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Focused visual attention distorts distance perception away from the attentional locus

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ABSTRACT

Several lines of evidence show that visual perception is altered at the locus of visual attention: detection is faster, performance better and spatial resolution increased. It is however not known whether attention can affect visual perception further away from its locus. In the present study, we specifically question whether and how visual attention influences spatial perception away from its locus, independently from any saccadic preparation. We use a landmark task in which subjects have to estimate the location of a bisection stimulus relative to two landmark stimuli 15° apart, while fixating one of them. This task is combined with a highly demanding discrimination task performed on one of the two landmarks. This allows us to test for the effect of spatial attention allocation on distance perception, as measured by the subject estimation of the landmarks midpoint. We show that the estimated midpoint is displaced towards the attentional locus, both when attention is instructed on the central landmark or on the peripheral landmark. These results suggest an overrepresentation of space around the attentional locus that can affect perception up to 8° away, and question the existence of an objective spatial representation. They are in line with reports of spatial distortion in hemineglect patients while they strikingly contrast with the spatial compression reported around the time of saccadic execution.

1. Introduction

Visual perception is the cognitive function by which information about our visual environment is made available to our consciousness and/or to guide our actions. It arises from a biased analysis of the visual world in which behaviorally relevant and intrinsically salient items are given more weight than other items. This biased analysis is in part achieved thanks to visual attention, a mechanism involving a stimulus-driven or/and a top-down selection of one or several spatial locations for enhanced processing.

Numerous studies on visual attention have demonstrated its strong effect on several aspects of visual perception. For example, an object presented at the locus of attention is detected faster (e.g. Bashinski & Bacharach, 1980; Posner, 1980; Sagi & Julesz, 1986) and better discriminated (Downing, 1988) than elsewhere. Contrast sensitivity is also increased at that location (Carrasco, Penpeci-Talgar, & Eckstein, 2000). It has been shown that attention enhances spatial resolution at its locus (Yeshurun & Carrasco, 1998, 1999) thus affecting the spatial representation locally. However, no indication exists that visual attention can affect perception elsewhere than locally around its locus.

A perceptual phenomenon affecting the whole visual representation has also been described during the execution of saccadic eye movements. Indeed, studies report a compression of space around the endpoint of an instructed eye-movement: flashed objects presented just before, just after, or at the time of the initiation of the eye movement are mislocalized closer to the saccadic endpoint than their actual location (Lappe, Awater, & Krekelberg, 2000; Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997). When several bars are presented close to each other, a percept of only one bar is experienced around the saccadic onset, revealing this compression phenomenon (Morrone et al., 1997; Ross et al., 1997).

Several lines of evidence have shown that visual attention and eye movements are intimately linked. For example, it is easier for subjects to detect a visual object if this object is presented at the endpoint of an imminent saccade (Chelazzi et al., 1995). The discrimination and the identification of a visual object are also facilitated if a saccadic eye movement is programmed towards its location, and spatially dissociating the eye movement endpoint from the discrimination location is nearly impossible (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995). Conversely, saccadic trajectories are deviated away from the location of an expected

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event (e.g. Sheliga, Riggio, & Rizzolatti, 1994; Sheliga, Riggio, Craighero, & Rizzolatti, 1995; though the saccade can also be deviated towards a distractor depending on the experimental conditions, for review see van der Stigchel, Meeter, & Theeuwes, 2006; Walker & McSorley, 2008), indicating an influence of the locus of attention on the ongoing eye movement metrics. At the neurophysiological level, the networks involved in saccades and visual attention are largely overlapping (human fMRI: e.g. Corbetta et al., 1998; Nobre, Gitelman, Dias, & Mesulam, 2000; monkey electrophysiology: e.g. Colby, Duhamel, & Goldberg, 1996; Moore & Amstrong, 2003; Moore & Fallah, 2001; Thompson, Biscoe, & Sato, 2005), thus supporting the premotor theory of attention (Rizzolatti, Riggio, Dascola, & Ulmita, 1987; Rizzolatti, Riggio, & Sheliga, 1994) which proposes that moving the eyes and directing attention in space are supported by the same central structures except for the very final oculomotor steps that control the extra-ocular muscles.

Considering these functional and anatomical links between saccade preparation and attention orientation, it seems reasonable to question the ability of visual attention to alter on its own visual perception and representation away from its locus, in a way similar to what is observed during saccadic compression.

The aim of the present study is to identify the influence of focused attention on the spatial representation *away from the attentional locus*. Subjects had to estimate the location of a flashed object relatively to two reference squares (landmark task). The locus of visual attention was manipulated thanks to a very demanding discrimination task on either of the two reference squares. We show a mislocalization of the flashed object suggesting that the expansion of space induced by a focused spatial attentional allocation has a perceptual effect up to 8° away from the locus of attention.

2. Methods

2.1. Experiment 1: landmark task along the horizontal axis

2.1.1. Subjects

20 subjects (11 males) participated in Experiment 1 (mean age = 23.1 years, range 20–29). All had normal or corrected-to-normal vision, but none was wearing glasses to prevent any disparity in the group concerning visual field dimension and contrast perception. All subjects were naive as to the purpose of the experiment. Our experiment involved a contrast discrimination task (see below). While most subjects had discrimination rates above chance both for central and for peripheral stimuli, one subject failed to correctly perceive the peripheral stimuli during the preliminary stair-case procedure and was excluded from the main experiment. All experimental procedures complied with the requirements of the Ethics Committee of the Université Claude Bernard-Lyon I, and subjects gave their written informed consent.

2.1.2. Experimental setup

Subjects sat in a chair at 32 cm from a 19″ computer monitor. Their head was restrained by a chin rest. Their arms were placed on a table next to a response box equipped with four buttons: up, down, right, and left. Vertical and horizontal eye position was monitored by direct current electro-oculography. Data acquisition, eye monitoring and visual presentation were controlled by a PC running the REX software package (Hays, Richmond, & Optican, 1982). Visual stimuli were presented by a second PC running, Spartacus, a software specifically developed in the laboratory. The REX and Spartacus PCs were connected via a dedicated communication interface.

2.1.3. Stimuli

The central stimuli were 0.65° wide squares (3.7 mm wide, i.e. 13 pixels with screen resolution of 1280 × 768). These stimuli could be of three types: uniform gray squares (mean luminosity of 3.9 cd/m^2); bicolor stimuli with the surround of the same gray as above but with the central 9 × 9 pixels lighter than the peripheral pixels (mean luminosity ranging from 4.3 to 6.4 cd/m^2 depending on the subject, see stair-case procedure below) or darker (mean luminosity ranging from 2.3 to 3.6 cd/m^2 depending on the subject).

The peripheral stimuli were 0.85° wide squares (4.9 mm wide, i.e. 17 pixels). As for the central stimuli, these stimuli could be of three types: uniform gray square and bicolor stimuli with the surround of the same gray as above but with the central 13 × 13 pixels lighter (mean luminosity ranging from 10.3 to 35.3 cd/m^2 depending on the subject) or darker than the peripheral pixels (mean luminosity ranging from 0.4 to 1.1 cd/m^2 depending on the subject).

The bisection stimulus was a 0.45° wide square (2.6 mm wide, i.e. 9 × 9 pixels) of 3.9 cd/m^2 of mean luminosity (see Fig. 1A). *The mask* was a random noise full screen wide stimulus of 13.4 cd/m^2 average luminosity (average luminance contrast of 2.4). *The background* was black (0.02 cd/m^2).

2.1.4. Experimental procedure

Each experimental session began by installing four electrodes around their eyes for an electro-oculography (EOG) eye movement monitoring (two for horizontal and two for vertical monitoring), and by explaining to the subjects the subsequent tasks and the use of the response box. This was done in a semi-dark environment in order to stabilize and reduce drifts in EOG signals (a significant reduction in such drifts could be seen 15–20 min following electrode placement). We then calibrated the offset and the gain of the eye signals. On a subset of three subjects, eye position was monitored using a video eye-tracker (Iscan™, sampling at 120 Hz, spatial resolution <1°).

In all experimental procedures described below, subjects had to fixate the central stimulus all throughout the trial and whenever fixation was disrupted the trial was aborted and presented later. The fixation was monitored both thanks to an eye tolerance window of 2° wide around the fixation stimulus and to an on-line calculation of eye velocity (velocities above 35°/s were considered as saccade initiations and the ongoing trial was aborted). Aborted trials were discarded when calculating the individual subject performance. In a given experimental block, trials were presented pseudorandomly.

Stair-case procedure. Each subject participated in a preliminary experiment aiming at calibrating the luminosity contrast between the surround and the center of the bicolor stimuli so as to determine the contrasts at which subjects achieved an average 80% discrimination performance. Each trial started with the presentation of a uniform gray central stimulus at (0°,0°) and a uniform gray peripheral stimulus at 15° along the horizontal axis, either to the left or to the right of the fixation point (balanced across subjects, see stimuli description above). In a first block, after 900 ms, the inner patch of the central stimulus became either lighter or darker for 80 ms. A full screen mask was then presented for 100 ms. The task of the subject was to orally report whether the inner patch of the central stimulus had become lighter or darker. In a second block, the central stimulus remained uniform and the subjects had to discriminate luminosity changes in the peripheral stimuli. The test order of block types was balanced across subjects. For each block type, a non adaptative stair-case procedure was applied every 20 trials as follows: starting from a 30 cd/m^2 luminosity difference between the center and the periphery of the stimulus to be discriminated (central or peripheral depending on the block type), this luminosity difference was either decreased or increased by 6% (resp. 25%) for the central discrimination blocks (resp. peripheral, see above for precise stimuli description). For each subject, a central and a peripheral bicolor stimulus each inducing an 80% discrimination performance were selected for the main task. The central stimuli had central/peripheral luminosities that ranged from 2.3/6.4 cd/m^2 to 3.6/4.3 cd/m^2. The peripheral stimuli had central/peripheral luminosities that ranged from 0.4/35.3 cd/m^2 to 1.1/10.3. One subject was excluded from the main experiments because he/she was unable to perceive any contrast difference in the periphery.

Main task. 19 subjects performed the main experiment. It consisted in a forced-choice landmark task, in which we manipulated the spatial allocation of attention of the subject by associating it to a contrast discrimination task. In a first block of trials (standard landmark block), there was no discrimination task associated with the landmark task. In a second block of trials (central block), subjects were required to discriminate the change in luminosity of the central stimulus. In a third block of trials (peripheral block), they were required to discriminate the change in luminosity of the peripheral stimulus. The test order of block types was balanced across subjects.

Standard landmark block. The task was essentially a landmark task (see Pohl, 1973 for the original task in the monkey) that proceeded as follows (Fig. 1A): at the beginning of each trial, the landmarks—a central and a peripheral uniform gray stimulus appear at (0°,0°) and at (±15°,0°) on the left or right side of the central point respectively. The subject was required to fixate the central landmark. Nine hundred milliseconds later, the bisection stimulus was presented for 80 ms equiprobably at one of the nine possible positions centered around the objective midpoint between the two landmarks and spaced by 2.6 mm (Fig. 2A) In order to prevent any screen and retinal persistence effects which could provide the subjects with cues while performing the landmark task, the bisection presentation was followed by a 100 ms full-screen mask. In the blocks in which the peripheral landmark was on the right (resp. left) of the central one, the task of the subject was to press the left (resp. right) button if he/she perceived the bisection square closer to the central landmark and on the right (resp. left) button if he/she perceived it closer to the peripheral landmark. Subjects were instructed that precision had priority over speed and had 3000 ms to produce this manual response.

Central block. Here, the landmark task was combined with a central contrast discrimination task. The temporal organization of the trials was similar to that of the standard landmark block trials, except that the presentation of the 80 ms bisection stimulus coincided with a change in *both* landmarks from uniform gray stimuli to bicolor stimuli of higher or lower luminance (pseudorandomly presented such that in a given block, each landmark changed to a higher luminance on 50% of the trials and to a lower luminance on 50% of the trials, see stimuli description above). All stimuli were then replaced by the 100 ms mask. The exact luminance values for the bicolor stimuli were chosen beforehand for each individual subject thanks to the stair-case procedure. The subject was instructed at the beginning of the block that he/she had to attend to the central landmark and that he/she had to provide two successive responses. First, he/she had to indicate whether the central patch became darker (lower button press) or lighter (upper button press). Second, he/she had to report the position of the bisection square with the left/right buttons as described for the *standard landmark block* above. In order to ensure the focus of attention on the attended landmark, the instructions emphasized the importance of being accurate in the discrimination task, over being accurate in the landmark task. As a result, reaction times for the landmark task were non informative and only the left/right responses were used to analyze the subject's perception of the bisection stimulus location.

Peripheral block. Here, the landmark task was combined with a peripheral contrast discrimination task identical to the one described for the *central block*, except for the fact that subjects were instructed to monitor the change in luminosity of the peripheral landmark instead of tracking that of the central landmark.

The standard landmark, central and peripheral blocks were tested both for the right and for the left visual field, resulting in six blocks of testing, the order of which was balanced across subjects (Fig. 1b). At the beginning of each block, the subject was instructed orally of the specific condition he/she was being tested in (block type, visual hemifield) and was reminded of the task he/she had to perform. 80 trials were collected per subject for each block.

2.1.5. Analysis

All analyses were carried out under matlab or R. For each subject, for each specific block configuration and for each possible objective location of the bisection stimulus, we counted the percentage of button presses that indicated that it was closer to the central landmark and the number of button presses that indicated that it was closer to the peripheral landmark. These values served for the individual subject response plots. A sigmoid fit was applied on each set of button press responses as a function of the objective position of the bisection stimulus (Figs. 3 and 4) as follows. The iterative fitting procedure consisted in determining the four parameters $a1$, $a2$, $a3$ and $a4$ that minimized the least square distance between the data and the following equation $a1 + (a2/(1 + \exp(-(x - a3)/a4)))$, where x stands for the objective position of the landmark midpoint. Each experimental block could thus be described by two sigmoid curves, the intersection of which was taken as the subjective midline estimate of the subject. For some subjects, the fitting procedure failed to converge on a given block because of noisy responses (the obtained sigmoid was a flat horizontal line, i.e. the least square distance between the data and the sigmoid equation was minimized for a slope parameter $a4$ equal to 0). These subjects were thus excluded from the specific analysis involving these blocks. All the remaining subjects were retained in the study. In these cases, an F-test comparing the variance explained (4 degrees of freedom) by the sigmoid fit with the residual variance (8 degrees of freedom) yielded a p-value below 0.05 and the visual validation of the fit was always satisfactory.

The performance of each subject on the discrimination task was also calculated in order to assess that attention was correctly allocated to the requested landmark. Note here that the general spatial configuration of the task is such that it was impossible for the subjects to monitor both landmarks at the same time. A specific analysis is presented in the Section 3 to assess whether subjects could orient their attention along a spatial gradient encompassing both the requested landmark and the bisection stimulus.

2.2. Experiment 2: landmark task along the vertical axis

14 subjects (7 males) participated in Experiment 2 (mean age = 22 years, range 20–30). All had normal or corrected-to-normal vision, but none was wearing glasses to prevent any disparity in the group concerning visual field dimension and contrast perception. All subjects were naive as to the purpose of the experiment. Three of them also participated in Experiment 1. The experiment and analysis procedures were exactly the same as in Experiment 1, except that the two peripheral landmarks were located at 15° up or down from the fixation point. The responses on the response box were adapted to this configuration: the subjects were asked to report their estimate of the bisection stimulus position with respect to the landmarks using the up/down buttons and to report the perceived change in luminance in the attended landmark using the left/right buttons. Only the central and peripheral block types were tested (no neutral blocks) and were identical to those described in Experiment 1, except that the peripheral stimulus could be either in the upper visual field or in the lower visual field.

3. Results

In the following, we will focus on how the allocation of spatial attention affects the subject's estimate of the location of a given stimulus with respect to stable landmarks in the visual field.

3.1. The midpoint between two stable landmarks is perceived closer to the fixation point

In the standard landmark task, subjects were required to judge the location of a bisection stimulus with respect to two landmarks constituting the extremities of an imaginary line. One landmark was positioned at the center and the second one at the periphery. We were thus able to measure their subjective midpoint estimate in the absence of any explicit spatial allocation of attention.

All but three subjects consistently perceived the midpoint closer to the fixation point than the peripheral landmark (17/19 subjects in the right hemifield blocks and 18/19 subjects in the left hemifield blocks). An individual example is presented in Fig. 2A. This discrepancy between the objective midpoint and the subjective estimate was small but statistically significant over the subjects group ($p < 0.001$, mean shift of −3.9 mm/−0.55° and −4.3 mm/−0.62° in the left and right hemifields respectively, a negative shift meaning that the midpoint was displaced *towards the center*). These group results are shown in Fig. 3 (SL condition). The major trends reported here did not depend on whether midpoint estimates were expressed in terms of distance projection onto the screen or in terms of visual angle (see Fig. 1C for a description of both measures), the following results will thus be reported only in distance.

3.2. Focusing attention on the fixation point accentuates the overestimation of central space

We then analyzed the effect of focused attention on distance perception along the horizontal axis by combining the landmark task and a hard visual discrimination task at the fixated landmark (central block, see Section 2). The discrimination task was calibrated so as to be very demanding for the subjects forcing them to focus their attention on the fixation point in order to achieve an above chance performance. Average subject performance was equal to 77.9% for the right hemifield block, and to 78.4% for the left hemifield block, i.e. close to the 80% performance selection criteria set during the stair-case calibration procedure for each individual subject (see Section 2). A midpoint could be estimated statistically for all subjects in both hemifield blocks except for one subject for whom the midpoint could not be estimated in the right hemifield configuration (inconsistent noisy responses). The results discussed below are thus obtained from 18 subjects in the right hemifield configuration and 19 subjects in the left hemifield configuration.

Most of the subjects estimated the landmarks midpoint closer to the fixation point when the landmark task was combined with the discrimination task than when it was not (11/18 in the right hemifield, 14/19 in the left hemifield). The response pattern of a representative individual subject is shown on Fig. 2B. This trend is confirmed at the group level (Table 1). The average displacement of the perceived midpoint towards the center as compared to the objective midline in the combined landmark/central discrimination task is of −6.3 mm and −5.7 mm for the left and right hemifields respectively ($p < 0.05$). Focusing attention on the fixation point thus resulted in an additional displacement of the perceived midpoint towards the center (as compared to the subjective midline measured in the simple landmark task) of −2.4 mm and −1.8 mm for the left and right hemifields respectively ($p < 0.05$). These results are presented in Fig. 3 (CD condition, compared to the SL condition).

3.3. Spatial distortion is centered on the locus of attention

Combining the landmark task with a contrast discrimination task at the peripheral landmark allowed us to investigate whether this influence of attention on space perception generalizes to other positions of the visual field. When combined with the landmark task, the peripheral contrast discrimination task proved to be very

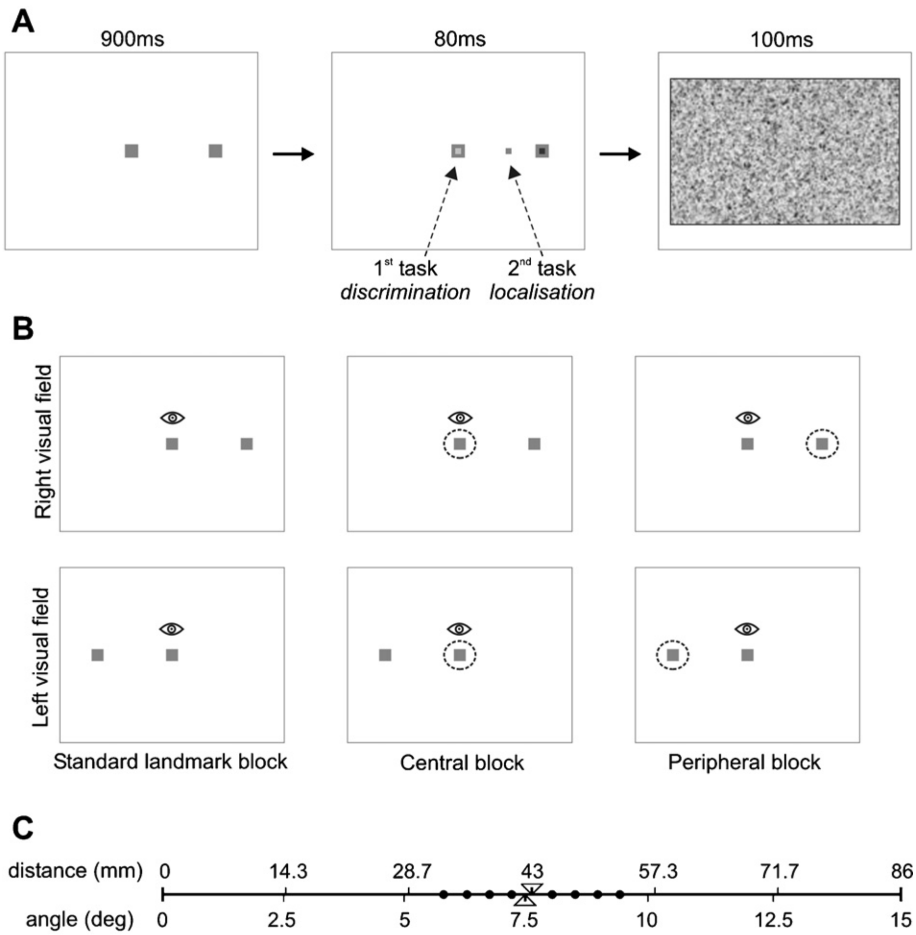

Fig. 1. Experimental design (horizontal configuration). (A) Single trial example of the central discrimination landmark task in the right hemifield. The central and peripheral landmarks are presented for 900 ms. Then, an 80 ms bisection stimulus is presented at the same time as the central most part of the landmarks change luminosity. A 100 ms mask is then presented to prevent persistence effects that could help the subject in performing the task. The subject had first to report if the central landmark became dimmer or lighter than its surrounds, and second to report if the bisection stimulus was located closer to the central or to the peripheral landmark. (B) The six experimental configurations. Fixation is always on the central landmark (eye symbol). During the discrimination landmark task, attention can either be focused on the central or on the peripheral landmark to discriminate, in blocks (dashed circle). (C) Objective midpoint location in distance and visual angle. The fixation point is located at 0 mm along the horizontal axis. The peripheral square is located at 86 mm/15° on the horizontal axis, either on the left or on the right, in blocks. The objective midpoint is slightly different depending on whether it is estimated in flat screen mm or in visual angles. Both possible values are represented by a triangle. During the experiment, the bisection stimulus is presented at nine possible positions centered on the objective landmarks midpoint and spaced by 2.6 mm, as indicated by a filled circle.

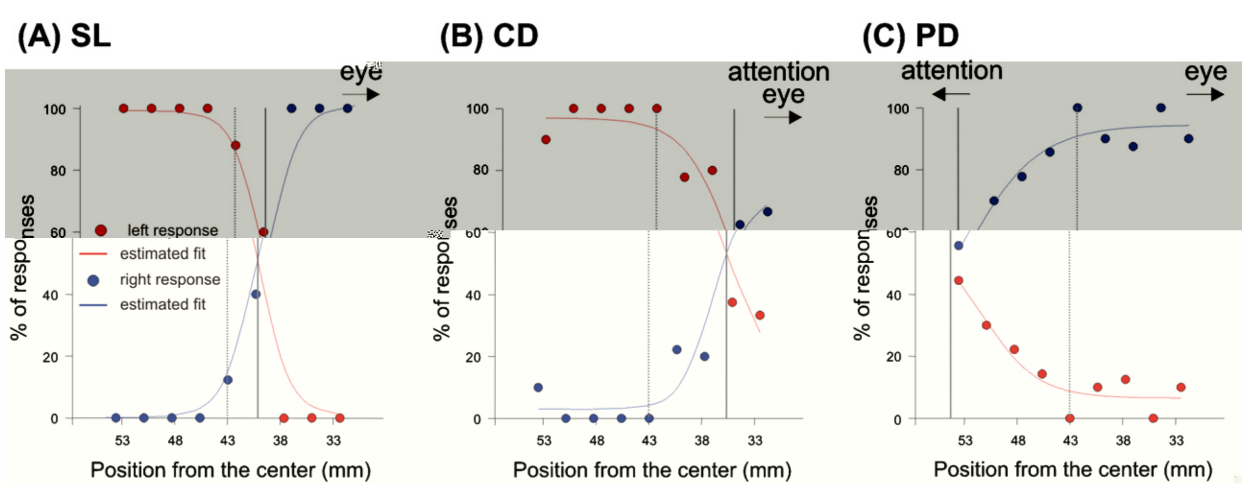

Fig. 2. Single subject example of the effect of fixation and spatial attention on the landmarks midpoint estimation. Percentage of left (red dots, bisection stimulus perceived closer to the periphery) and right button presses (blue dots, bisection stimulus perceived closer to the center) as a function of the location of the bisection stimulus, during a standard landmark task (SL) (A) a central discrimination landmark task (CD) (B), or a peripheral discrimination landmark task (PD) (C) in the left hemifield. The red and blue lines represent the estimated sigmoid fit of the response profiles (see Section 2). The dotted gray line represents the objective landmarks midpoint, the gray line represents the subjective midpoint estimate. The left peripheral landmark is located on the left of the figure at 86 mm, the central landmark on the right at 0 mm. Neither appears on the plots. (For interpretation of the references to color in text, the reader is referred to the web version of the article.)

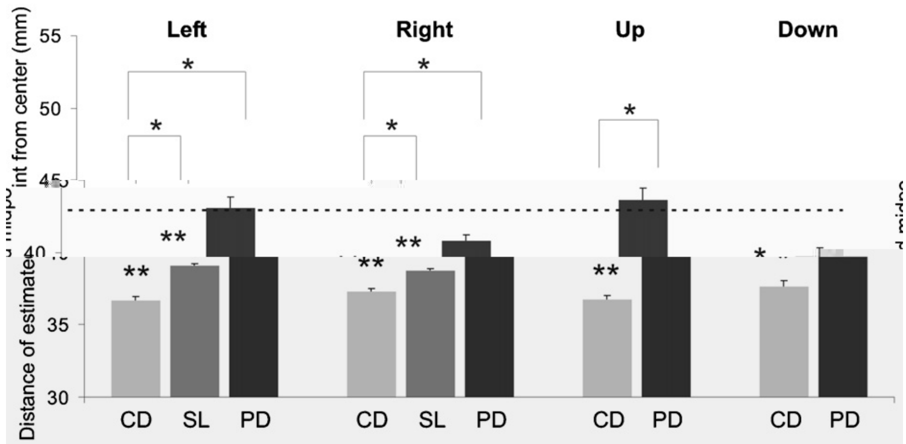

Fig. 3. Effect of fixation and spatial attention on the landmarks midpoint estimation for the groups of subjects. Position of the estimated midpoint in mm for the standard landmark task (SL), the central discrimination landmark task (CD) and the peripheral discrimination landmark task (PD) for the left, right, upper and lower visual fields. The dashed line indicates the location of the objective midpoint between the two landmarks; *t*-tests either between the estimated and objective midpoint locations, or between the estimated midpoints locations in two conditions: $^{**}p < 0.001$, $^{*}p < 0.05$.

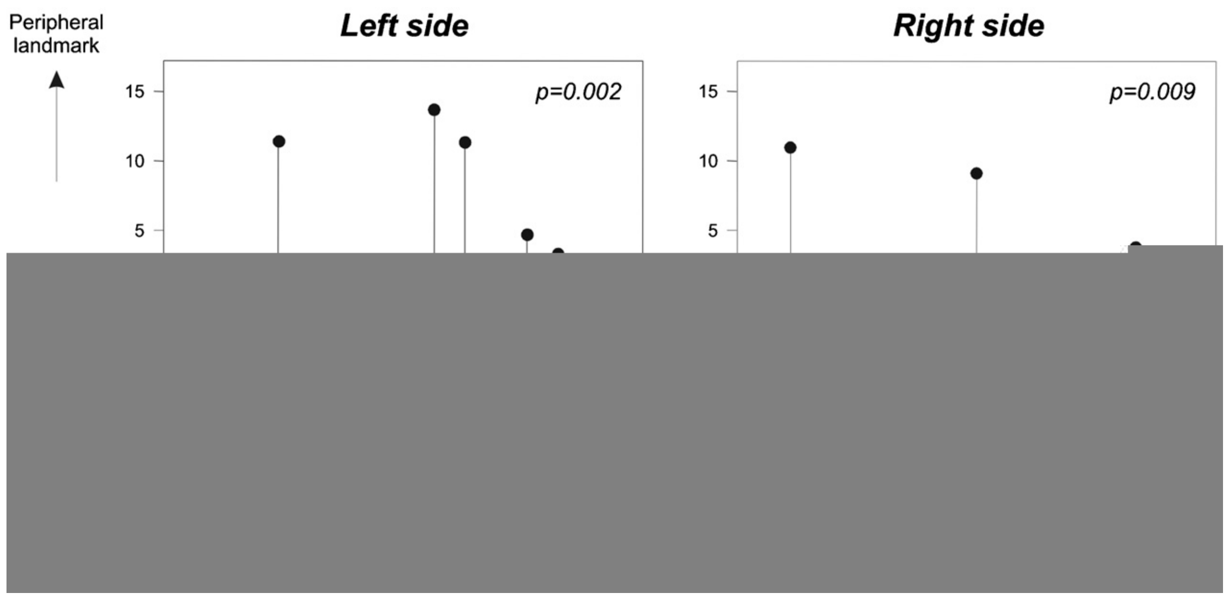

Fig. 4. All subjects effect of the locus of attention on the landmarks midpoint estimation in the horizontal axis. The location of the midpoint estimation relatively to the objective midpoint is represented for all the subjects during the central discrimination landmark task (open circles), during the peripheral discrimination landmark task (black circles) and during the standard landmark task (gray crosses). For each subject showing a trend congruent to the group effect (i.e. a midpoint in the peripheral condition which is estimated closer to the periphery than estimation derived in the central condition), a continuous line joins the midpoints estimates derived for each attentional condition. The *p*-value corresponds to that obtained for a paired *t*-test comparing the location of the perceived midpoint in both attentional conditions.

difficult. Subjects with performance at chance level were excluded from the analysis (three in the left hemifield). Moreover, for three subjects in the left hemifield and four subjects in the right hemifield, it was not possible to statistically estimate the subjective midpoint. For one subject, this estimate followed the group general effect, except that the amplitude of this effect was such that it fell out of the range of the spatial positions tested and could thus not be included in the quantitative analysis (i.e. whatever the position of the bisection, this subject consistently perceived it as closer to the central landmark and only a fraction less so for the most peripheral position of the bisection tested; thus, his/her estimation of the midpoint was strongly biased towards the peripheral landmark

Table 1
Influence of focused central attention on the location of the midpoint estimation.

	Left hemifield ($n = 19$), mean ± std	Right hemifield ($n = 18$), mean ± std
Fixation only (1)	−3.90 ± 2.64	−3.96 ± 3.04
Fixation + attention in the center (2)	−6.31 ± 4.99	−5.73 ± 3.90
Shift (2 − 1)	−2.41 ± 4.07	−1.77 ± 3.38
p-Value	0.021	0.04

Mean ± std location of the perceived landmarks midpoint compared to the objective midpoint, when the landmark task is performed alone (fixation only) and when it is combined with the central discrimination task (fixation + attention) in the left and right hemifields. The results are expressed in mm. A negative value indicates that the perceived midpoint is closer to the center than the objective midpoint. The *p*-value is obtained for a paired *t*-test comparing the midpoint estimation in both conditions.

Table 2
Influence of the locus of attention on distance estimation along the horizontal axis.

	Left hemifield (n = 13), mean ± std	Right hemifield (n = 15), mean ± std
Attention in the center (1)	−6.39 ± 4.47	−5.93 ± 4.27
Attention in the periphery (2)	+0.11 ± 8.40	−2.21 ± 6.05
Shift (2 − 1)	+6.50 ± 5.76	+3.72 ± 4.79
p-Value	0.002	0.009

Mean ± std location of the midpoint estimations compared to the objective midpoint, during the central and peripheral discrimination blocks, in the left and in the right hemifields. The results are expressed in mm. A negative value indicates that the perceived midpoint is closer to the center than the objective midpoint. The p-value is obtained for a paired t-test comparing the midpoint estimation in both conditions.

when his/her attention was focused on the peripheral landmark; however, our sampling for the bisection locations was too narrow around the objective midline to obtain a sigmoid fit of the left and right responses and thus to estimate his/her subjective midpoint in this condition). For the other two subjects, the responses were too noisy and too close to random to allow for the estimation of a midpoint location. The data of 13 and 15 subjects were thus retained for the left and right hemifield analyses respectively. Discrimination performances in these subjects were equal to 77.4% (resp. 77.5%) correct at the center on left blocks (resp. right blocks) and 69.9% (resp. 67.1%) at the periphery. While the peripheral performance is significantly lower than the 80% performance obtained in the calibration procedure (Wilcoxon test $p < 0.05$ for both hemifields), it is not significantly different from the central performance (Wilcoxon test $p > 0.05$) suggesting that the level of attentional engagement was the same on central and on peripheral blocks. When engaged in a double task, subjects can either focus on the required landmark (central or peripheral) or share their attention between the landmark and the bisection stimulus. We hypothesized that if the focus of attention encompassed both stimuli, then performance should be better when the bisection is closer to the landmark than when it is further away (see Section 4). We found no significant effect of the bisection location on the discrimination performance (Kruskal–Wallis, 3 groups of locations close/middle/far consisting of 3 bisection locations each, $p > 0.1$ both for the central and for the peripheral blocks), suggesting that subjects essentially monitored the landmark rather than both the landmark and the bisection.

For most subjects (11/15 in the right hemifield configuration, 13/13 in the left hemifield configuration), the position of the subjective midline was significantly attracted towards the focus of attention, as seen when comparing the midline estimate in central and peripheral blocks. The response profile of an individual subject is presented in Fig. 2C. At the group level, the estimated midpoint was displaced by +6.5 mm (paired t-test, $p = 0.002$) and +3.7 mm ($p = 0.009$) for the left and right visual fields respectively (Table 2; Fig. 3, PD condition compared to CD condition).

The detailed individual results for all subjects are presented in Fig. 4. The amplitude of the midpoint shift varies across subjects, ranging from −2.3 mm to +18.6 mm (i.e. −0.4–3.2°). The eye fixation tolerance window being 2°-wide, this raises the question of

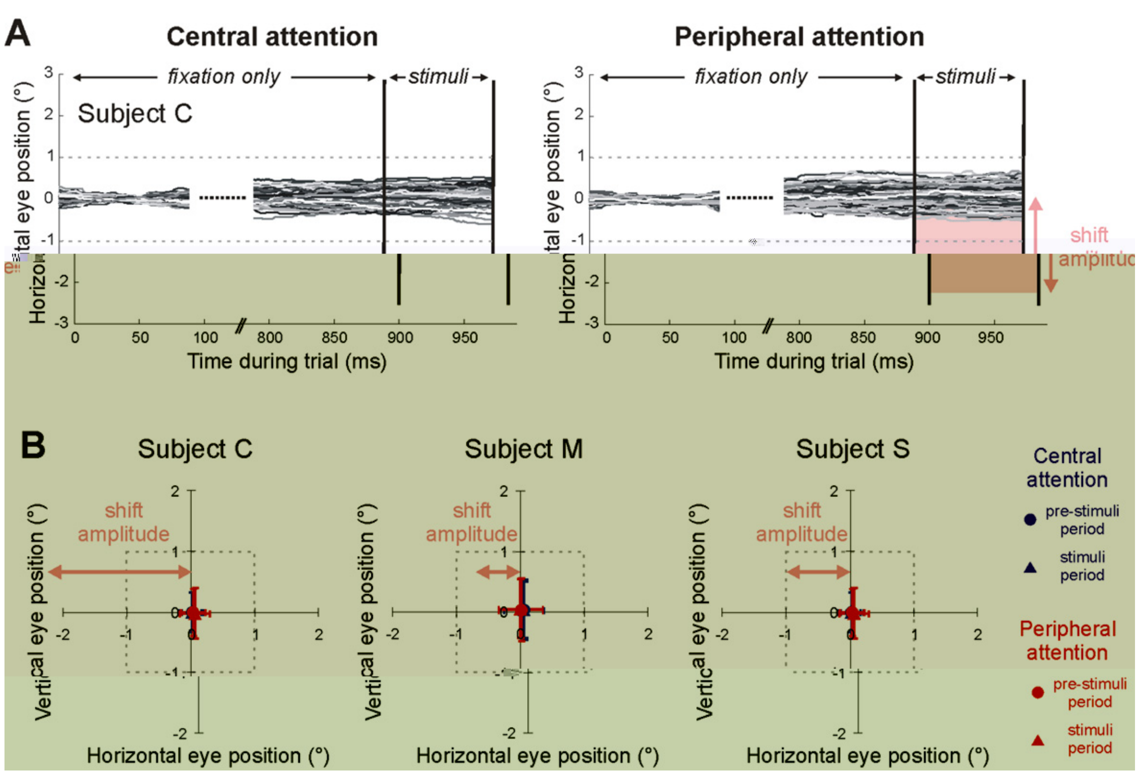

Fig. 5. Eye position during the central and the peripheral attentional tasks in the left hemifield in 3 subjects. A. Horizontal eye traces for all trials are displayed for the central and the peripheral attention landmark tasks performed by subject C. The dashed gray lines correspond to the limits of the fixation window. The pink area depicts the amplitude of the midpoint shift estimate between the peripheral and the central condition. The landmarks and bisection are presented in the left hemifield (towards negative values in°). B. Mean (+std) of average eye position during the pre-stimuli period (circles) and the stimuli presentation period (in which the subjects still had to fixate, triangles), for the central (blue) and peripheral (red) attention conditions. No statistical differences were observed (see Section 3). The pink arrows represent the amplitude of the midpoint shift between the peripheral and the central condition for each of the 3 subjects. The dashed gray box corresponds to the fixation window. (For interpretation of the references to color in text, the reader is referred to the web version of the article.)

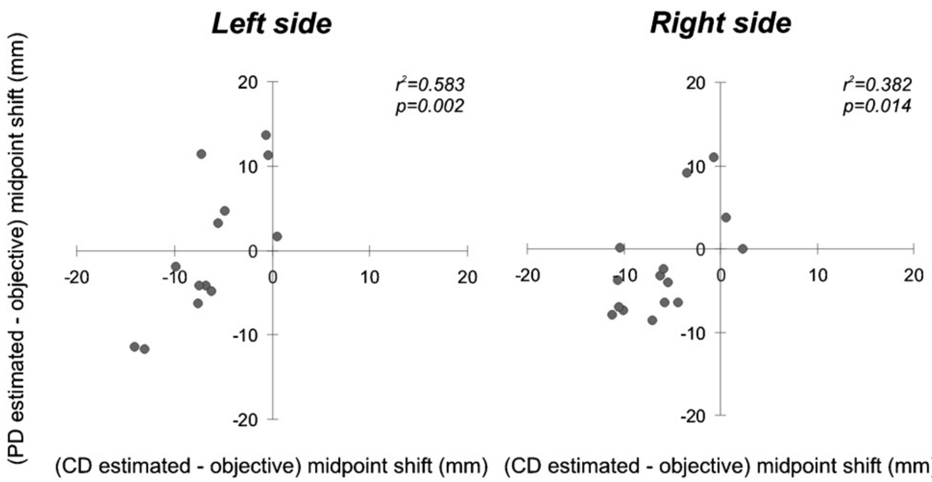

Fig. 6. Correlation between the central and the peripheral attentional landmarks midpoint shifts with respect to the objective midpoint. The shift of the landmarks midpoint estimate with respect to the objective midpoint during a central discrimination landmark task is plotted against the same shift during a peripheral discrimination landmark task for all the individual subjects in both hemifields. The *r*-square and *p*-value of the corresponding linear regression are indicated.

whether part of our effect can be explained by systematic fixation drifts between the central attention and the peripheral attention conditions or microsaccades biased by the attentional state. Our initial setup could monitor the eye position online but did not record the eye traces. To specifically address this question, the eye traces of three additional subjects were thus recorded using a video eye-tracker (Iscan^{TM}) while they were performing the central and peripheral landmark task in the left hemispace. These three subjects reproduced the main trend described in the subjects group, i.e. they estimate the midpoint closer to the peripheral landmark during the peripheral attention condition than during the central attention condition (midpoint shift ranging between 3.4 mm and 12.7 mm). Fig. 5A shows horizontal eye position traces of one of the three subjects for all the trials in both the central and the peripheral attention conditions. An increase in eye trace variability can be noted between fixation onset (time = 0 ms) and later in the task course. However, this latter pattern of eye traces is not affected by test stimuli onset nor by the mask presentation (data not shown). In particular, no saccades and no systematic eye drifts can be observed. Fig. 5B shows the mean eye position during the pre-stimuli presentation and the stimuli presentation periods for the 3 subjects. Interestingly, these means are in the range of 0.01–0.1° and the corresponding standard deviations are below 0.5 degrees. No statistical differences in eye trace positions were observed (1) between the pre-stimuli and the stimuli periods, for either attentional condition; (2) between the pre-stimuli periods of the central and peripheral attention conditions; (3) between the stimuli period of the central and peripheral attention conditions (*t*-tests on the horizontal and vertical eye position, $p > 0.05$ for all the tests). In addition, for each specific subject, the difference in the mean horizontal eye position during the pre-stimuli and the stimuli periods is statistically different from his/her subjective perceptual midline shift ($p < 0.00001$ for all subjects). All this taken together demonstrates that our effect cannot be attributed to systematic drift in eye position due to attentional orientation.

The individual data of Fig. 4 shows that while the midpoint is consistently estimated closer to the fixation point when attention is focused at the center of the visual field than when it is focused at the periphery, these two subjective values do not necessarily lie on each side of the objective landmark midpoint or on each side of the midpoint estimate in the standard landmark task (gray crosses in Fig. 4) as this is the case for the individual subject presented in Fig. 2. This suggests that while distance estimation as probed by the standard bisection task calls on neuronal processes that are preserved across subjects, cognitive operations over space such as attention focusing may be very variable from one subject to another. Nevertheless, several aspects of the data suggest that attentional focusing induces consistent spatial deformations for each subject. Indeed, we observe a significant correlation between the deviation of the subjective midpoint in the central versus peripheral condition, and this whatever the hemifield considered ($p < 0.02$, Fig. 6). Overall, when there is a very large shift of the landmarks midpoint estimate towards the center in the central attention condition, we observe that in the peripheral attention condition, this estimate is drawn towards the center but does not necessarily cross over the objective midline towards the peripheral landmark. On the opposite, when the shift towards the center in the central attention condition is small, we observe that in the peripheral attention condition, the estimate is strongly shifted towards the periphery. This suggests that the distortion of space perception under the influence of attention is submitted to certain common constraints across subjects reflected by a linear relationship. These constraints seem to generalize across the visual field. Indeed, the overall effect of central attention versus peripheral attention on midpoint estimation is significantly correlated across hemifields for the 12 subjects retained on both the right and the left block configurations (Fig. 7). Thus, subjects that show a strong effect of attention on space perception on right blocks also tend to show a strong effect on left blocks, and vice versa. This shows that the amount of distortion introduced by attention varies across subjects, but is consistent across visual space in each subject. No correlation could be observed between the position of the estimated midpoint and the performance in the discrimination task, both for the central and for the peripheral discrimination task. However, as we have not explicitly manipulated task difficulty for a given attentional state, we do not know whether the spatial distortion rules described above vary as a function of task difficulty or not.

3.4. Spatial distortion induced by attentional focus along the vertical axis

14 subjects performed Experiment 2, which is similar to Experiment 1 except for the fact that the different visual stimuli are presented along the vertical axis, and that no standard landmark blocks were tested. Eleven subjects were retained for the upper field configuration (discrimination performance of 78.6% correct in the center attention blocks and 68.1% in the peripheral attention blocks, Wilcoxon test $p > 0.05$) and 10 subjects for the lower field

Table 3
Influence of the locus of attention on distance estimation along the vertical axis.

	Upper field (n = 11), mean ± std	Lower field (n = 10), mean ± std
Attention in the center (1)	−6.25 ± 2.95	−5.39 ± 4.10
Attention in the periphery (2)	+0.60 ± 8.92	−3.27 ± 5.42
Shift (2 − 1)	+6.85 ± 8.49	+2.12 ± 4.41
p-Value	0.023	0.165

Mean ± std location of the midpoint estimations compared to the objective midpoint, during the central and peripheral discrimination tasks, in the upper and in the lower hemifields. The results are expressed in mm. A negative value indicates that the perceived midpoint is closer to the center than the objective midpoint. The p-value is obtained for a paired t-test comparing the midpoint estimation in both conditions.

(discrimination performance of 81.6% correct in the central attention blocks and 71.8% in the peripheral attention blocks, Wilcoxon test $p > 0.05$). As for the Experiment 1, we excluded the subjects that had responses that were too noisy and too close to random and did not allow for a robust estimation of a midpoint location.

For most of the subjects in the upper field blocks (10/11), the estimated midpoint was closer to the periphery when the attention was focused on the peripheral square than when it was focused on the central square. This was also the case in the lower field blocks, but only for 6 of the subjects (6/10). At the group level (Table 3, Fig. 3), a significant effect of the position of attention can be seen in the upper visual field (paired t-test $p = 0.023$) but only a trend is observed for the lower visual field (paired t-test $p = 0.165$). The landmarks midpoint estimate difference between the two attentional conditions is estimated on average at +6.85 mm (resp. +2.12 mm) for the upper hemifield configuration (resp. lower, $p < 0.01$ for the upper visual field configuration).

In order to describe the general effect of the location of attention, we used a mixed effects analysis (performed in R) in which we tested several linear models in order to find the optimal fit to our data. The models respectively considered that the estimated midpoint (1) was constant; or depended on (2) the location of attention (center/periphery); (3) the hemifield tested (left/right/up/down); (4) both the location of attention and the hemifield tested; (5) the location of attention, the hemifield tested and their interaction. In all those models, the location of attention and tested hemifield were fixed factors, and the subjects were used as random factor. The data were best described by the model #2, considering that the estimated midpoint was a linear function of the location of attention (estimate of the effect of location of attention: 0.845 with std 0.184, $t = 4.581$, $p = 1.866 \times 10^{-5}$; estimate of the intercept −1.024 with std 0.164, $t = 6.225$, $p = 2.745 \times 10^{-8}$; across-subjects std of intercept (random factor): 0.466 with confidence interval [0.244,0.887]; std of residual errors 0.904; data expressed in degrees). The effect of location of attention was highly significant (ANOVA between models #2 and #1: $p < 10^{-4}$). There was no effect of the hemifield (models #3 vs. #1: $p = 0.78$; models #4 vs. #2: $p = 0.66$), nor significant interaction with the location of attention ($p > 0.15$ for all the interactions; models #5 vs. #2: $p = 0.33$). Considering the variability of the effect of location of attention on the estimation of the midpoint, displayed for example in Fig. 4, we also tested a model in which this effect was taken as a random factor. This model did not describe our data better (ANOVA with model #2: $p = 0.062$), which suggested that the effect of location of attention was primarily stereotypical although a small subject-dependent effect probably exists (Fig. 4).

These analyses confirmed our previous findings for each hemifield separately: there is a consistent effect of the location of attention on the perception of the midpoint location between the two landmarks.

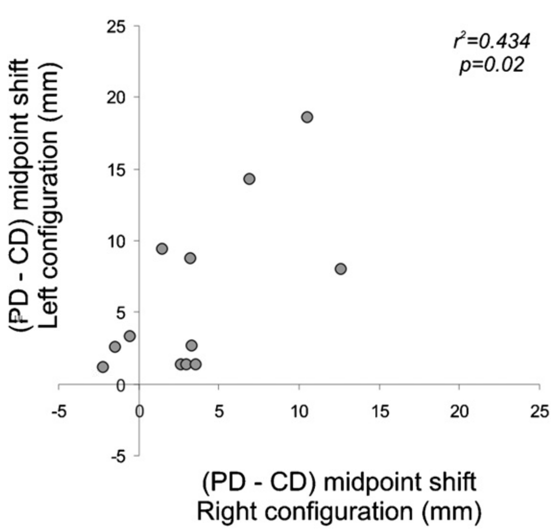

Fig. 7. Correlation between the amplitude of the landmarks midpoint estimate shift between the central and peripheral discrimination landmark tasks in the left and in the right hemifields. The difference in the location of the perceived landmarks midpoint between the peripheral and the central discrimination landmark blocks in the right hemifield is plotted as a function of the corresponding difference obtained in the left hemifield configuration, for the 12 individual subjects available for this comparison. The r-square and p-value of the corresponding linear regression are indicated.

4. Discussion

The present results show that visual attention affects spatial perception and distance estimation *away* from the attentional locus. Indeed, we show that subjects perceive the midpoint of the distance between two landmarks closer to the landmark on which attention is focused. This mislocalization of the midpoint suggests an *expansion* of the spatial representation around the locus of attention that can affect distance perception up to 8° away from it.

4.1. Distance estimation during fixation

In the absence of any attentional load, locking one's eyes on a given position of space affects distance estimation away from the fixation locus. In particular, the midpoint of two landmarks is perceived closer to the fixation point than to the peripheral landmark, whatever the hemifield the bisection is presented in. This suggests an overrepresentation or expansion of space around the fixation point. Our results are very close to those obtained by Nielsen, Intriligator, and Barton (1999) when presenting subjects with prebisected lines during the central fixation of one extremity of the line. Their subjects perceived the midline closer to the fixation point than the actual objective midline by 2–5% of the length of the line for different line lengths (4.5–5% in our experiment). All this taken together suggests that passive fixation induces distortions in the subjective representation of space.

This result is quite new as most of the studies on distance or length representation do not control for eye position and allow for a free exploration of the stimuli (McCourt & Jewell, 1999; McCourt & Olafson, 1997). In addition, subjects are often asked to perform a manual bisection rather than a perceptive judgment (e.g. Bradshaw,

Bradshaw, Nathan, Nettleton, & Wilson, 1986; Nichelli & Rinaldi, 1989). In such experimental conditions, subjects tend to bisect a line or a distance slightly towards the left of the actual midpoint. This phenomenon is called pseudoneglect (for review see Jewell & McCourt, 2000) and is different from our present results as the bias is systematically to the left, whereas the biases we observe here depend on the hemifield the stimuli are presented in.

4.2. Effect of the position of attention

The effect of eye fixation on distance estimation described above could be an artifact of the over-representation of the central space throughout the visual system. Alternatively, it could be due to the fact that in most spontaneous situations, attention is locked on the position on which the eyes are fixating. In order to test the effect of the position of attention, we estimated the midpoint between the two landmarks when attention was focused on one of them. A discrimination task performed on the landmark of reference allowed for an indirect measure of this spatially selective attentional allocation. We find that the estimated midpoint is biased towards the location of attention. These results are consistent with an expansion of the representation of space around the attentional locus and suggest a dynamic deformation of space metrics as a function of attention.

Our results are consistent in the left, right and upper hemifields while only a smaller effect can be observed in the lower visual field. Asymmetries between the upper and lower visual fields have been described in numerous attentional tasks and the lower visual field has been shown to have a higher attentional and/or visual resolution (e.g. He, Cavanagh, & Intriligator, 1996; Intriligator & Cavanagh, 2001; Talgar & Carrasco, 2002). As if to compensate the lower spatial resolution of the upper field, attention has been shown to have a greater effect on discrimination performances in the upper than the lower field (Kristjansson & Sigurdardottir, 2008; Rezec & Dobkins, 2004, but see Talgar & Carrasco, 2002). Our results are consistent with these data as we observe a reduced effect of attention on spatial estimation in the lower than in the upper field.

4.3. Where exactly is attention in the different block types?

We have voluntarily excluded to discuss the difference between the standard landmark blocks and the blocks including the discrimination task. Even if on average the estimated midpoint in the former condition falls between the estimated midpoints in the two attentional conditions, there is no way to know where attention is really directed. It could be focused on the fixation point (but with a lower attentional load than when a discrimination task has to be performed), in the interval between the two landmarks where the bisection will appear, or shifting between the two landmarks in order to optimize performance on the bisection task.

On the central and peripheral discrimination blocks, the discrimination performance provides us with an indirect measure of attentional allocation. The discrimination task has been rendered very demanding such that it could not be achieved without paying attention to the stimuli to be discriminated. Thus, on these types of trials, the locus of attention could have been either (1) large enough to include the bisection stimulus as well as the discrimination locus, (2) divided between both locations, (3) shifting between the two locations or else (4) focused only on the landmark to optimize the discrimination. In order to test for the first alternative, we calculated the discrimination performance as a function of the bisection location, reasoning that, if the attentional locus encompassed both the landmark and the bisection, then performance would decrease when both stimuli were furthest apart (the zoom lens model proposes that visual attention covers more or less space with inverse proportional resolution, Eriksen & St James, 1986). Performance remained constant whatever the bisection position, suggesting that the first alternative does not hold. The second alternative is based on the fact that visual attention can be split between several locations (e.g. Awh & Pashler, 2000; Müller, Malinowski, Gruber, & Hillyard, 2003). However, this split seems to take effect across hemifields, but rarely within a given hemifield, especially when task difficulty is important (Ibos, Duhamel, & Ben Hamed, 2009; Kraft et al., 2005), thus precluding this alternative. Several studies show that attentional displacements can be as short as 50 ms (Ibos et al., 2009; Wolfe, Alvarez, & Horowitz, 2000). The bisection and the discrimination stimuli were presented simultaneously for 80ms. Given the reported attentional shift dynamics, it is quite improbable that both the analysis of the discrimination stimulus and the shift of attention between the landmark and the bisection stimulus could operate sequentially in this 80 ms time window. All this taken together suggests that, on average, attention was specifically oriented towards the discrimination locus before the presentation of the discrimination and bisection stimuli (blocked presentation).

4.4. Relationship with visuospatial neglect

In visuospatial neglect, usually following large lesions of the right parietal cortex, patients tend to ignore objects on the contralesional side of space. One of the most common tests used to quantify neglect is the line bisection test in which patients have to mark the midpoint of a line. They usually consistently mark it on the right of the objective line midpoint. If for some patients this behavior is explained by a motor reluctance to initiate a movement towards the contralesional hemispace (hypokinesia), most of the time, this behavior reflects a perceptual deficit with an attentional and/or representational origin (Milner, Harvey, Roberts, & Forster, 1993). In this context, the mislocalization of the line midpoint can be interpreted as a size or length perception problem. It has for example been shown that the horizontal size of an object has to be increased when presented in the contralesional space in order to appear identical to the isometric object in the ipsilesional space, suggesting either an underestimation of length in the contralesional space, or an overestimation in the ipsilesional space (Irving-Bell, Small, & Cowey, 1999; Milner & Harvey, 1995; Milner, Harvey, & Pritchard, 1998). In reference to the attentional origin of neglect hypothesis, this would mean that the distribution of attentional resources over space influences length perception. Our data are in complete agreement with this proposal as they suggest that an attentional bias towards the ipsilesional side of space results in an expansion of the spatial resolution on that side of space compared to the contralesional space, as reported in neglect patients for length perception. We thus show a direct effect of spatial attention on spatial representation, which means that the theoretical dissociation between attentional and representational neglect might be irrelevant.

Other studies have tried to estimate the effect of attention on size and length perception in the context of understanding visuospatial neglect symptoms. They show that, in normal subjects, attracting attention towards the extremity of the line to bisect (or the pre-bisected line to judge) biases the manual bisection and the perception of the midline towards the cued extremity (Harvey, Pool, Robertson, & Olk, 2000; Milner, Brechmann, & Pagliarini, 1992; Nichelli & Rinaldi, 1989). However, these studies have not precisely controlled for attention both in space and in time. Indeed, subjects were asked to read a letter at the extremity of the line, or mark the extremity of the line, or attend to the experimenter marking the extremity of the line. These tasks are not really demanding and there is no way to know what precise operations are carried out by the subjects when thereafter bisecting or judging the location of the bisection. Moreover, in these studies, subjects were allowed to fixate any region of interest and in particular the line endpoints. We show in our data that fixation has a major influence on spatial perception and we can wonder whether the effects shown in these studies are due to fixation, attention, or both. In contrast, our results clearly show that both these factors contribute to a dynamic representation of space and distance, suggesting that there is no such thing as an objective space but rather that space representation is modulated as a function of the ongoing endogenous or exogenous constraints. The specific rules subserving this dynamics and their functional significance remain to be explored, as well as their alteration in neglect patients.

4.5. Relationship with saccadic compression

The design of our experiment is very different from the design of saccadic compression experiments (Morrone et al., 1997; Ross et al., 1997), preventing any precise comparison. However, two aspects of our results point to differences between the perceptual effects we observe and those described during saccadic compression. First, in the saccadic compression phenomenon, any point in the visual scene is mislocalized towards the saccadic endpoint, resulting in a compression around that point (i.e. the distance between one point and the saccadic endpoint is perceived as smaller) while in our experiment, the perceptual midpoint between the two landmarks is located closer to the attentional locus (i.e. the smaller distance between the perceived midpoint and the locus of attention is considered as equal in length to the longer distance between the perceived midpoint and the unattended landmark) indicating an expansion of space around the attentional locus. Second, the two phenomena are very different in amplitude. Indeed, while during saccadic compression, the mislocalization is estimated between 50 and 90% of saccade amplitude, the spatial effects observed in our experiment are in the range of 4–8% of the distance between the two landmarks. All this taken together suggests that the perceptual effects we observe are subserved by different processes than those at work during saccadic compression.

4.6. Attention-induced spatial representation dynamics and possible neuronal mechanisms

Our results suggest an expansion of the spatial representation around the position of fixation position and the locus of voluntary attention. Within the visual areas, a gradient-like overrepresentation of the central few degrees is observed correlated with the higher density of visual sensors than peripheral sensors on the retina (magnification factor, e.g. Tolhurst & Ling, 1988; Virsu & Rovamo, 1979). Our results concerning the influence of eye location could be explained by this basic neuronal organization.

Spatially focused attention has been shown to improve visual performance (e.g. Bashinski & Bacharach, 1980; Downing, 1988; Posner, 1980; Sagi & Julesz, 1986) and enhance spatial resolution (Yeshurun & Carrasco, 1998). These effects decrease away from the attentional locus, either linearly (Kinsbourne, 1970) or following a Mexican hat spatial rule (e.g. Müller, Mollenhauer, Rösler, & Kleinschmidt, 2005). The extent of space affected around the locus of attention depends on the task and the level of attentional engagement (e.g. LaBerge, 1983). In the present study, we observe a mislocalization of an object located 7–8° away from the locus of attention. This is to our knowledge the first time that an effect of spatial attention is described at such a distance from the locus of attention. The effects reported here can correspond either to a genuine continuous expansion of space around the attentional locus up to several degrees away. Alternatively, they can be due to a more local deformation of the spatial representation around the attentional locus affecting the perceptual judgment of distance between this locus and any other point in space. Testing the extent of the genuine deformation of the spatial representation will be a key element to understand the neuronal processes underlying this phenomenon. In any case, we expect the extent of these attentional spatial effects to depend on the eccentricity of the peripheral attentional locus (15° in the present report) and we predict that the observed mislocalization will be enhanced when attention is placed further away in the periphery.

Attention has been shown to modulate neuronal responses in nearly all visual areas. In particular, it has been shown that neurons have a consistently different response (usually higher) when attention is directed towards their receptive field than away (e.g. Colby et al., 1996). But attention and eye movements do not only affect neuronal discharge rates but can also modify the shape and/or location of the neuronal receptive field. For example, in areas V2, V4 and inferotemporal cortex, when both a target and a distractor are present within the receptive field of the recorded cell, as identified in a passive receptive field visual mapping task, the neuronal response is determined primarily by the response of the neuron to the target presented alone, as if the receptive field had shrunk around the target (Luck, Chelazzi, Hillyard, & Desimone, 1997; Moran & Desimone, 1985). Such a dynamic change in the receptive field profile can account for an increased spatial resolution at the attentional locus. Changes in receptive fields shape and shift of their location have also been observed just before a saccadic eye movement in V4 and parietal area LIP (Ben Hamed, Duhamel, Bremmer, & Graf, 1996; Tolias et al., 2001). In the same line, neurons in area LIP show a more resolutive representation of central space during attentive fixation than during free gaze (Ben Hamed, Duhamel, Bremmer, & Graf, 2002). This neuronal dynamics could correspond to the neuronal substrates of attention-induced spatial representation dynamics during fixation and attentional engagement as suggested by our results. Cumulative human data suggest that the parietal cortex would indeed be involved in the attentional and/or representational mechanisms involved in our experiment (e.g. Chen, Marshall, Weidner, & Fink, 2009). In addition to that, functional imaging shows that the intraparietal sulcus is one of the key structures activated during both perceptual and motor bisection tests (Çiçek, Deouell, & Knight, 2009).

5. Conclusions

We show that both fixation and spatial allocation of attention bias the estimation of distance and localization of visual objects. Our results suggest that the spatial representation of the visual scene is expanded around the eye location and the attentional locus. Thus our representation of the external world seems to be dynamically biased by voluntary top-down attention and fixation. This questions the existence of an internal stable subject-free representation of space approaching the outside objective space.

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