in the center of the line, a transector following left-sided cues had to be shifted significantly to the left of the position where it was perceived to be centered after right-sided cues. PSEs differed from the true midpoint of the line after left-sided cues $t(7) = 2.9$, $p = 0.01$ and when no cue was presented, $t(7) = 2.22$, $p = 0.03$. Thus, without any cue, a line had to be transected 3.22′ left of the true center in order to be perceived in 50% of the cases as symmetrically bisected, consistent with the pseudoneglect phenomenon. Right-sided cues were able to counter this bias, and gave rise to relatively symmetrical performance. With right-sided cues, the transector needed to be shifted slightly but not significantly to the right in order to be perceived at the midpoint, whereas with left-sided cues observers needed the transector to be shifted significantly to the left in order to perceive the line as symmetrically bisected. Without any cues, the perceived middle lay between the two cue conditions.

2.5. Discussion

The results of Experiment 1 provide clear evidence of ARE when observers had to estimate the position of a transector in a landmark-type horizontal line. This generalization of the ARE, which was originally shown with vernier stimuli, supports the hypothesis that exogenous attention influences the perception of location: the position of the vertical transector is subjectively displaced towards the uncued extremity of the line either because the vertical transector is repelled by the cue or the nearer segment of the horizontal line is perceived as longer, or both.

However, a potential concern with these results is that a fixation cross was present throughout the entire duration of the trial. Since the line stimuli were centered within the display, then observers could conceivably use the location of the fixation cross to make their judgments of transector location. Observers did not use this information optimally, since their PSEs were biased in the various conditions, but this possibility remains a problematic potential confound. Experiment 2 was performed to address this concern.

3. Experiment 2

Five observers (two males and three females, aged 22–31 years) participated in Experiment 2. All were right-handed according to the Edinburgh laterality inventory, (mean score, 83.25; SD, 33.50). The procedure was identical to Experiment 1, with the following exception: at variance with Experiment 1, where the fixation cross was present throughout the experiment, in Experiment 2 the fixation cross was

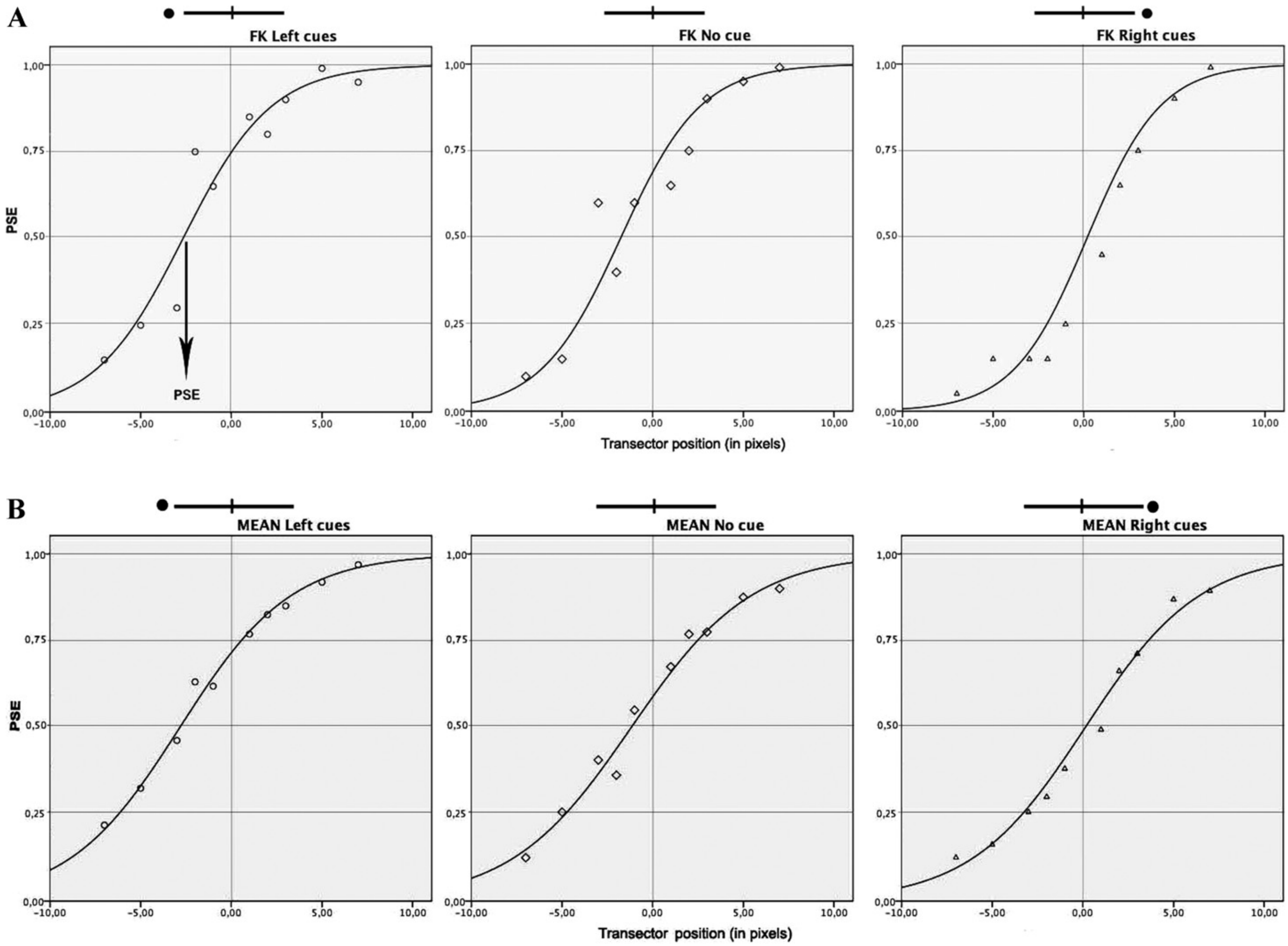

Fig. 2. Experiment 1: A, representative curve fit for one observer based on the proportion of 'seen at right' responses. B, curve fits for mean results of all eight observers.

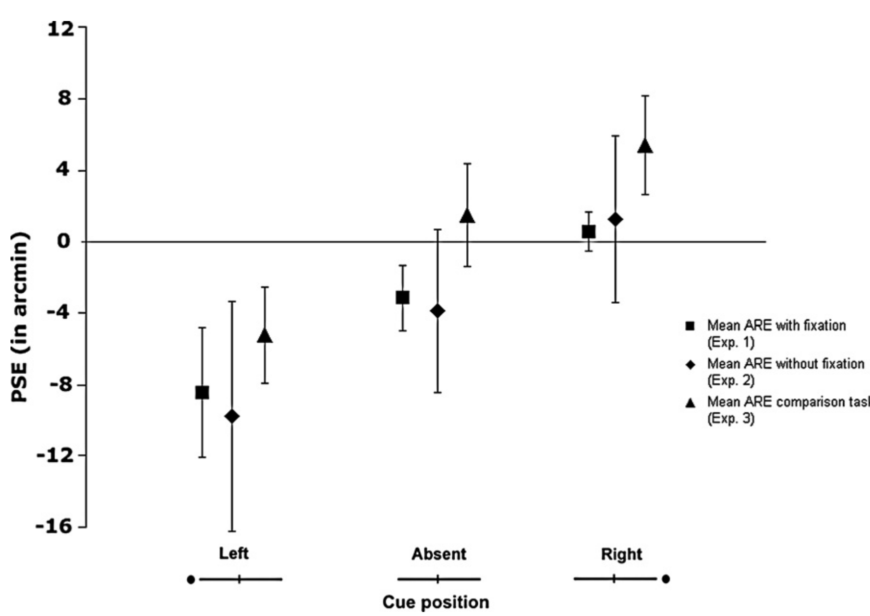

Fig. 3. Arcmin-transformed PSEs for performances obtained in the three experiments, showing the locations where participants had symmetrical performance, with 50% of responses indicating a target to the right, 50% to the left, as a function of the different cue conditions. Negative values, left-sided locations; positive values, right-sided locations. The vertical error bars represent ±1 SD.

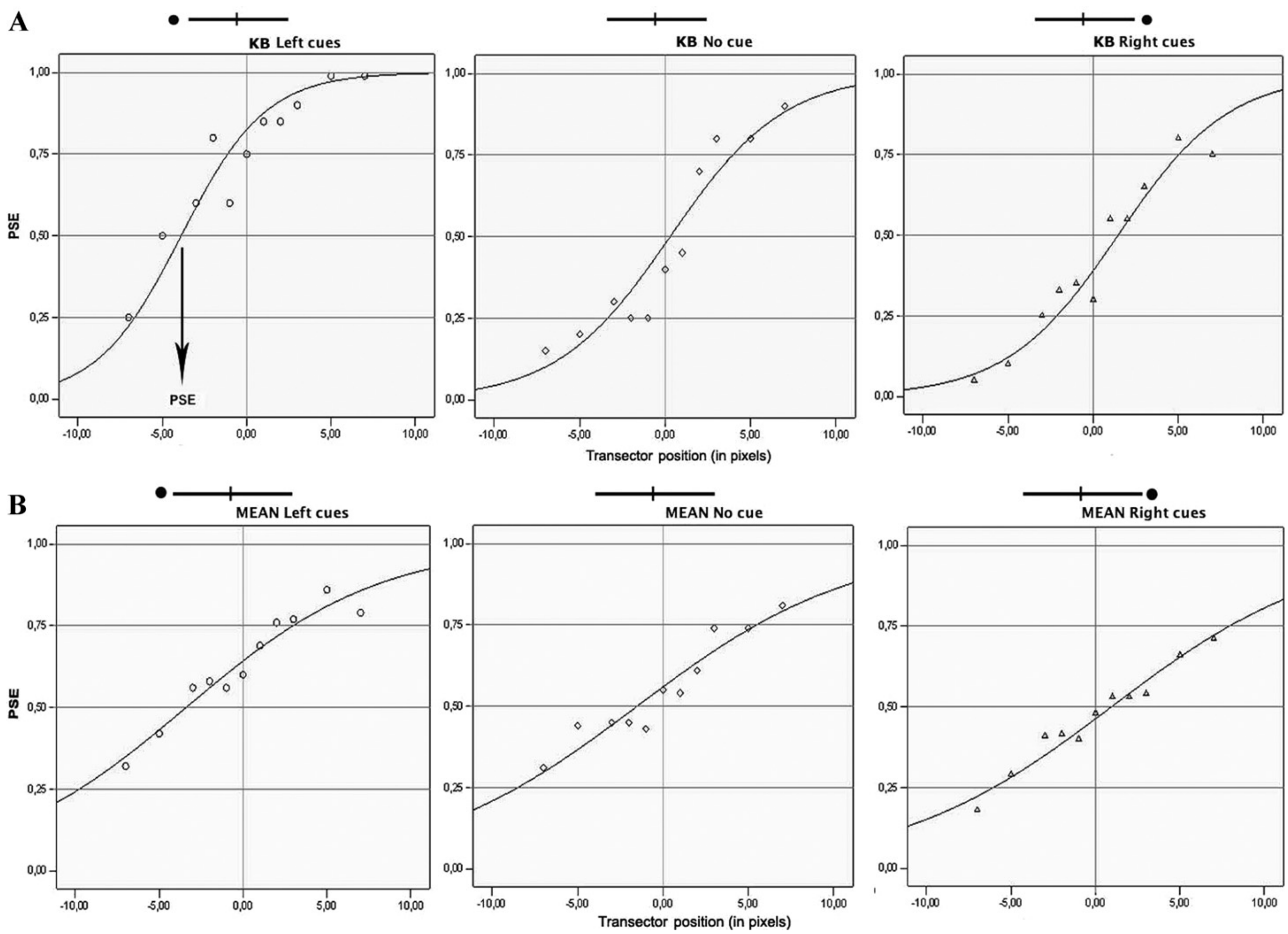

Fig. 4. Experiment 2: A, representative curve fit for one observer based on the proportion of 'seen at right' responses. B, curve fits for mean results of all five observers.

present only at the beginning of the trial for 700 ms, before the sequence started. Then the fixation cross disappeared and the events developed as in Experiment 1. Observers responded from the onset of the bisected line and indicated whether the transector appeared to the right or to the left of the true center of the line. As in the previous experiment, before the test, participants had to complete a training period of 33 practice trials or more as needed.

3.1. Results

The percentage of 'seen-at-right' responses (i.e., when observers judged the transector as being to the right of the true center) was calculated for each of the 11 transector positions. Despite the absence of a fixation point during cue presentation, a repulsion effect was obtained for all five observers. As in Experiment 1, lateral cues shifted the apparent bisection point contralaterally and the magnitude of the effect was larger after left-sided cues than after right-sided cues.

Fig. 4A (one observer) and B (means) shows the same pattern observed in Experiment 1, with the curve in the left-cue condition being shifted towards the left (pattern observed for the individual performances of all five subjects), whereas the curve with right-sided cues is shifted towards the right (as observed for the individual performances of all observers). The curve for the no-cue condition lay in the middle, between the curves obtained for left- and right-sided cues.

The amount of the offset necessary for subjects to see the bisection marker as being at midpoint of the line (see Fig. 3) was 9.79′ to the left of the true midpoint for the left-cue condition; for right-sided cues, the perceived midpoint was again slightly (1.22′) to the right of the true midpoint. A repeated measures ANOVA revealed a significant main effect of the cue position $F(2,4) = 21.74$, $p = 0.0001$. Post-hoc comparisons (Tukey HSD) indicated that the means obtained in the left-cue and right-cue conditions were different ($p = 0.0003$). The no-cue condition differed from both the right-cue ($p = 0.03$) and left-cue ($p = 0.01$) conditions. Without any cue, a line had to be transected 3.92′ left of the true center in order to be perceived in 50% of the time as symmetrically bisected, consistent with the pseudoneglect phenomenon. With left cues subjects needed the transector to be 9.79′ left of the true center in order to perceive the line as symmetrically bisected, with right cues the pattern was reversed, because subjects needed the bisector at 3.91′ right from the true center. Thus, despite the fact that the fixation cross disappeared before cue onset, the results of Experiment 2 were very similar to those of Experiment 1. A further comparison, between observers' performance on the two experiments revealed no significant difference between the means obtained in each condition (ANOVA, all $Fs < 1$).

3.2. Discussion

In Experiment 2 subjects obtained results similar to those of Experiment 1, thus providing clear evidence that despite experimental manipulations like the presence/absence of the fixation point, an ARE still occurs when participants estimate horizontal lengths. If in the Experiment 1 participants did not use the information provided by the fixation cross optimally (as shown by the cue-induced modulation of PSEs), in Experiment 2 that information was not available at all when the cues appeared. The absence of a fixation cross during the perceptual estimation, however, did probably render the task more difficult, as suggested by the greater interindividual variability relative to Experiment 1 (see Fig. 3).

Having thus established that an ARE occurs with pre-bisected lines, we asked whether similar effects would occur by using the typical landmark instructions, that is the comparison of the lengths of the two segments of a pre-bisected line.

4. Experiment 3

In the first two experiments, observers indicated the side of apparent displacement of the transector. On the landmark test used to test neglect patients, however, other types of responses are more usual. For example, observers are typically asked to state which of the two segments appears to be longer or shorter. In the present context it was thus important to see whether the response type changed the pattern of results. In Experiment 3, seven students (four males and three females, aged 22–37 years), all right-handed (mean score, 84.6; SD, 27.2, according to the Edinburgh

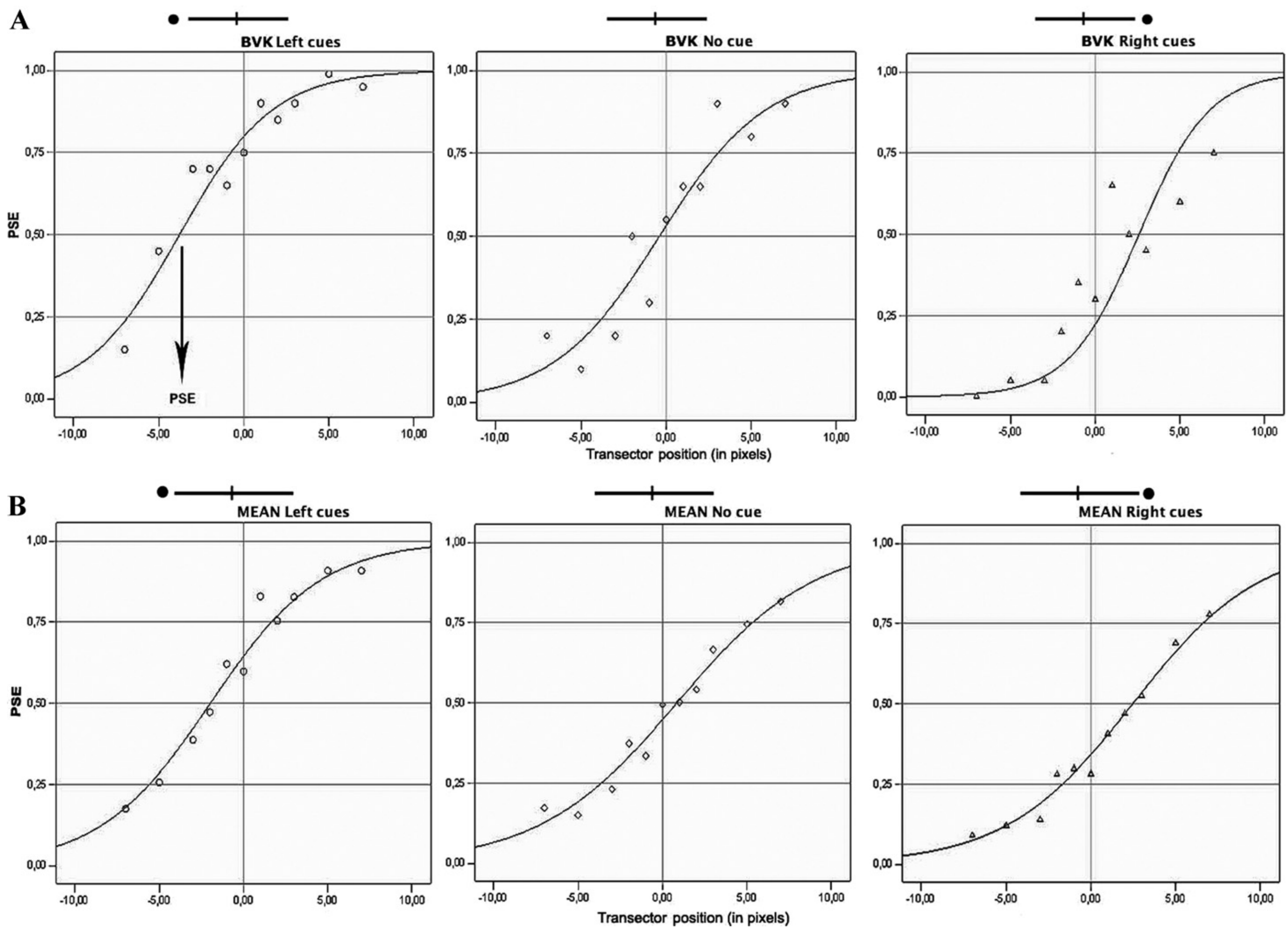

Fig. 5. Experiment 3: A, representative curve fit for one observer based on the proportion of 'seen at right' responses. B, curve fits for mean results of all seven observers.

laterality inventory) stated on each trial which segment (left or right) appeared shorter (four observers) or longer (three observers). In all other respects, Experiment 3 was identical to Experiment 1. As in the two previous experiments, before Experiment 3 participants completed a training period of 33 practice trials or more, as needed.

4.1. Results

The percentage of 'seen-at-right' responses (i.e., when observers considered the longer or shorter segments, depending on the group, as being to the right of the true center) was calculated for each of the 11 transector positions.

We compared subjects' PSEs obtained in the comparison task conditions (long segment versus short segment). Paired t tests did not show any significant difference between results obtained respectively for conditions with left cues ($t(6) = -0.92$, $p = 0.46$), right cues ($t(6) = -1.42$, $p = 0.29$) or no cues ($t(6) = -2.71$, $p = 0.11$). Thus, we merged all these results in one group in order to compare performances with those obtained in Experiment 1, in which subjects simply indicated whether the transector appeared to the right or to the left of the true center of the line.

A repulsion effect was again obtained for all observers, despite some variability in absolute magnitude. As in the previous experiments, right-sided cues shifted the apparent bisection point more to the left than did left-sided cues.

Fig. 5A (one observer) and B (means) shows the same result patterns as the other experiments. The curve for the left-cue condition is shifted further to the left (pattern observed in individual performances of six out of seven subjects), whereas the curve with right-sided cues is shifted further to the right (as observed in individual performances of all observers). The curve for the no-cue condition was in the middle, between the left-cue curve on the left and the right-cue curve on the right (pattern observed in individual performances of six observers).

Fig. 3 shows the amount of the offset necessary for subjects to perceive the bisection marker as being at the midpoint of the horizontal line. For left-sided cues, the mean displacement necessary to see the line as being symmetrically bisected was 5.22′ to the left of the midpoint; for right-sided cues, the perceived midpoint was 5.39′ to the right of the true midpoint. For the no-cue condition, the bisector had to be shifted 1.45′ to the right of the midpoint in order to appear centered. A repeated measures ANOVA revealed a significant main effect of the cue position $F(2,6) = 15.86$, $p = 0.0001$. Post-hoc comparisons (Tukey HSD) indicated a difference between the mean obtained in the left-cue and right-cue conditions ($p = 0.0005$) and between the left-cue and the no-cue conditions ($p = 0.01$). There was no significant difference between the mean obtained in the no-cue condition and right-cue condition. PSEs differed significantly from the true midpoint of the line after left-sided cues $t(6) = 2.29$, $p = 0.05$ and also after right-sided cues, $t(6) = 2.28$, $p = 0.05$, but not in the no-cue condition when subjects were relatively accurate.

In order to assess the effect on performance of task instructions (assess the transector position versus compare the lengths of the left and right line segments), we compared PSEs obtained in Experiments 1 and 3. The ANOVA showed no reliable difference between the means obtained in the left-cue conditions ($F(1,13) = 0.73$) and either the right-cue ($F(1,13) = 3.94$) or the no-cue conditions ($F(1,13) = 2.83$; all *ps* ns).

4.2. Discussion

Experiment 3 demonstrated the ARE phenomenon by using a length comparison task, that is the typical landmark task of the clinical literature (Milner et al., 1993). Despite the change in task instructions, the results were qualitatively similar to those of the previous experiments. In Experiment 3, the effect of right-sided cues was larger relative to the previous experiments. With both left-sided and right-sided cues, observers needed the transector to be shifted significantly towards the ipsilateral endpoint in order to perceive the line as symmetrically bisected. Without any cue, the perceived middle still lay between the two cue conditions, but this time it was situated to the right of the midpoint. This was the only qualitative difference in the results of Experiment 3 relative to the two previous experiments. However, the rightwards deviation failed to reach significance when compared to the true midpoint, and was variable among observers, four of whom obtained PSE values at the left of the true midpoint, as in the two previous experiments.

5. General discussion

5.1. Summary of results

Three experiments assessed the presence, direction and magnitude of the attentional repulsion effect (ARE, Suzuki & Cavanagh, 1997) with pre-bisected lines. Observers perceived the transector of pre-bisected lines as being shifted contralaterally to a peripheral visual cue, consistent with the ARE phenomenon previously demonstrated with vernier offsets (Pratt & Arnott, 2008; Suzuki & Cavanagh, 1997). Cues-induced exogenous attention repelled the perceived location of the bisection marker away from the attentional focus; as a consequence, observers required the mark to be closer to the attentional focus for it to be judged as lying at the midpoint. In the no-cue condition observers often perceived the transector as being situated to the right of its true position, consistent with a relative overestimation of the left-sided line segment (pseudoneglect phenomenon).

Similar effects have been previously obtained with different paradigms (see McCourt et al., 2005, for review and data), but the goal here was to explore these issues with pre-bisected lines similar to those used in the clinical literature. Moreover, we demonstrated for the first time that similar results can be observed with different response type (forced-choice line bisection protocol used in Experiments 1–2 against landmark task instructions used in Experiment 3), despite the fact that attention could be deployed differently in the two cases and the two strategies could use partly distinct brain structures (Fink, Marshall, Weiss, Toni, & Zilles, 2002).

5.2. ARE, spatial attention and neglect

The principal aim of this study was to link attentional phenomena observed in normal participants to the performance of patients with left neglect on line length estimation. Patients with right brain damage and left neglect typically show, among other deficits, a rightward bias in exogenous orienting of spatial attention, with a concomitant deficit in leftward orienting (Bartolomeo & Chokron, 2002).

While attentional deficits can easily explain patients' impaired performance on visual search or response time tasks, their relation to biased length estimation is more controversial. "Attentional magnification" can at least in part account for neglect patients' errors on line bisection and on perceptual judgments made on pre-bisected lines. Patients' magnification of the right side of the line would subjectively elongate this portion and draw the perceived midpoint of the line rightward into the elongated region.[1] Despite several suggestions in this sense, based on performance of both normals (Bultitude & Aimola Davies, 2006; McCourt et al., 2005) and neglect patients (Marshall & Halligan, 1990; Urbanski & Bartolomeo, 2008), there is a relative lack in the literature of convincing demonstrations of the role of spatial attention in tasks actually used with neglect patients, such as line bisection and the landmark task. Thus, "non-attentional" hypotheses have been advanced to explain patients' behavior on these tasks, e.g. the occurrence of a pathological anisometry of spatial coordinates (Bisiach et al., 1996; Savazzi et al., 2007) or of directional hypokinesia, whereby patients would produce hypometric movements towards the left when bisecting horizontal lines (Heilman, Bowers, Coslett, Whelan, & Watson, 1985; Marshall & Halligan, 1995).

The ARE phenomenon is a good candidate to provide a link between length estimation and orienting of spatial attention, because its attentional nature has been convincingly demonstrated. The original study (Suzuki & Cavanagh, 1997) already ruled out alternative interpretations in terms of figural aftereffects or apparent-motion-based illusions. Accounts based on perceptual grouping of lines and cues (Mattingley, Pierson, Bradshaw, Phillips, & Bradshaw, 1993), seem inconsistent with the original observations by Suzuki and Cavanagh (1997) that ARE is similar in magnitude for different cue–vernier distances (2.1°, 4.9° and 7.7°).[2] In addition, to assess more directly the potential effect of perceptual grouping in our paradigm, we collected pilot data with two participants (aged 30 and 31, both scored 100 at the Edinburgh inventory). The experimental parameters were identical to those of Experiment 1, with the exception that cues were presented 2° above the position used in the main experiments, which rendered perceptual grouping less plausible. Results demonstrated an ARE similar to that obtained in the main experiments, with a mean displacements of $6.01'$ to the left of the midpoint for left-sided cues, $1.62'$ to the right of the midpoint for right-sided cues and $2.67'$ to the left of the midpoint for the neutral condition. These results reasonably exclude perceptual grouping effects with the present experimental paradigm.

The repulsion of the midline transector in Experiments 1 and 2 replicates the displacement of the single vernier target in Suzuki and Cavanagh's (1997) original experiment. Suzuki and Cavanagh (1997) described the repulsion as a consequence of attention's influence on the underlying receptive fields, both sharpening their tuning and shifting their centers. The shifting of the receptive field centers toward the cue (Connor et al., 1997; Womelsdorf et al., 2006) would lead to a magnification of space around the cue. This magnification would lead to the stretching in the perceived locations away from the cue lengthening the apparent extent of the nearest portion of the horizontal test and shifting the apparent location of the vertical test away from the cue. Since Suzuki and Cavanagh (1997) presented a single vertical vernier line segment as a test, there was only blank space between the cue and the test. That study could not examine the expansion of any line segment between the cue and the vertical test as we did here.

The present results generalize the ARE phenomenon to stimuli, such as pre-bisected lines, that are directly relevant to the assessment of spatial neglect. Another novel feature of this study is the demonstration of the occurrence of the ARE phenomenon when participants have to judge which segment of the line is longer or shorter, which is the typical response modality for the landmark task in neglect patients. Thus, the present Experiment 3 provides direct evidence that exogenous orienting of attention can manipulate the perception of horizontal lengths when stimuli (pre-bisected lines) and responses (identify the longer/shorter segment) directly mirror those used with neglect patients. This demonstration opens the way to parsimonious interpretations of neglect patients' behavior as resulting, among other deficits, from rightward-biased exogenous orienting of attention. As a consequence, it is unnecessary to stipulate hypotheses based on putative asymmetries of the metrics of spatial representations, such as the anisometry hypothesis, to account for patients' patterns of performance (see Bartolomeo et al., 2004, for similar considerations and further data against the anisometry hypothesis). Concern-

[1] A similar account may apply to the pseudoneglect phenomenon shown by normal subjects, with the additional assumption that the normal right hemisphere specialized for spatial attention would bias normal observers' attention towards the left side of the line (McCourt et al., 2005).

[2] Moreover, pilot data reported by Suzuki and Cavanagh (1997) suggest that for very short distances between cue and target, which in principle should maximize perceptual grouping, attraction can be observed instead of repulsion. This suggests that perceptual grouping might result in attraction instead of ARE.

ing directional hypokinesia, patients' perceptual asymmetries with pre-bisected lines in the absence of hand movements (Milner et al., 1993) already demonstrated that it cannot be the sole determinant of biased line bisection (although it may well contribute to it). Our result that purely perceptual asymmetries with pre-bisected lines can occur as a result of attentional manipulations further substantiates this evidence.

Previous similar results were obtained by McCourt et al. (2005) in two experiments devoted to explore the relationships between changes in perceived length evoked by peripheral cues and by variations in the shape of pre-bisected stimuli. Peripheral cues influenced judgments of length in the sense of an overestimation of the cued segment, consistent with the present results. However, their stimuli (lines, transectors, and cues) differed in a number of ways from stimuli used in clinical tests of neglect. Lines were elongated rectangles or wedges composed of white and black bands, whose intersections constituted the transector. Cues were briefly presented circular cosine functions, which overlapped the subsequent lines. It was thus important to see whether peripheral cues affected the perceived length of stimuli directly relevant to the clinical literature, such as the typical landmark lines used in the present study.

Can processes analogous to the attention magnification that underlies ARE be at work in the lateral bias shown in neglect patients' line bisection? The present research on neurologically healthy participants cannot directly answer to this question, but, as outlined in Section 1, it can at least provide a proof of principle by demonstrating the implication of attentional processes in line bisection. Neglect patients typically show an early orienting bias of attention, which is "magnetically" captured by right-sided items (Gainotti et al., 1991) and remains afterwards, as it were, "stuck" on these items (Bartolomeo & Chokron, 2002; Posner et al., 1984; Rastelli, Funes, Lupiáñez, Duret, & Bartolomeo, 2008). A problem in using the present evidence to interpret neglect behavior is the different time scale in which these phenomena occur: less than 200 ms for the ARE, several seconds for pathological performance on line bisection. This might suggest that different attentional processes are involved. Against this interpretation, we note that unbalanced fronto-parietal networks in neglect, with relative overactivity of left hemisphere networks (Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005; Koch et al., 2008), may induce repeated cycles of rightward orienting, thus sustaining in time attentional magnification of right-sided items. Moreover, the interaction of orienting problems with more general, nonlateralized attentional impairments (Robertson, 2001), which determine a general slowing of attentional operations, might result in the impairment of more sustained forms of attention. If so, rightward bias in line bisection would be the result of a competition between the right and the left parts of the line (Marshall & Halligan, 1990), with the right portion being overestimated (Urbanski & Bartolomeo, 2008), perhaps as a consequence of increased perceptual salience of the right segment of the line (Anderson, 1996; Bultitude & Aimola Davies, 2006).[3]

The present results obtained in normal participants, while being of course neutral about the possible mechanisms of biased line bisection in neglect patients, do demonstrate that exogenous orienting of attention, here manipulated by using peripheral visual cues, plays a role in the subjective length estimation of horizontal lines. In this way, attentional magnification of the cued side of the line suggests a possible basis for neglect patients' behavior. Rightward shifts of the bisection mark would be a consequence of patients' overestimation of the right portion of the line, resulting from their attention being exogenously captured by the right extremity of the line. Abnormal activation of structurally intact fronto-parietal networks related to orienting of spatial attention in left neglect patients (Corbetta et al., 2005) is a plausible neural underpinning of this tendency to right attentional capture. Also ERP and fMRI results in normals indicate that activity in frontoparietal networks in the right hemisphere correlates with perceptual judgments on pre-bisected lines (Fink, Marshall, Weiss, & Zilles, 2001; Foxe, McCourt, & Javitt, 2003). Temporary electrical inactivation of these networks during neurosurgery led to dramatic rightwards deviations on line bisection (Thiebaut de Schotten et al., 2005). The present results add to this accumulating evidence in demonstrating a basic mechanism linking exogenous attention and length estimation. On the other hand, they suggest a plausible attentional basis for patterns of performance sometimes attributed to a distortion of putative spatial coordinates (Bisiach et al., 1996, 1998; Savazzi et al., 2007), thus rendering possible more parsimonious accounts of these phenomena.

5.3. ARE and pseudoneglect

In Experiments 1 and 2, when no cue was presented, the PSE was shifted towards the left, as if observers tended to overestimate the left portion of the line. In a meta-analysis of performance factors in line bisection, Jewell and McCourt (2000) reported the same pattern of results, in which both leftward cues and the no-cue control conditions produced leftward bisection errors relative to rightward cues. Thus, our results are consistent with the pseudoneglect phenomenon (Bowers & Heilman, 1980). Left-sided cues exacerbated this perceptual asymmetry, whereas right-sided cues decreased it. This suggests that right-sided cues countered a left-directed orientation bias, consistent with the hypothesis of an attentional bias toward the left endpoint of the line, perhaps due to a right-hemisphere specialization for spatial attention (Heilman & Van Den Abell, 1980; Mesulam, 1999), and exacerbated by scanning strategies in left-to-right readers (Chokron & Imbert, 1993). Our result, that pseudoneglect can be modulated by exogenous attentional cueing (see McCourt et al., 2005, for previous similar data and review of earlier evidence), further support the hypothesis of an attentional component of this effect.

6. Conclusion

By experimentally manipulating exogenous attention, we biased normal participants' perception of horizontal lengths, in ways consistent with attentional interpretation of neglect patients' biased line bisection behavior and of the pseudoneglect phenomenon. Importantly, and at variance with previous similar studies, our stimuli were the pre-bisected lines typically used in the clinical literature. Moreover, we showed that observers' response pattern did not substantially change with different strategies of response (assessing the transector position versus comparing the segment lengths). The present psychophysical evidence can thus constrain hypotheses concerning the functional locus of origin of important aspects of visual perception in normal subjects and brain-damaged patients.

It will be informative in future studies to test the attentional repulsion effect in neglect patients, taking care to adjust the timing to match the generally slowed attentional processes of these patients. Similarly, studies of illusory line motion (Faubert & Von Grunau, 1995) in neglect patients may also tap the same exogenous components of attention as the ARE. Finally, neuroimaging studies on normal participants might also provide converging evidence for the attentional bases of these phenomena by highlighting the activity of fronto-parietal networks, especially in the right hemisphere.

[3] With stimuli such as inverted Ls, which do not extend into the right hemispace, left underestimation may also contribute to neglect patients' performance (Charras & Lupianez, 2010).

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