Simulating unilateral neglect in normals using prism adaptation: implications for theory

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Abstract

Rightward deviation on line bisection is considered one of the most classic clinical signs of unilateral visual neglect—a cognitive disorder of spatial processing that commonly follows right brain damage. Recently, short-term adaptation to wedge prisms has been shown to significantly reduce neglect on this and other conventional diagnostic tasks. Our previous study has shown that visuomotor adaptation in normals produces a similar pattern of directional bias on a line bisection task. Based on the good working knowledge of how neglect patients perform on different versions of the standard diagnostic task, we showed here that using leftward-deviating prisms in normals, it is possible to produce: (1) a reliable bias on line bisection, (2) a rightward specific deviation, (3) a modulation of rightward deviation, which depends on the relative spatial location of the target lines and (4) a line length effect. A final experiment confirmed that these after-effects are specific to prism adaptation rather than passive prism exposure. Collectively, these findings confirm that adaptation to left-deviating prisms in normals produces a reliable right-sided bias and as shown by a previous visuospatial judgement task, these findings cannot be adequately explained by the symmetric sensori–motor effects of prism adaptation. Taken together with the improvement of spatial neglect shown by right-deviating prisms only, the present study suggests that low level sensori–motor adaptations play a greater role in right hemisphere organisation for spatial cognition than previously thought.
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Keywords: Prism adaptation; Spatial neglect; Bisection; Space representation; Plasticity; Visuomotor

1. Introduction

Unilateral neglect is a well-established neuropsychological disorder that comprises a family of lateralised symptoms that commonly follow unilateral (right) brain damage [15]. Despite the recent proliferation of dissociations, two common features have been used to unify this heterogeneous condition. First, much of the clinical evidence supports a hemispheric asymmetry for neuropsychological processes mediating spatial cognition; neglect after right hemisphere lesions is more frequent, long lasting, and severe than after equivalent lesions of the left hemisphere and typically produce rightward deviation and hence "left neglect" on a variety of simple diagnostic measures [12,58].

The second feature concerns the level of neuropsychological processing where the disorder takes place. The standard definition of neglect since the 1970s is unambiguous in maintaining that the disorder cannot be "attributed to either sensori or motor defects" [15]. From a neuropsychological perspective, it is now generally accepted that neglect is a heterogeneous disorder whose different symptoms can be explained in terms of damage to (at least) one of three different cognitive mechanisms mediating *attention* (e.g. [14]), *intention* [59] and/or space *representation* [3]. Recently, however, evidence that various symptoms of visual neglect can be improved following short adaptation periods to a 10° right prismatic shift of the visual field [50,51] has begun to challenge the traditional distinction in the standard clinical definition between low level sensori–motor deficits and those assumed to involve higher level/cognitive systems.

Prism adaptation consists of active pointing to visual targets while the subject wears prismatic goggles that deviate the visual field unilaterally. The prisms produce a visuo-proprioceptive conflict which initially (a) induces a

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pointing error in the same direction as the optical deviation (i.e. right-shifting prisms initially induce a rightward pointing error). However, after several pointing trials, subjects (b) adapt their pointing responses and pointing errors gradually disappear. The after-effects of such adaptation, (c) in normal subjects, are well established as quantitative measures of the adaptation (see [60]) and have been traditionally described as recruiting low level sensori–motor systems (e.g. [43]). These after-effects compensate for the visuo-proprioceptive discrepancy introduced by the prisms. These sensori–motor after-effects typically last for a brief time period [23] of

usually no more than the exposure period since the normal system de-adapts or re-adapts just as rapidly when movements are permitted under normal vision. Although varying the cognitive load on these tasks has been shown to interfere with prism [41,42] or visuomotor [18] adaptation, the converse (producing significant after-effects on cognitive tasks following adaptation in patients or healthy individuals) had not been documented until recently [50].

The perceived midline (evaluated by manual demonstration) of neglect patients can be shifted to the left following adaptation to prisms [50]. In addition, several standard
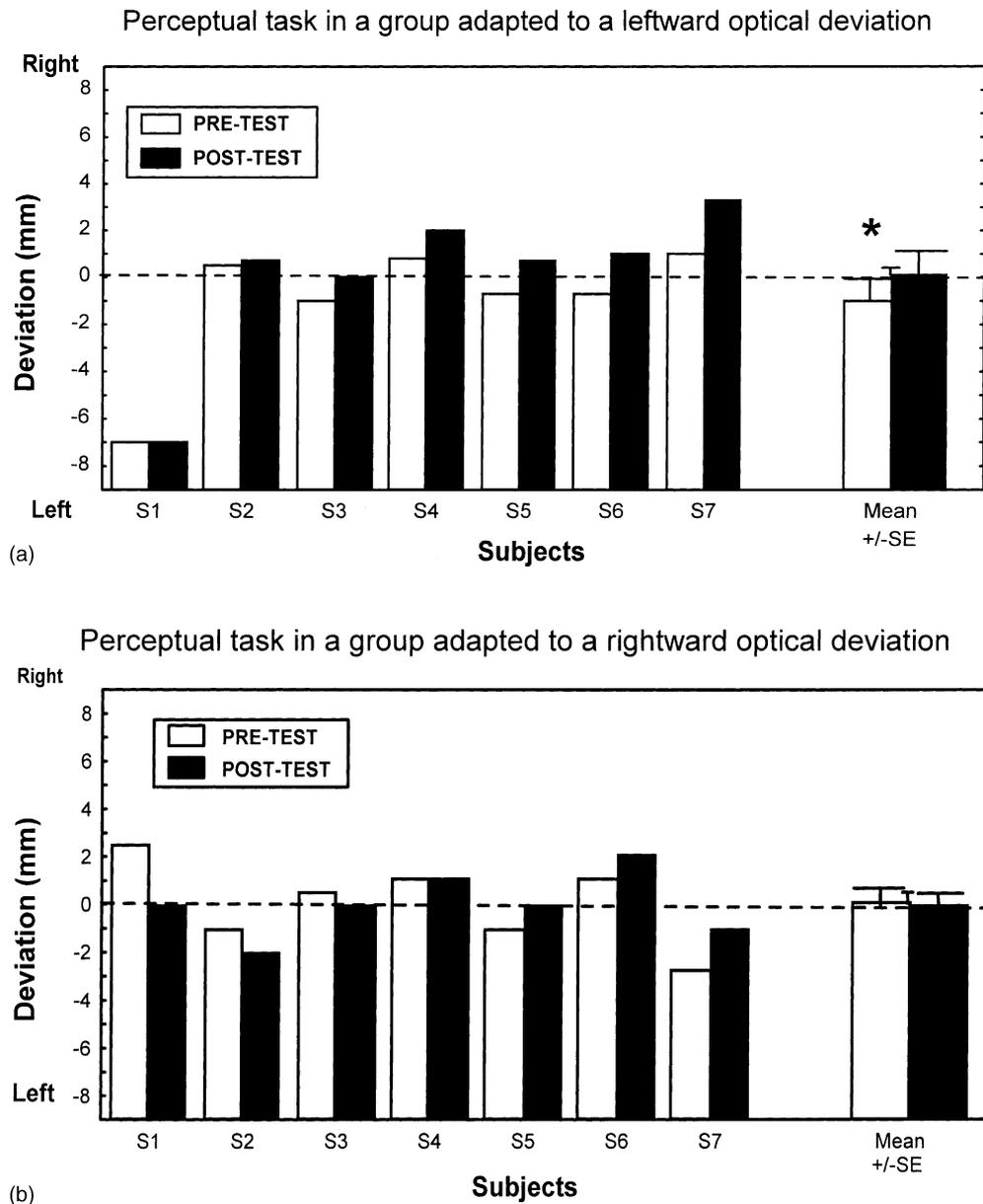

Fig. 1. Results observed in perceptual line bisection task in our previous work (redrawn from [7]). The results are presented in increasing size of the after-effect (difference between performances obtained in post- and pre-test). Variability of the effect of prism adaptation is shown by the small standard error bar between the mean group values for pre- and post-tests. (a) Perceptual estimation of the line centre in the group adapted to a leftward visual shift. A significant rightward shift of the estimation of the centre of lines was observed ($P < 0.02$). (b) On the contrary, no significant bias was observed in the group adapted to a rightward deviation ($P > 0.9$).

neuropsychological tests showed beneficial and reliable effects including line bisection, copying a simple drawing, drawing of a daisy from memory and reading. In some patients, this corrective effect was found to last up to several days [32,40,51] (review: [49]). Subsequently, it was shown that prism adaptation could produce a similar beneficial effect on tasks that depended on effectors other than the exposed hand (body posture: [57]) or solely on higher levels of spatial representation (mental representation: [47]). Hence, in contrast to the standard definition of neglect, simple prism adaptation (involving low level sensori–motor processes) modulated visuospatial neglect performance in a directionally specific way on many of the established clinical tests thought to assess the effects of damage to high level spatial cognition. Collectively, these findings question the assumption that only higher level cognitive disorders (e.g. attention, intention and/or representational) are involved in producing the characteristic clinical picture of unilateral neglect. Moreover, they suggest that left neglect after right hemisphere damage may result from an interaction of sensori–motor changes and higher cognitive processes [51]. There are many varied lateralised systems in the brain that can interact in the detection and exploration of "ambient changes in the environment" [22]. Consequently, it is possible that some of the spatial features of unilateral neglect following right damage might be determined by intrinsic low level neural organisational features specific to the right hemisphere. To establish this hypothesis it is necessary to show that post-pathology activation by prism adaptation can modulate neglect performance (1) beneficially, (2) for a temporally extended period of time and (3) more importantly demonstrate qualitatively similar transient disturbance in normals. The purpose of the present study relates to the latter of these objectives namely to extend previous findings [7] by using prism adaptation to further demonstrate the qualitative effects on line bisection.

Line bisection, a spatial judgement task that requires subjects to indicate the centre of a line is one of several traditional clinical tests commonly used to diagnose and define visual neglect [3,11]. The test has the advantage of being simple, quantitative, and reproducible [12,13]. At present two main versions of the test are currently used [35]: a manual version, in which subjects place a mark at the centre of a horizontal line and a perceptual judgement version (Landmark test), where subjects are simply requested to judge whether a line has been transected to the left or the right of its true centre. Both were employed in the current study to control for the possible independent effects of prisms on motor and perceptual aspects of task performance.

Two main aims were followed in the present series of experiments:

First, to replicate the directional bias previously observed in normals (Fig. 1) [7] on a line bisection task and then establish whether two further well-established clinical features of clinical line bisection/judgement performance could also be observed: (a) the position effect; (b) the length effect. In accordance with the position effect, the extent of the rightward bias for bisection in neglect patients is greatest when lines are presented to the left of the subject's midline, moderate for lines presented straight-ahead and is substantially reduced for lines presented to the right of the subject's midline. In accordance with the length effect, for lines presented straight-ahead, the extent of the rightward bias remains a function of line length (e.g. [36]). In addition, we tested whether the directional bias observed after prism exposure on line bisection is specific to the adaptation caused by the active pointing compared to a condition of "passive" exposure to prisms. The prediction is that only the former would produce a directional bias if the cognitive effects are dependent on the adaptation to prisms.

Second, simulating the characteristics of neglect-like symptoms in healthy individuals following prism adaptation would provide a tool to explore the interaction between low level sensori–motor processes and spatial cognition. Further, our study allows us to discuss the significance of these and other recent findings for understanding the neuropsychological mechanisms of the neglect syndrome.

2. Experiment 1

In Experiment 1, we explored whether the extent of the spatial bias following prism adaptation varies with the relative hemispatial location of the lines. In patients with neglect, the rightward bias for estimating the centre of horizontal lines strongly depends on the spatial location of the stimuli, e.g. the typical rightward bias is greater when lines are located to the left of the patient's midline [12]. According to our previous results [7], we should observe a rightward bias in the estimation of the centre of the line after prism adaptation. If this rightward bias is explained by sensori–motor after-effects of prism adaptation, it would be observed: (1) for the same absolute amplitude independent from the spatial location of the line, as it is known that adaptation after-effects generalise linearly over space [2] and (2) not for the perceptual bisection (i.e. relative coding), as it is known that wedge prisms affect absolute location but not relative location coding [44]. By contrast, if the rightward bias can be assimilated to a neglect-like symptom, (1) it would mainly be observed in the perceptual bisection task [13] and (2) it should increase from right- to left-sided locations.

2.1. Method

2.1.1. Subjects
Ten right-handed and normal-sighted healthy subjects participated in this experiment (three females, seven males; age: 24–46 years (mean = 30.3 years; S.E. = 3.2 years)).

2.1.2. Materials
For the manual bisection task, 18 black lines of 250 mm length and 1 mm width were presented one by one on A3

sheets. The set of lines was randomly distributed across three spatial locations (left, right and central to the subject's midline). For the perceptual line bisection task, a total of 105 pre-transected 250 mm lines (bisected accurately or at 2, 4 or 6 mm to the right or to the left of the true centre) were used.

2.1.3. Procedure

Subjects were seated at a table, facing the experimenter. In the manual bisection task, subjects performed 18 trials in which they were given a pencil and asked to place a mark on the centre of each line presented by the experimenter. Special attention was paid to the subjects' movements in order to avoid contamination from the sensori–motor control involved in pointing movements (i.e. from sensori–motor after-effects): arm movement amplitude was kept as short as possible and slowness of the hand movement was imposed (see Fig. 4a). During the perceptual task, subjects were requested to judge (forced-choice) whether pre-transected lines were bisected to the left or to the right of their centre. Following the pre-tests, subjects underwent the prism adaptation procedure as in [7]. They wore prismatic goggles producing a 15° leftward visual shift of the visual field. They performed a simple pointing task to visual targets for 20 min. Subjects were asked to point to each of the 10 visual targets as fast as possible. Vision of the starting position of the hand was occluded to ensure the optimal development of the adaptation [45]. After removal of the goggles the post-tests were performed. Effective development of the adaptation (to assess sensori–motor after-effects) was checked with an "open-loop" pointing task in which subjects could not see their hand. The same experimental procedure was used as during the pre-test. Subjects were asked to keep their eyes closed between each trial in order to slow down the de-adaptation process. In perceptual and manual line bisection tasks, the location of lines (left, right or centre) were randomly presented in front of the subject's body midline or 33 cm to the right or to the left of the body midline. In the central position, the viewing distance was approximately 45 cm.

2.1.4. Data analysis

Evidence of sensori–motor after-effects—assessed on an open-loop pointing task—were considered present if subjects produced systematic pointing errors. As per tradition, negative values were attributed to leftward errors and positive values to rightward errors. For the manual bisection task, the subjective centre of each line was measured to the nearest millimetre. For the perceptual bisection task (or Landmark) a simple convergence method was used to illustrate the results. The point of equiprobability of 'left' and 'right' responses provided a measure of the subjective centre of the line (the spatial definition of this method was 0.1 mm; Fig. 2). In pre-test, a repeated measure ANOVA was used to test the effect of location on the manual and perceptual bisection tasks. A two-way repeated measure

ANOVA was used with test Period (pre versus post) and line Location (left, centre or right) as factors.

2.2. Results

2.2.1. Sensori–motor after-effects: open-loop pointing task

Rightward sensori–motor after-effects were reliably induced by prism adaptation. The open-loop pointing performances showed a significant rightward shift (mean $\pm$ S.E. $= 13.2° \pm 1.5°$) between the post-test ($12.4° \pm 1.5°$) and the pre-test ($-0.8° \pm 1.0°$) ($F(1; 9) = 55.43$; $P < 0.001$).

2.2.2. Manual bisection task

As in previous studies, repeated measure ANOVA demonstrated a significant effect of spatial location in the pre-test. The manual estimation of the centre of lines was -0.6 mm (mean) ± 0.9 mm (S.E.) for the left-sided lines (lines presented left of the body midline), 0.1 mm (± 0.7 mm) for central lines (lines presented centre of the body midline) and 4.6 mm (± 1.1 mm) for the right-sided lines (lines presented right of the body midline; $F(2; 18) = 11.62$; $P < 0.001$). The two-way ANOVA revealed a main effect of adaptation with the manual estimation of the centre of lines being shifted to the right after prism adaptation ($F(1; 9) = 21.41$; $P < 0.002$). Furthermore, a significant location effect was observed ($F(2; 18) = 9.42$; $P < 0.002$), such that the rightward bias was greater for lines presented to the right side of the subject. The interaction between adaptation and location was not significant ($F(2; 18) = 2.00$; $P > 0.15$). However, as indicated in Fig. 3a, a contrast analysis performed to assess the effects of prism adaptation for the right-sided location was far from significance ($F(1; 9) = 0.002$; $P > 0.96$). Taken together with the adaptation main effect, the effects of prism adaptation on the manual line bisection therefore depend on spatial location. The rightward shift of the manual estimation was 2.1 mm ± 0.9 mm (pre-test: -0.6 mm ± 0.9 mm; post-test: 1.5 mm ± 1.1 mm) for left-sided lines, 2.1 mm ± 0.6 mm (pre-test: 0.1 mm ± 0.7 mm; post-test: 2.2 mm ± 0.6 mm) for central lines and 0.0 mm ± 0.67 mm (pre-test: 4.6 mm ± 1.06 mm; post-test: 4.6 mm ± 0.93 mm) for right-sided lines.

2.2.3. Perceptual bisection task

In pre-test the repeated measure ANOVA did not show any effect of spatial location on performance. The two-way ANOVA revealed only an effect of adaptation ($F(1; 9) = 8.54$; $P < 0.02$) indicating that the perceptual estimation of the centre of lines was shifted to the right after prism adaptation. The results obtained in pre-test and post-test for each location are presented in Fig. 3b. The rightward shift of the perceptual estimation of the centre of lines decreased from left- to right-sided lines: 1.0 mm ± 0.4 mm (pre-test: 0.0 mm ± 1.1 mm; post-test: 1.0 mm ± 1.1 mm) for the left-sided lines, 0.7 mm ± 0.3 mm (pre-test: -0.3 mm ± 0.3 mm; post-test: 0.3 mm ± 0.5 mm) for the central lines and -0.00 mm ± 0.42 mm (pre-test: 0.6 mm ± 0.51 mm;
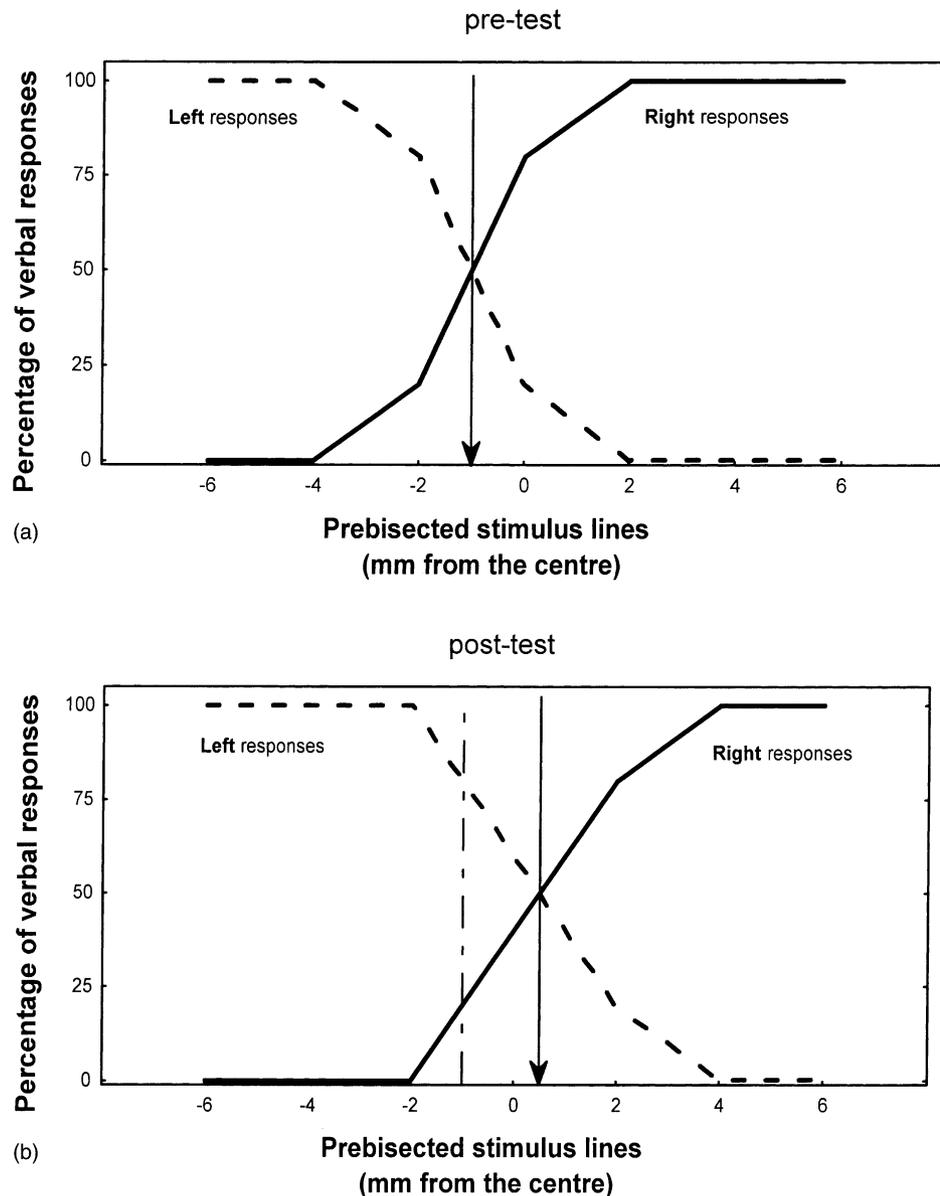
pre-test

(a)

post-test

(b)

Fig. 2. Graphic illustration of the method used to determine the subjective centre in perceptual bisection. (a) Pre-test: the same method is used for each subject. This graph presents the percentage of 'Right' and 'Left' verbal responses obtained for each mark deviation from the objective centre on pre-bisected lines (perceptual stimulus), in the central position, for one typical subject participating in Experiment 1. The dotted line represents the percentage of left responses and the continuous line illustrates the percentage of right responses. The converging point of the two lines, where the percentage of right responses is equal to left responses, indicates the subjective centre. For this subject, the perceptual centre is located on the left of the true centre. (b) Post-test: after adaptation to a leftward optical deviation the perceptual centre of the same subject is shifted by 1.5 mm to the right.

post-test: $0.6 \, \text{mm} \pm 0.60 \, \text{mm}$) for the right-sided lines. However, no significant effect of spatial location ($F(2; 18) = 0.18$; $P > 0.81$) and no significant interaction between adaptation and spatial location ($F(2; 18) = 1.75$; $P > 0.20$) was found. As for the manual bisection, a contrast analysis performed to assess the effects of prism adaptation for the right-sided location was far from significance ($F(1; 9) = 0.0001$; $P > 0.99$). Considered with the adaptation main effect, this shows that the effects of prism adaptation on the perceptual bisection also depend on spatial location as indicated in Fig. 3b.

2.3. Discussion

The results of this experiment show that after prism adaptation a significant rightward shift is observed both in manual and in perceptual bisection tasks but not for right-sided lines. These effects cannot be directly explained by simple after-effects of prism adaptation, known to generalise homogeneously over space [2]. It may be the case that enlarging the workspace used in the task (i.e. because three locations were used) influenced the current results by virtue of two possible mechanisms. First, there was an increase of the

Manual task for three line locations

(a)

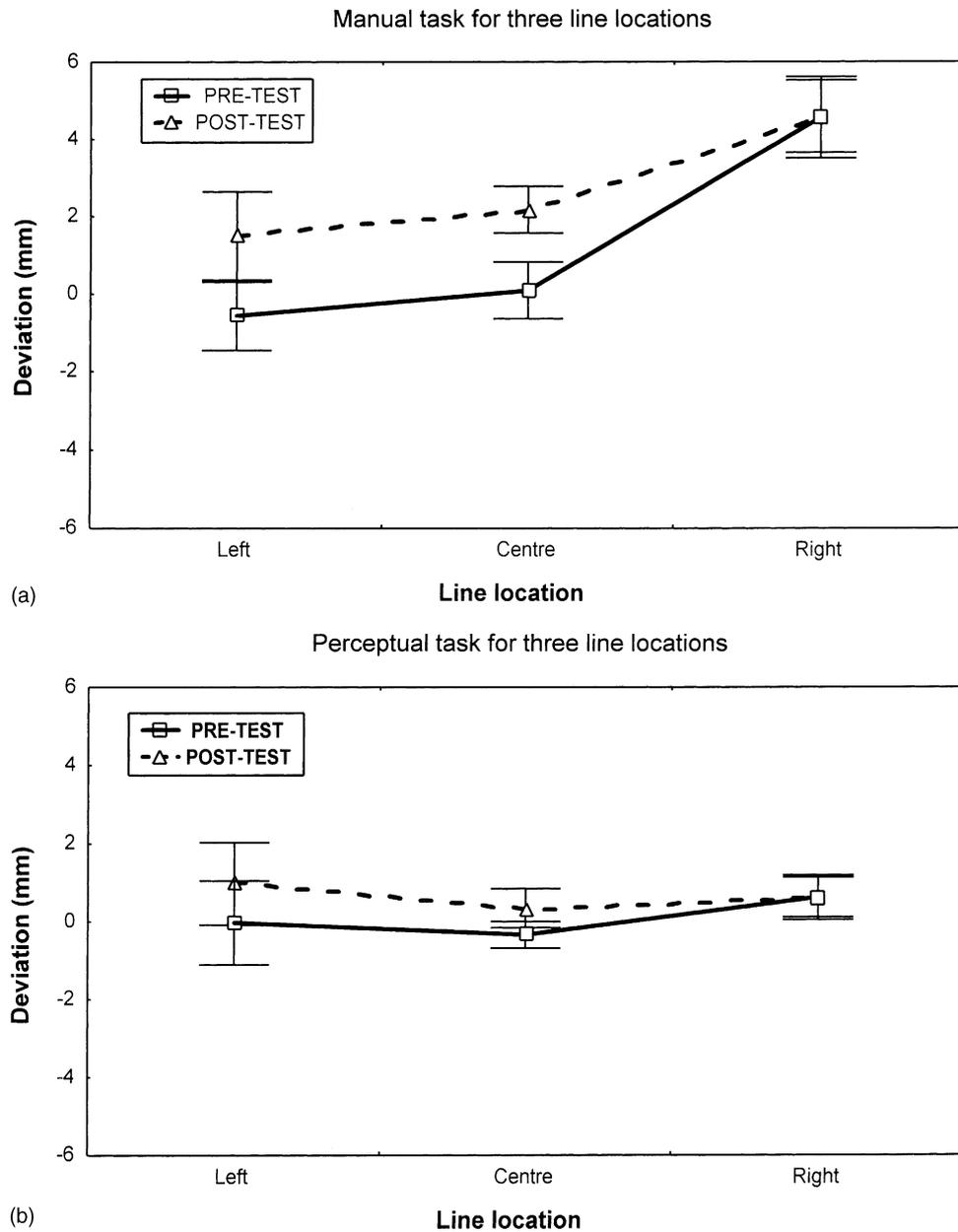## Perceptual task for three line locations

(b)

Fig. 3. Estimation of the centre of lines for the three locations: performance in manual and perceptual line bisection tasks for lines with heterogeneous locations (left, centre and right) in the group of subjects participating in Experiment 1. In both manual and perceptual tasks, a similar trend was observed. The rightward bias induced by prism adaptation was greater for left-sided lines. (a) Manual bisection task: a rightward shift of the manual estimation of the lines is observed after prism adaptation for the left and central lines. An adaptation effect ($P < 0.002$) and a location effect ($P < 0.002$) were observed. (b) Perceptual bisection task: a rightward shift of the perceptual estimation of the lines was observed after prism adaptation for the left and central locations. An effect of adaptation was observed ($P < 0.02$).

motor contribution to the task. It is possible that the effects of prism adaptation do not only induce a perceptual bias thereby producing a pre-motor bias by a leftward directional hypokinesia for objects located within the affected hemispace. The pre-motor facilitation might decline progressively as a function of leftward location in space as in neglect patients [34]. Second, using three locations resulted in an enlarging of the horizontal extent of attention. As shown in

neglect patients [27], having to diversify the allocation of attention over space within an experimental session is likely to increase the spatial span of attention. This factor may explain why we observed a weaker amplitude in the bisection bias for lines presented in front of subjects when compared with previous occasions [7]. The following experiment explored whether or not changes in the line length would also alter the effects of the prism adaptation on line bisection.

3. Experiment 2

The performance of neglect patients on line bisection typically shows an increase of the rightward proportional bias with increase in the length of the lines (e.g. [4,12,36]). In the second experiment, we investigated the after-effects of prism adaptation on line bisection (manual and perceptual) for lines of different lengths in healthy subjects. According to our previous results [7], we predicted a rightward bias in the estimation of the centre of the line after prism adaptation. As argued for the effect of position, if the rightward bias observed can be mainly explained by sensori–motor after-effects of prism adaptation, it would be observed (1) with the same amplitude irrespective of the length of the line and (2) not for the perceptual bisection task because it involves relative position coding that is not altered by wedge prisms (see [44]). By contrast, if the rightward bias can be thought of a neglect-like symptom caused by prism adaptation, (1) it would be observed in the perceptual bisection task and (2) it should increase faster than the stimulus line length (Fig. 4a).

3.1. Method

3.1.1. Subjects

Seven right-handed and normal-sighted healthy subjects participated in this experiment (five females, two males; age: 21–30 years (mean = 24.57 years; S.E. = 1.15 years)).

3.1.2. Materials

In the manual bisection task, before (pre-test) and after (post-test) prism adaptation, six black lines of 125, 250 and 375 mm length and 1 mm width were presented one by one horizontally and centrally on A3 sheets. The lines were presented in front of the subject's body midline. The order of presentation of the three line lengths (long, medium and short) was counterbalanced. In the perceptual bisection task, a total of 105 pre-transected lines was presented. For each length (125, 250 and 375 mm) the lines were bisected accurately or bisected at 2, 4 or 6 mm to the right or left of the true centre. Lines were randomly presented. The viewing distance was approximately 45 cm.

3.1.3. Procedure

The experimental procedure was identical to Experiment 1.

3.1.4. Data analysis

Repeated measure ANOVA was used to test the effect of line length on manual and perceptual bisection separately.

3.2. Results

3.2.1. Sensori–motor after-effects: open-loop pointing task

The open-loop pointing performances showed a significant rightward shift (mean ± S.E. = 13.4° ± 2.8°) between the post-test (12.6° ± 2.8°) and the pre-test (−0.8° ± 1.0°) ($F(1; 5) = 24.20$; $P < 0.003$). As in Experiment 1, rightward sensori–motor after-effects were induced by prism adaptation to a leftward visual shift.

3.2.2. Manual bisection task

In the pre-test, a repeated measure ANOVA did not reveal a significant effect of line length. Fig. 4b shows a slight tendency to the right in the manual estimation of the centre of the lines after prism adaptation. This tendency increased from short lines to long lines. However, the two-way ANOVA did not reveal a significant effect of length, adaptation and no interaction (all three $P > 0.1$).

#### 3.2.3. Perceptual bisection task

In the pre-test, repeated measure ANOVA did not show a significant effect of line length (Fig. 4c). There was however a rightward shift of the perceptual estimation in the post-test condition, which was modified by line length. That is, the rightward shift in estimations increased from short lines to long lines. This shift was 0.1 mm (mean) ± 0.2 mm (S.E.) (pre-test: 0.2 mm ± 0.2 mm; post-test: 0.3 mm ± 0.3 mm) for the short lines, 0.65 mm ± 0.5 mm (pre-test: 0.05 mm ± 0.4 mm; post-test: 0.7 mm ± 0.55 mm) for the medium lines and 1.9 mm ± 0.5 mm (pre-test: −0.3 mm ± 0.6 mm; post-test: 1.6 mm ± 0.8 mm) for the long lines. The two-way ANOVA revealed a significant effect of adaptation ($F(1; 6) = 11.47$; $P < 0.02$) and a significant interaction between adaptation and line length ($F(2; 12) = 4.85$; $P < 0.03$). However, as indicated in Fig. 4c, a contrast analysis performed to assess the effects of prism adaptation for short lines was clearly not significant ($F(1; 6) = 0.002$; $P > 0.63$). Taken together with the adaptation main effect, this implies that the effects of prism adaptation depend on line length. It should be emphasised that the rightward bias in bisection was 19 times greater for the longest lines than for the shortest lines despite the fact that the longest line was only three times longer than the shortest.

3.3. Discussion

First, as in our previous study [7] the bisection bias caused by prism adaptation dominated in the perceptual version of the task. Second, the modulation of the bias by line length can be clearly distinguished from the prediction based on sensori–motor after-effects and resembles the typical pattern described in left neglect patients in bisection (e.g. [12,36]) and visual exploration tasks [21]. Third, the average amount of bias observed in the experiment is much smaller than expected by a pure sensori–motor effect measured by the theoretical open-loop condition. The small amplitude of this bias confirms that the slow and short hand movements performed in our manual bisection task are only marginally, if at all, contaminated by the visuomotor discrepancy caused by the adaptation to the prismatic shift. The rightward bias in the perceived centre of medium lines induced by prism adaptation is weaker in the current experiment than in our
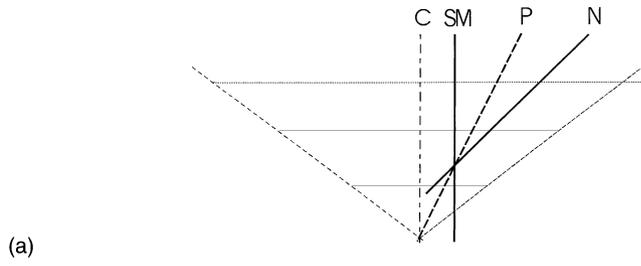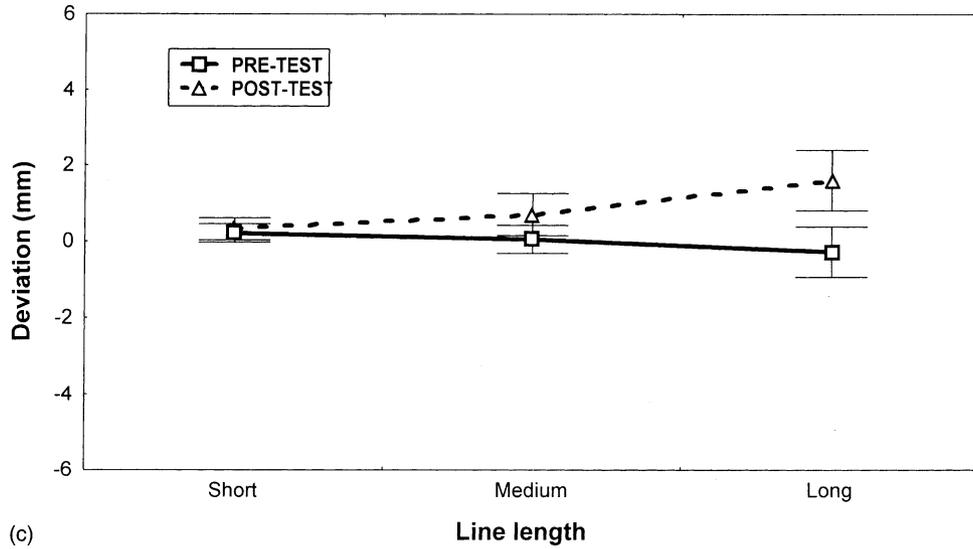
(a)

Manual task for three line lengths
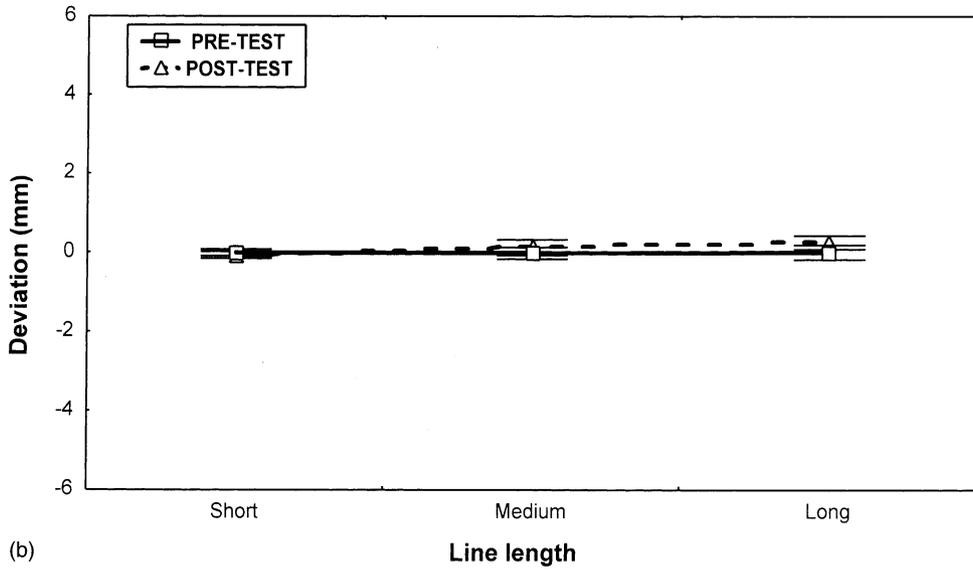
(b)

Perceptual task for three line lengths

(c)

previous results [7]. The enlargement of workspace induced by longer lines may lead subjects to underestimate the length of the medium lines [27]. No effect of line length was observed on the performance of the pre-test in the present experiment, as in previous studies [27,54]. It is interesting that only following prism adaptation normal subjects become affected by line length, which is an intrinsic characteristic of neglect patients [27].

4. Experiment 3

The first two experiments showed a clear cognitively mediated bias in line bisection tasks following adaptation to a leftward visual shift. It could however be questioned whether the cognitive bias was specific to prism *adaptation* or can be observed following prism *exposure* regardless of sensori–motor after-effects. Active movements during the prism exposure (compared with no or passive movements) are necessary for the development of the adaptation to prisms [16,17]. However, several others studies showed that passive exposure to prisms could give rise to a significant, though slower, adaptation [38]. Although it is generally admitted that active pointing provides the optimal condition for the development of prism adaptation [23,60], it was necessary to check whether the repetition of the bisection task itself or the increase in arousal caused by the heavy goggles or the lateral deviation of the visual field could be responsible for a cognitive bias. In order to demonstrate that the results of Experiments 1 and 2 are *attributable* to prism adaptation, Experiment 3 compared passive versus active prism exposure. We compared the performance of two groups of subjects, one performing an active pointing task during prism exposure ('active group') while the other group did not perform any such task during prism exposure ('passive group').

4.1. Method

4.1.1. Subjects

Twenty right-handed and normal-sighted healthy subjects participated in the third experiment. The 'active group' comprised four females and six males ranging in age from 15 to 44 years (mean = 29.4 years; S.E. = 3.3 years); the 'passive group' three females and seven males ranging in age from 18 to 52 years (mean age = 40 years; S.E. = 8 years).

4.1.2. Material

In the manual bisection task, before (pre-test) and after (post-test) prism exposure, 10 black lines of 250 mm length and 1 mm width were placed horizontally and centrally on A3 sheets of paper, one line on each sheet. For the perceptual line bisection task, a total of 78 pre-transected 250 mm lines (transected accurately or mis-bisected at 2, 4, 6, 8, 10, 12 mm to the right or to the left of the true centre) were presented at a viewing distance of approximately 45 cm. All subjects were tested in identical conditions before and after prism exposure.

4.1.3. Procedure

The experimental procedure was identical to the first two experiments. The 'active group' performed a simple visual pointing task while wearing prisms. In contrast to the 'active group', the 'passive group' made no hand movements during prism exposure and visual feedback of the hand was not available.

4.1.4. Data analysis

A two-way repeated measure ANOVA with a between group factor was performed.

4.2. Results

4.2.1. Sensori–motor after-effects: open-loop pointing task

The two-way ANOVA revealed a significant effect of group ($F(1; 18) = 33.35$; $P < 0.001$), a significant effect of adaptation ($F(1; 18) = 23.15$; $P < 0.001$) and an interaction between group and prism adaptation ($F(1; 18) = 1.52$; $P < 0.001$). As shown by previous studies, the 'active group' showed a significant rightward effect (mean$\pm$S.E. = $10.4° \pm 2.0°$) of prism adaptation on the open-loop pointing task between the post-test ($13.7° \pm 1.3°$) and the pre-test ($3.3° \pm 1.5°$) (contrast analysis: $F(1; 18) = 56.13$; $P < 0.001$). As expected, the 'passive group' showed no significant effect between the pre- and the post-tests (pre: $-0.2° \pm 1.3°$; post: $-1.3° \pm 1.5°$; contrast analysis: $F(1; 18) = 0.47$;

Fig. 4. (a) Schematic representation of theoretical and predicted biases observed in the manual bisection: three lines of increasing length (1, 2, and 3 units) are presented. The line C indicates the true centre of the lines. The line P corresponds to a theoretical bias proportional to the line length (i.e. a constant percent deviation across all line lengths). The line labelled SM illustrates a manual response that would be obtained if the bias was explained solely by sensori–motor after-effects of prism adaptation. Two implications result from this theoretical case: (1) The bias (in absolute value) would not vary with line length if the task was performed in visual open-loop conditions (i.e. without visual feedback). In the case of Experiment 2, the manual estimation of the centre should be placed 5.3 cm to the right of the true centre irrespective of line length. (2) This SM bias would be reduced when visual feedback is available and negatively correlated with the amount of visual feedback (e.g. the SM bias should increase for fast vs. slow movements). The line labelled N shows a pattern typical of neglect patients, i.e. where the percent deviation increases with line length (and hence the absolute bias increases faster than line length) [4,27]. (b and c) Estimation of the centre of lines for the three line lengths: manual and perceptual line bisection tasks for lines with heterogeneous length (long, medium and short) in Experiment 2. In both manual and perceptual tasks, a similar trend was observed. The rightward bias induced by prism adaptation was greater for longer lines. (b) Manual estimation of the line centre: there was no effect of length, no effect of adaptation and no interaction (all $P > 0.1$). (c) Perceptual estimation of the line centre. A rightward shift of the perceptual estimation of the lines was observed after prism adaptation for the longer lines. There was a significant effect of adaptation and a significant interaction ($P < 0.03$).

$P > 0.5$). Only active pointing during prism exposure reliably produced sensori–motor after-effects on the pointing task. It can be concluded that the current experimental conditions applied to our passive group did not allow the development of adaptation.

4.2.2. Manual bisection task

A two-way repeated measure ANOVA with a between group factor showed only a significant interaction between the group and the adaptation effects ($F(1; 18) = 4.56$; $P < 0.05$). In the 'active group', adaptation to a leftward visual shift produced a bias in the manual estimation of the centre of the lines (mean ± S.E. = 2.4 mm ± 1.2 mm) between the post-test (2.3 mm ± 1.3 mm) and the pre-test (−0.13 mm ± 1.0 mm; contrast analysis: $F(1; 18) = 6.48$; $P < 0.03$; Fig. 5a). The 'passive group' did not show any bias in the estimation of the centre of lines between the post-test (2.6 mm ± 1.2 mm) and the pre-test (3.0 mm ± 1.3 mm; contrast
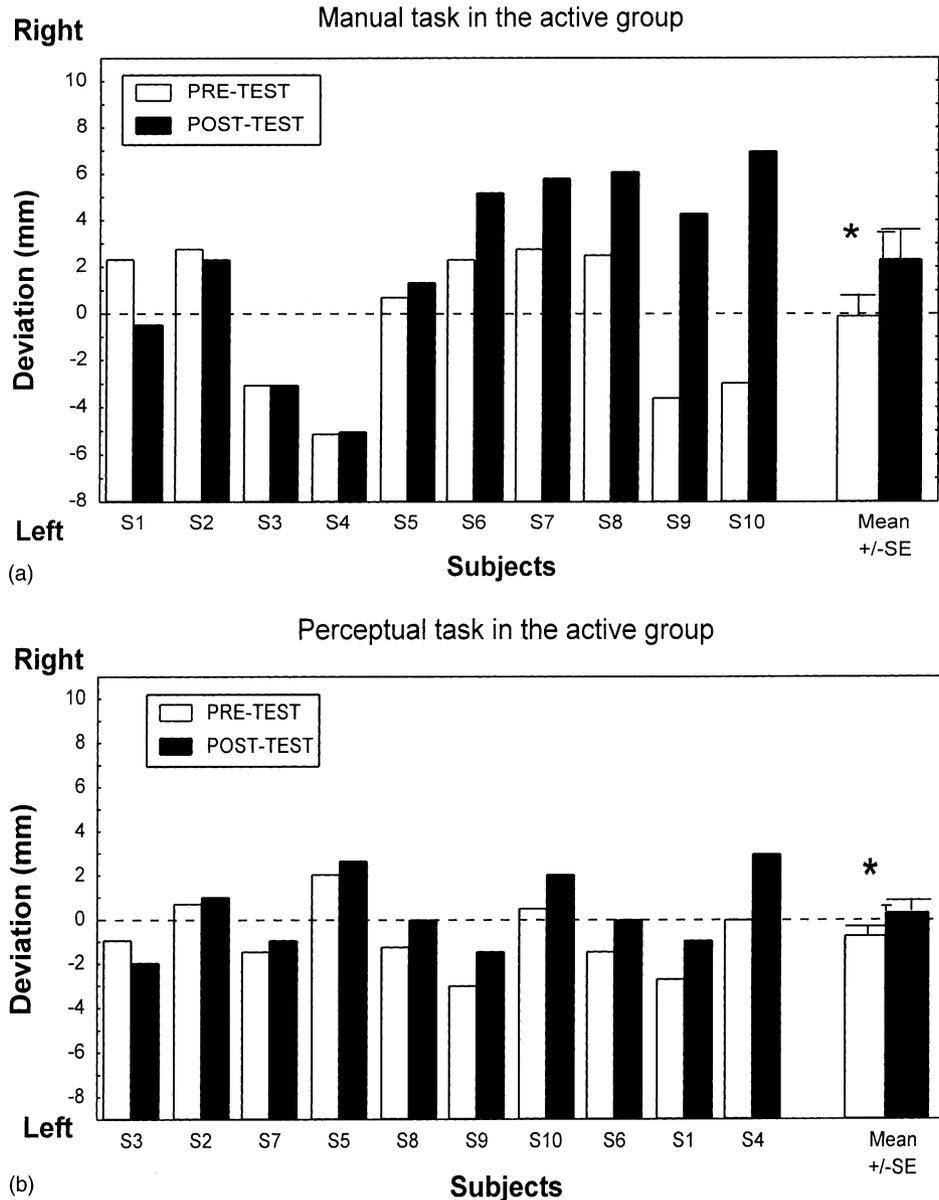

Fig. 5. Active vs. passive prism exposure: perceptual and manual estimation of the centre of lines in the two groups are presented. The results are presented in increasing size of after-effect (difference between performances obtained in post- and pre-test). Variability of the effect of prism adaptation is shown by the small standard error bar between the mean group values for pre- and post-tests. Manual bisection task in the active group (a): in this group, which performed an active pointing task during prism exposure, a significant rightward effect is observed (contrast analysis: $P < 0.03$). Perceptual bisection task in the active group (b): in the same group, a significant rightward perceptual effect is observed (contrast analysis: $P < 0.02$). Manual bisection task in the passive group (c): on the contrary, in the 'passive group' no significant shift of the manual estimation of the centre of lines was observed (contrast analysis: $P > 0.6$). Perceptual bisection task in the passive group (d): in the same group, no significant shift of the perceptual estimation of the centre of lines was observed (contrast analysis: $P > 0.5$).
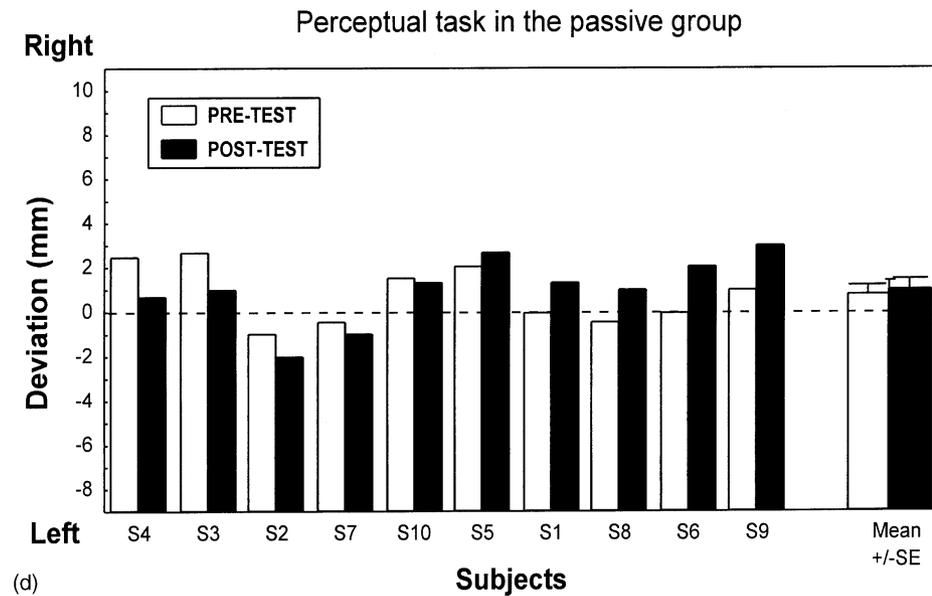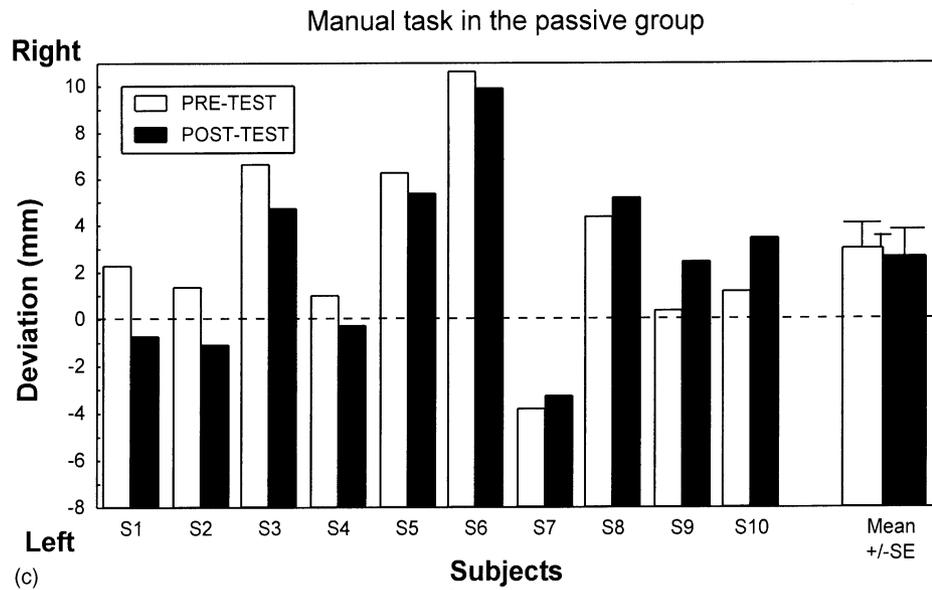
Fig. 5. (*Continued*).

analysis: $F(1; 18) = 2.22$; $P > 0.6$; Fig. 5c). Prism *adaptation* (versus passive exposure) to a leftward visual shift induced a rightward-sided shift of performance.

4.2.3. Perceptual bisection task

A two-way repeated measure ANOVA showed only a significant effect of adaptation ($F(1; 18) = 5.43$; $P < 0.04$). The 'active group' presented a rightward shift of the perceptual estimation of the centre of lines (mean ± S.E. = $1.1\,\text{mm} \pm 0.3\,\text{mm}$) between the post-test ($0.3\,\text{mm} \pm 0.6\,\text{mm}$) and the pre-test ($-0.8\,\text{mm} \pm 0.5\,\text{mm}$; contrast analysis: $F(1; 18) = 7.39$; $P < 0.015$). This rightward effect was observed in all but one subjects (S3), ranging in amplitude

from 0.3 to 3 mm (Fig. 5b). In contrast, no modification of the perceptual estimation of the centre of lines was observed in the 'passive group' between the post-test ($1.0\,\text{mm} \pm 0.5\,\text{mm}$) and the pre-test ($0.8\,\text{mm} \pm 0.4\,\text{mm}$; contrast analysis: $F(1; 18) = 0.33$; $P > 0.5$; Fig. 5d). Thus, a perceptual bias was only observed when subjects performed an active pointing task during prism exposure.

4.3. Discussion

The results of Experiment 3 clearly demonstrate that sensori–motor after-effects of prism adaptation depend on active pointing during prism exposure, i.e. on the

development of adaptation. This was also true for cognitive after-effects assessed by both verbal and manual bisection responses. That is, the perceptual judgement of the middle of horizontal lines was only affected in the 'active' group. The question may arise of why the motor bisection is significantly affected in the present experiment whereas this was not the case in Colent et al. [7]. Altogether it appears that both perceptual and motor bisection performance are shifted to the right following adaptation. The difference in significance of these results may be explained by variability factors. It is obvious that pre-test measures are more variable for the motor than the perceptual task (Fig. 5a and b; Fig. 2 of [7]). However, the variability of the effect of prism adaptation can be dissociated from (and smaller than) the variability of pre-test measure (see Fig. 1 of [50]). In both [7] and the active condition of Experiment 3, the variability of the prism adaptation effect is about four times greater for the manual task than for the perceptual task whereas the variability of the pre-test performance is only about twice larger for the manual task. Thus, prism adaptation might produce a neglect-like effect for both perceptual and manual bisection but the effect produced on the perceptual task appears more reliable.

5. General discussion

Sensori–motor after-effects following prism adaptation are well established in normal subjects. By comparison, the after-effects of prisms on tasks considered to be assessing higher level cognitive processes have received attention only recently [50]. Recent research demonstrating a dramatic improvement in neglect at both the sensori–motor and cognitive levels following prism adaptation [50] has motivated a reconsideration of the traditional distinction. The aim of the present study was two-fold: first, we wanted to explore in healthy controls the effects of the sensori–motor prism adaptation on traditional neuropsychological tasks thought to be sensitive to high level cognitive processes. Second, we wanted to compare the qualitative patterns of performance between controls and patients with neglect on tests generally considered to be sensitive to cognitive or high level spatial processing. Previous results [7] in conjunction with the present results provide the basis for some tentative conclusions.

5.1. Asymmetric effects of prism adaptation and the neglect syndrome

5.1.1. Sensori–motor effects of adaptation

Can the asymmetry observed on line bisection in normals be explained in terms of non-cognitive processes, i.e. in terms of low level sensori–motor transformations? Prism adaptation in normal subjects produces sensori–motor after-effects of similar amplitudes, regardless of the left or the right direction of the prismatic shift (e.g. [61]).

Therefore, the asymmetrical after-effects observed on line bisection tasks cannot simply be explained away as the product of symmetrical sensori–motor after-effect. By contrast, several arguments favour a cognitive explanation for the observed rightward bias. If the observed bias was due to sensori–motor after-effects it would mainly be observed on the manual bisection task; the amplitude of the bias in the manual bisection task would be independent of the spatial location of the line; the amplitude of the bias in the manual bisection task would be independent of the line length and finally the bias would be in the opposite direction of the prismatic displacement for both left and right deviations. None of these patterns were demonstrated, further supporting the view that the bisection bias observed following prism adaptation is mediated indirectly by cognitive rather than by sensori–motor mechanisms. Nevertheless, these effects confirm that sensori–motor integration can structure spatial cognition (e.g. [50,51]) and hence that sensori–motor and cognitive representation of space are not fully dissociated [48].

5.1.2. A right hemisphere bias?

The fact that unilateral brain damage produces stronger left-side than right-side neglect is a well-established clinical observation [15,55]. Several directionally specific improvements in neglect have already been reported for vestibular, optokinetic, transcutaneous and TENS stimulation (see review [49]). None of these stimulations have produced the same qualitative characteristic clinical performance on different standard visuospatial tasks of visual neglect in normals. Extending several previous attempts to produce neglect in normal individuals (e.g. [10]), the bias observed here provides a clear demonstration of this claim for two main reasons. Line bisection tasks were performed with identical stimuli presented in identical conditions in the compared conditions, i.e. before and after prism adaptation. There are no obvious artefacts responsible for attentional cueing [34], no visual illusions [10,29], no sensori stimulation *during* our bisection test such as optokinetic effects induced by rotatory self-motion [52]. On the other hand, the cognitive effects (i.e. the characteristic pattern of high level deficits on clinical tasks attributable to attention disorders) reported in our previous work [7] are directionally and consistently asymmetrical whereas other sensori stimulation (neck muscle vibration and caloric vestibular stimulation [20] or optokinetic stimulation [28]) used in normals always produced fairly symmetrical effects.

As mentioned, the rightward bias in controls following prism adaptation mirrors many of the task specific biases during line bisections that are seen in patients with unilateral neglect. Given that neglect is commonly observed following right temporo-parietal lesions, it may be the case that the right hemisphere is differentially sensitive to prism adaptation. The improvement of neglect symptoms using prism adaptation suggests the involvement of the inferior parietal cortex through its neural representation of the visual

space. In addition, the rightward bias found on perceptual line bisection is generally more robust and severe than leftward manual biases in normal subjects [46]. It is therefore possible that a hemispheric imbalance induced by prism adaptation in normals may affect the attentional functions of each hemisphere differentially. Application of repetitive transcranial magnetic stimulation (rTMS) to the right parietal cortex has been shown to produce the same directional rightward bias [8]. Taken altogether the cerebellar substrate of adaptation could inhibit the right parietal cortex via an indirect neural network. Alternatively, it may interfere with the influence of the parietal cortex by acting of the level of its projections onto crucial target areas. This is coherent with recent functional imaging studies [9] employing the Landmark task suggest that while the cerebellum may be critically important, the responsible locus of this inherent neural bias remains the right parietal lobe—at least for those tasks involving explicit linear judgements.

The anatomical structures involved in prism adaptation are not well known. However, several clinical findings suggest that the cerebellum plays a crucial role in the adaptation process [56,6] (for review: [19]). In non-human primates, prism adaptation is abolished by disruption of visual afferents to the cerebellum [1]. However, positron emission tomography (PET) studies have shown activation of the posterior parietal cortex but not the cerebellum during reaching with displacing prisms in normals [5]. On the other hand, recent studies on patients with bilateral damage have shown that the posterior parietal cortex exhibits no deficit for adaptation to prisms [39]. The reciprocal connections (at least indirectly) between the cerebellum and the parietal cortex could provide an anatomical substrate to support cerebellar participation in higher-order cognitive processing [53]. Our recent PET investigations also suggest that the cerebellum is involved in the therapeutic effects of prism adaptation [24]. It is therefore necessary that future investigations consider how the action of prism adaptation at cerebellar level can simulate neglect in normals (see [49]).

5.2. Effects of spatial position

Several studies (e.g. [14]) have shown that the spatial position of the stimulus lines to be bisected can significantly influence patients' performance. Compared with presentation in front of the patient, left neglect may be reduced by placing the stimulus in right space and increased by placing the stimulus in left space.

Milner et al. [35] suggested that the underestimation of horizontal extent may result from an attentional deficit in left hemispace and that rightward line bisection errors in patients with neglect may be due to a misperception of the left part of the horizontal line compared to the right part, when the left is perceived shorter. Milner argued that this distortion might be greater within left hemispace and this hypothesis receives support from data showing that the bias in bisection is larger when lines are placed in the

contralateral space [33]. For normal subjects, previous research has demonstrated a leftward spontaneous bias in line bisection (e.g. [25,34]), in a direction opposite to the bias observed in neglect patients (pseudoneglect; e.g. [30,31,34]). This effect of spatial location was found here in normal subjects in the manual bisection of the pre-test for Experiment 1 but not for perceptual bisection. It should be noted that during the manual bisection task two factors, perceptual (attentional) and premotor (intentional) operate together [34] and the enlargement of the workspace may have overly increased the motor contribution to the performance. The main result in Experiment 1 was the rightward bias obtained after prism adaptation, which increased for the lines from right to left visual space (Fig. 3). Once again, this bias emulates the response seen in neglect patients.

5.3. Effects of line length on bisection

Several studies (e.g. [4,11]) have reported that the extent of deviation in neglect is a function of line length. When comparing deviations obtained for several line lengths it is found that the extent of deviation increases to a greater degree than line length (see Fig. 4a) [4,27]. In Experiment 2, the rightward bias produced in normals also increases to a greater degree than line length. In addition, it is also interesting to compare the present result with our previous experiment. When a single line length (equal to the current medium line) was used [7] a significant perceptual bias was induced by the adaptation. In contrast, when several line lengths are presented within the same session (Experiment 2), a significant bias was observed only for the longest line and not for the medium line. Notably, such effect of block versus randomised presentation of lines of different lengths has been described in neglect patients [27]. Also interesting is the fact that an increased variability was shown in normal subjects with longer lines (see [37]). This less precise performance may reflect a less stable spatial representation, possibly related to the greater difficulty in building up an internal representation of a larger stimulus.

5.4. Differential effects of adaptation for perceptual and manual bisection

Since prism adaptation requires an overt motor behaviour the manual bias could have been expected to be larger than that of the perceptual one. Several studies have reported a predominance of perceptual on motor symptoms of neglect when the same task is explored with two types of responses (review: [49]). These findings suggest that neglect may affect perceptual processes more markedly than motor behaviour (but the reverse pattern may be observed in some cases (see [26]). In Experiment 2 of the present study, the rightward manual bias was too variable (with respect to the perceptual response) to reach significance (as in [7]). Nevertheless, Experiment 1 demonstrated a significant rightward bias in both perceptual and manual tasks. Compared with

the simple task used previously (one line length and one location) [7], Experiment 2 varied only the stimuli and kept a stereotyped manual response whereas Experiment 1 produced a variation in both perceptual and motor sides.

Another reason for not expecting a stronger motor than perceptual bias following the adaptation is that movements of small amplitude performed under visual control are not altered by visual and proprioceptive discordance [44]. During our manual line bisection task both the lines and the hand initial position were visible and the movements were slowly performed (see Fig. 4a), which can explain the absence of direct sensori–motor effects on the manual performance.

6. Conclusion

Prism adaptation to the right improved left neglect in patients while prism adaptation to the left produced a moderate neglect-like behaviour in normals. More importantly, several of the main characteristics of neglect observed on line bisection task were qualitatively simulated in healthy normals following prism adaptation. None of these effects can be attributed to simple sensori–motor after-effects of the adaptation. Collectively, the neglect-like behaviours obtained in this and the previous studies [7] following prism adaptation suggest that plastic changes of inter-sensori and sensori–motor processes can systematically affect higher cognitive processes traditionally believed to be only involved in spatial representation. The asymmetrical effect revealed by prism adaptation on tasks of spatial cognition reflects an inherent neural organisational bias for spatial representation—a bias that can be modified as in the case of prism adaptation in normals and following lesions of the relevant cortical areas. Consequently, rather than consider the symptoms of neglect to be the sole effect of damage to cortical brain areas it is possible that some of the lateralised symptoms observed in the condition originate from secondary maladaptative responses such as those following uninhibited adaptation between intact left hemisphere and cerebellum (see [49]).

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