

Sensorimotor effects on central space representation: prism adaptation influences haptic and visual representations in normal subjects

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Abstract

Prism adaptation improves visual and haptic manifestations of left neglect, and can induce a small but reliable simulation of left visual neglect in normal individuals. Here, we present two experiments in which the effects of prism adaptation on the representation of space were explored. In Experiment 1, normal subjects were required to locate the centre of a haptically explored circle, before and after adaptation to leftward displacing prisms. In Experiment 2, a visual circle centring task was used. In both tasks, prism adaptation induced a significant rightward shift of performance. In addition, in both experiments, three classical measures of visuo-manual adaptation were taken: the visual shift, the proprioceptive shift and the total shift. The effects found on the haptic and visual tasks did not correlate with any of these measures. This suggests that the effects of prism adaptation on the circle centring tasks did not depend directly on the sensorimotor consequences of the adaptation. These results imply that prism adaptation can affect noetic levels of space representation in normal subjects, supporting the hypothesis that this low-level sensorimotor intervention can exert a bottom-up structuring influence on higher levels of cognitive integration. © 2004 Elsevier Ltd. All rights reserved.

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1. Introduction

Unilateral neglect is a syndrome in which patients fail to respond or orient towards stimuli located in the space contralateral to a brain lesion (Halligan, Fink, Marshall, & Vallar, 2003). Although most frequently observed immediately following a unilateral brain injury, signs of neglect may be found months or even years later (Gainotti, 1968; Cassidy, Lewis, & Gray, 1998). Furthermore, left neglect has been shown to be responsible for poor functional recovery from stroke, and a reduced ability to benefit from the treatment of impaired motor functions (Denes, Semenza, Stoppa, & Lis, 1982). It is not surprising then that several physiological techniques (e.g. vestibular stimulation, optokinetic stimulation, vibratory or electrical stimulation of neck muscles) that are capable of temporarily ameliorating the symptoms of unilateral neglect have attracted the attention of many researchers (see Vallar, Guariglia, & Rusconi, 1997; Rossetti & Rode, 2002 for reviews).

Recently, it was shown that a brief period of adaptation to a rightward prismatic displacement of the visual field can improve left neglect for at least 2 h (Rossetti et al., 1998). Subsequent studies have greatly extended the range of neglect-related phenomena on which prism adaptation is known have an ameliorative effect, and have shown that these effects may be relatively long-lived (see Rossetti & Rode, 2002; Rode, Pisella, Rossetti, Farné, & Boisson, 2003 for reviews). These findings, together with the simple and non-invasive nature of the treatment, make prism adaptation a potentially powerful tool for the rehabilitation of neglect. The generality and persistence of its effects suggest that it may exert its influence close to the core of the neglect syndrome, perhaps stimulating a reorganisation of the representation of space that continues to develop autonomously following treatment (Rossetti et al., 1998; Farné et al. 2002). Studies of the relationships between prism adaptation and spatial representation may therefore be of great importance for understanding the neglect syndrome and the underlying cognitive functions in normal individuals.

The majority of studies showing an effect of prism adaptation on neglect have focused on visually based tasks. Nevertheless, neglect may also be observed on non-visual

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tasks requiring tactile and kinaesthetic exploration of space (e.g. De Renzi, Faglioni, & Scotti, 1970; Chedru, 1976; Weintraub & Mesulam, 1987; Gentilini, Barbieri, De Renzi, & Faglioni, 1989; Caneman, Levander, & Tegnèr, 1992; Beschin, Cazzani, Cubelli, Della Sala, & Spinazzola, 1996), which we shall refer to as the “haptic” manifestations of neglect. However, haptic neglect has been most often observed on spatial exploratory tasks, and has been surprisingly absent on non-visual bisection tasks (Fujii, Fukatsu, Kimura, Saso, & Kogure, 1991; Hjaltason, Caneman, & Tegnèr, 1993; Chokron et al., 2002). One reason for the lack of significant neglect on non-visual line bisection may be that patients with impairments of spatial cognition can compensate for these problems by adopting counting strategies (Hatta & Yamamoto, 1986; McIntosh, 1999). One solution to this problem was suggested by McIntosh (1999), who devised a task in which patients are required to locate the centre of a haptically explored circle. It was argued that this task, by rendering counting strategies unhelpful, should force subjects to rely on explicitly spatial representations of the stimulus. McIntosh, Rossetti and Milner (2002) administered the task to a patient with chronic left neglect before and after prism adaptation. Prior to adaptation, the patient showed a marked tendency to locate the centre of the circle to the right of the true centre. Prism adaptation induced a clear improvement of neglect on this task as well as on tests of visual neglect. These cross-modal effects were interpreted as suggesting that prism adaptation not only induces changes in visuomotor coordination, but also stimulates reorganisation at higher levels of spatial representation.

The first study reported in the present paper was conducted primarily to investigate whether prism adaptation could influence the performance of normal subjects on the haptic circle centring task used by McIntosh et al. (2002). The fact that prism adaptation can also induce some neglect-like behaviour on visual bisection tasks in normal subjects was shown for the first time by Colent, Pisella, Bernieri, Rode and Rossetti (2000) and replicated by Michel et al. (2003a). Similar results have been obtained by Berberovic & Mattingley (2003), who found that prism adaptation could influence normal subjects’ bisection performance in both peripersonal and extrapersonal space. A positive effect on a haptic task in normal subjects would further demonstrate that prism adaptation affects higher cognitive functions in normal subjects, and not only in left neglect. As noted by McIntosh et al. (2002), however, it is unclear whether the reduction of rightward errors in their neglect patient was due to an improvement in the patient’s ability to represent the stimulus circle, or to a reduction of a rightward manual bias. This question is highly relevant because, in the last 100 years, many studies have shown that prism adaptation can bias manual responses in normal subjects, with the induced bias being directionally opposite to the prismatic displacement (e.g. Redding & Wallace, 1997). As a consequence, if it is possible to find any effect of prism adaptation in normal subjects on the haptic circle centring task, it is also

necessary to assess whether this effect is produced at a sensorimotor level or at a higher level of space representation.

The second aim of Experiment 1, therefore, was to investigate whether any effect of prism adaptation on the haptic task was correlated with classical measures of the sensorimotor realignment induced by the adaptation. The presence of a significant correlation would suggest that the effect induced on the haptic task is a simple reflection of changes at the sensorimotor level or, at least, that it depends directly on such changes. If no such correlation were observed, however, it would seem more likely that the effect on the haptic task arises at a more central cognitive level.

Finally, on the basis of the results of Experiment 1, Experiment 2 was mainly designed in order to verify the hypothesis that the effect found in Experiment 1 could be replicated in a visual version of the task employed in the previous experiment: the main difference between the two tasks was that the mental representation of the stimulus circle was fed with either haptic (Experiment 1) or visual (Experiment 2) information.

2. Experiment 1

2.1. Methods

2.1.1. Subjects

Eleven right-handed subjects (mean age: 31.8 years; S.D.: 10.55; range: 21–56) with no history or evidence of neurological or psychiatric illness participated in this study.

2.1.2. Haptic circle centring task

All subjects performed a haptic circle centring task, adapted from McIntosh et al. (2002). A 30 cm diameter circular groove cut centrally into a 10 mm thick square of transparent perspex (37.5 cm × 37.5 cm) was used (see Fig. 1). Subjects were blindfolded and the stimulus circle was placed on a table in front of them, centred on their body midline, at a distance of 25–30 cm. The task was performed using a pen held in the right hand. On each trial, the pen was placed by the experimenter in the circumference groove at one of two points: left or right with respect to the subject. The subject was then asked to make one full (clockwise or counter clockwise) exploration of the circumference groove. While the subject did this, the experimenter placed a finger at the original starting point so as to block further movements of the pen. When the subject felt his/her exploration blocked in this way, he/she was required to indicate, with the pen, the centre of the explored circle. This task is referred to as “haptic” since tactile and kinaesthetic information are gained actively by the subject. However, kinaesthesia presumably provides the primary source of useful information concerning the stimulus circumference. The experimenter recorded (to the nearest mm) the lateral and radial coordinates of the response from 1 mm scaled paper centred on the circle. Rightward and distal errors

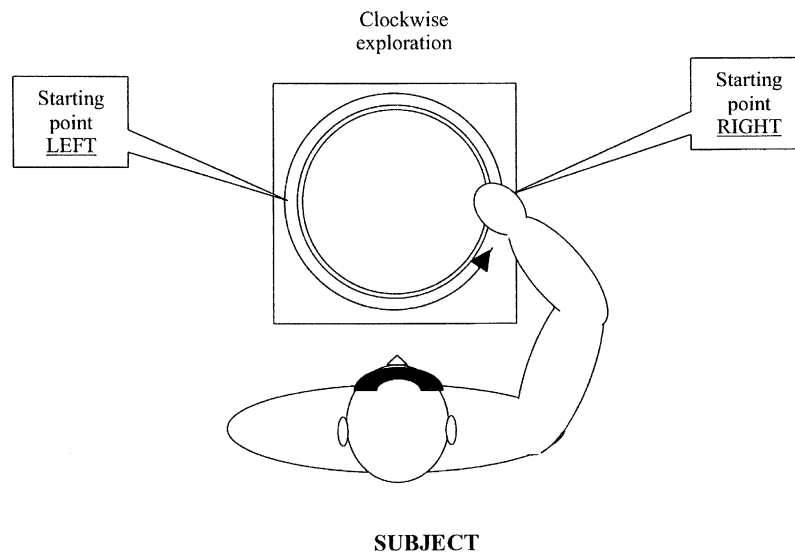


Fig. 1. Experiment 1. The haptic circle centring task: subjects were blindfolded and, on each trial, were requested to explore the circle circumference with the right hand starting from the left or the right of the circle and moving clockwise or counter clockwise (arrow in the figure).

were scored with positive values. Leftward and proximal errors were scored with negative values. Each subject performed 24 trials at each administration of the task: 12 trials with the hand starting on the left and 12 with the hand starting on the right (total duration: approximately 20 min). Direction of exploration (clockwise and counter clockwise) and starting position of the hand (left and right) were counterbalanced, and trial order was randomised. Subjects were free to move their head and trunk. Each subject performed the task twice: once before and once after adaptation to leftward displacing prisms.

2.1.3. Prism adaptation procedure

The adaptation procedure lasted approximately 20 min. The head was stabilised in a chin rest, and subjects wore a pair of goggles fitted with wide-field point-to-point lenses creating a leftward optical shift of 15° (Optique Peter, Lyon, France). The total visual field sustained by the goggles was 105° , including 45° of binocular vision. Adaptation to the prisms was obtained by asking the subjects to point with fast but comfortable movements of the right hand towards each of 20 dots, distributed evenly across a sheet of white A3 paper. The sheet of paper was located in front of the subject with its longer side parallel to the subject's horizontal plane and centred on the subject's body midline. Target order was randomised.

2.1.4. Measures of sensorimotor adaptation

For each subject, three classical estimates of sensory and motor references were obtained. These measures were taken in a dark room and with the subject's head stabilised in a chin-rest. The apparatus used for obtaining all estimates was similar to that used by Redding & Wallace (1996). It consisted of a two-layer rectangular black wooden box-like frame (30 cm high, 80 cm wide and 80 cm deep) placed on

a table and opened on the side facing the subject. Subjects were seated in front of the structure and placed their arms within it. Their head was kept aligned with the body's mid-sagittal axis using a chin-rest situated on the top of the box. The lower horizontal surface of the box was covered by electrosensitive paper that allowed responses to be recorded via a metallic thimble attached to the tip of subjects' index finger. This apparatus produced measurements with an accuracy of 0.1° . The following three measures were taken.

1. *Visual*: subjects were required to judge when a red LED, moving horizontally in front of them at eye level (approximate speed: $2^\circ/s$), passed directly in front of the body midline. At each administration, the subject made 12 judgements. The LED moved six times from right to left and six times from left to right, with direction of movement alternated between trials.
2. *Proprioceptive*: subjects made 12 straight-ahead pointing responses with the right hand at each administration of the task. The instruction provided to the subject was to point straight ahead of their navel such that their fingertip coincided with their body midline.
3. *Visual-proprioceptive*: subjects were required to point with the right hand towards a red LED located directly in front of the body midline at a distance of about 80 cm. Twelve responses were made for each administration of the task.

These three measures were taken, in the above order, twice for each subject: immediately following the first administration of the haptic circle centring task (prior to prism adaptation), and immediately following prism adaptation (prior to the second administration of the haptic task). The differences between the pre- and post-adaptation estimates of subjective body midline location furnished three measures of sensorimotor adaptation: visual shift (VS), proprioceptive

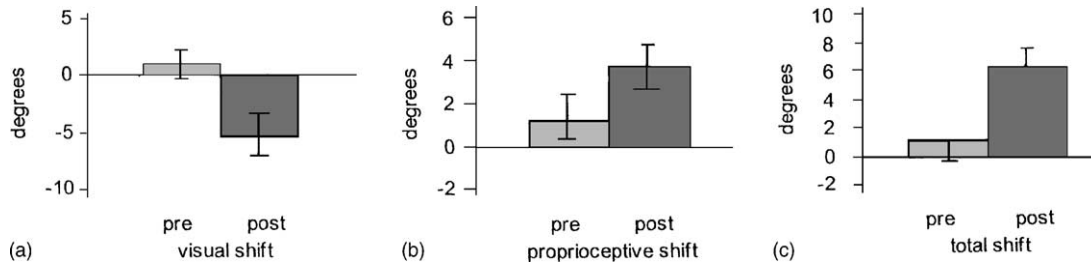


Fig. 2. Experiment 1. Average performance for the three measures of subjective midline before (pre) and after (post) the prism adaptation procedure (values are expressed in degrees and the value 0 represents the true body midline): (a) visual shift; (b) proprioceptive shift; (c) total shift. In all cases, positive values indicate a rightward displacement from the midline and negative values indicate a leftward displacement.

shift (PS), and total shift (TS), respectively (e.g. McLaughlin & Bower, 1965; Hay & Pick, 1966; Warren & Platt, 1975; Melamed, Beckett, & Haley, 1979).

As far as VS is concerned, after adaptation to prisms, the subjects' visual estimate of body midline location is usually shifted in the same direction as the visual displacement induced by the prisms. For the PS, performance is usually shifted in the direction opposite to the prismatic displacement. TS is a global measure of adaptation that is usually opposite in direction to the prismatic displacement. Although the relative weighing of VS and PS varies across subjects, TS magnitude approximates to the sum of the magnitudes of VS and PS (e.g. Wilkinson, 1971). These classical effects are usually interpreted as an example of the plasticity of the human sensorimotor system: VS is considered to reflect realignment in the eye-head system, PS to reflect realignment in the hand-head system and TS to reflect the total realignment in the eye-hand coordination loop (e.g. Redding & Wallace, 1997).

2.2. Results

2.2.1. Measures of sensorimotor adaptation

Fig. 2 shows the group mean estimate of subjective body midline location, prior to and after prism adaptation. For

each measure separately, a paired *t*-test was used to compare pre- and post-prism performance. As expected, VS was significantly leftwards, i.e. in the direction of the prismatic displacement ($t[10] = 4.78$; $P < 0.001$). PS was opposite in direction to VS, though just failing to reach significance ($t[10] = -1.94$; $P = 0.08$). Finally, TS was significantly rightwards ($t[10] = -6.99$; $P < 0.0001$).

2.2.2. Haptic circle centring task

Fig. 3 illustrates the mean lateral and radial errors produced in the haptic circle centring task, prior to and after prism adaptation. A repeated measures ANOVA by adaptation condition (pre, post) and hand starting position (left, right) was conducted for lateral and radial errors separately. For lateral errors the effect of condition was significant ($F[1, 10] = 8.64$; $P < 0.02$), indicating the presence of a global rightward shift induced by prism adaptation. The effect of starting position was highly significant ($F[1, 10] = 21.41$; $P < 0.001$), showing that when subjects started from the right, responses were further leftward than when starting from the left. The interaction between the two factors did not attain significance ($F[1, 10] = 2.89$; $P = 0.12$).

For radial errors the effect of condition was not significant ($F[1, 10] = 0.62$; $P = 0.45$), but the effect of starting position was ($F[1, 10] = 5.38$; $P = 0.04$), indicating that

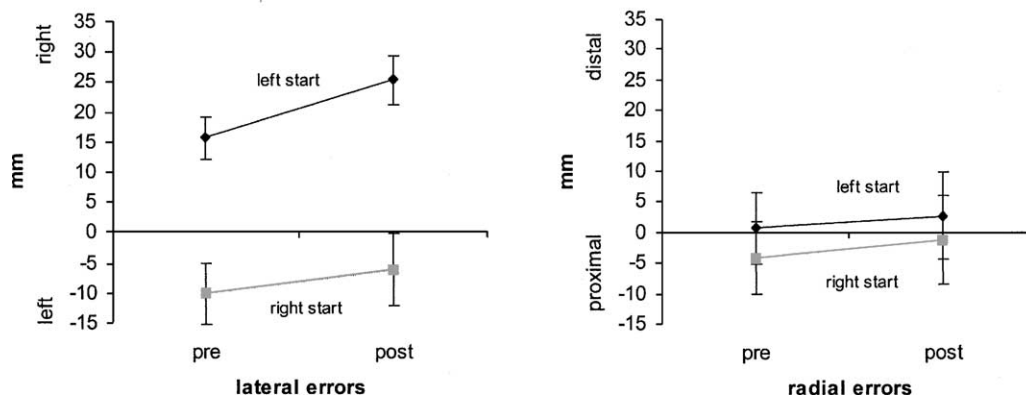


Fig. 3. Experiment 1. Results obtained on the haptic circle centring task. The left panel shows the average lateral errors. The right panel shows the average radial errors. Values are expressed in mm and indicate the distance from the objective centre of the circle: rightward and distal errors are indicated with positive values; leftward and proximal errors are indicated with negative values.

when the hand started from the right, responses were globally more proximal than when the hand started from the left. The interaction between the two factors was not significant ($F[1, 10] = 0.13$; $P = 0.72$).

Single-sample t -tests against zero, collapsed across hand starting position, were conducted in order to identify significant biases in the centring responses prior to or after adaptation. For lateral errors, mean pre-adaptation performance (+2.76 mm) did not differ significantly from zero, but the mean performance in the post-adaptation condition (+9.15 mm) was significantly shifted rightwards ($t[10] = -2.4$; $P < 0.05$). For radial errors neither pre- (−1.81 mm) nor post-adaptation performance (−0.02 mm) deviated significantly from zero.

2.2.3. Correlations between the measures of sensorimotor adaptation and the effect of prism adaptation on the haptic circle centring task

A series of bivariate correlations was computed to examine the relationships between the effects of prism adaptation on lateral and radial haptic circle centring errors (mean post-adaptation performance minus mean pre-adaptation performance) and each of the three measures of sensorimotor adaptation. No significant correlations were observed (all $r < 0.36$).

2.3. Discussion

The main aim of the present experiment was to investigate whether adaptation to a leftward prismatic displacement could induce a rightward shift of the performance in normal subjects on a task where no visual information was available. Leftward adaptation was found to induce a reliable rightward lateral shift of performance, but had no effect on radial errors. Accordingly, this treatment can simulate neglect behaviour in normal subjects, not only on visual line bisection tasks (Colent et al., 2000; Michel et al., 2003a; Berberovic & Mattingley, 2003), but also on a haptic version of visual line bisection. This supports the view that prism adaptation induces cross-modal effects at higher cognitive levels (i.e. the mental representation of space) (McIntosh et al., 2002), and extends this conclusion to normal brain functioning.

As noted in the Section 1, one alternative explanation for the present results might be that the rightward shift of performance does not reflect an alteration of the subjects' mental representation of the stimulus circle, but rather the induction of a rightward manual response bias similar to the classical proprioceptive shift, which is usually interpreted as a direct sensorimotor effect of prism adaptation. However, the absence of a significant correlation between the effects of prism exposure on performance of the haptic task and the proprioceptive shift argues against this hypothesis. Indeed, the effect found on the haptic task did not correlate with any of the measures of sensorimotor adaptation. Thus, it would appear that the effects found on the haptic task do not depend directly on the low-level sensorimotor effects

of prism adaptation, but rather on cognitive or noetic levels of space representation (Redding & Wallace, 1997). If this is indeed the case, then we might predict that a similar effect of prism adaptation should be found regardless of the sensory modality involved. The primary aim of the experiment reported in the following section will be to test this prediction in a visual circle centring task.

A collateral finding of Experiment 1 was that, prior to prism adaptation, normal subjects tended to err slightly rightward rather than leftward: that is, subjects did not show the so-called "pseudoneglect" phenomenon (Bowers & Heilman, 1980). This is interesting in light of the results of Sampaio & Philip (1991): these authors found that pseudoneglect was evident on a rod bisection task where both tactile and kinaesthetic information was available, whilst a reversed pseudoneglect (a small rightward bias) appeared on a purely kinaesthetic rod bisection task. Our results are therefore consistent with the idea that the haptic circle centring task relies on kinaesthetic factors. However, if the task is genuinely analogous to the visual line bisection task, then it could be predicted that, if the task were executed with the aid of visual information, pseudoneglect should appear. Experiment 2 tests this hypothesis.

Finally, we found that the pre-test performance in Experiment 1 was sensitive to where the hand movement started at the beginning of each trial: when the hand started from the left side of the circle, subjects tended to err rightward, whereas they erred leftward when the hand started from the right. An effect of hand starting position on radial errors was also observed: when the hand started moving from the left side, subjects tended to err away from the body, whereas they erred towards the body when the hand started from the right. One simple interpretation might be that the lateral overshooting is due to imprecision in the use of sensory feedback to correct movements. To explain the pattern of radial errors, one would additionally need to propose that, when making lateral movements with the right hand, there is a slight tendency for the movement to describe an arc, since it is natural for the right forearm to rotate around the elbow. The consequence would be a tendency for right-to-left movements to err slightly proximally with respect to the intended target, and vice versa for left-to-right movements. These overshoot biases would be amplified by the absence of visual feedback (Prablanc, Echallier, Komilis, & Jeannerod, 1979a; Prablanc C., Echallier, Jeannerod, & Komilis, 1979b). One consequent hypothesis is that the effect of hand starting position on both lateral and radial errors should be reduced if visual feedback is available. The final aim of Experiment 2 is to test this hypothesis.

3. Experiment 2

In Experiment 1, we showed that prism adaptation to a leftward visual displacement could induce a rightward bias on a haptic task and that this effect could be interpreted as

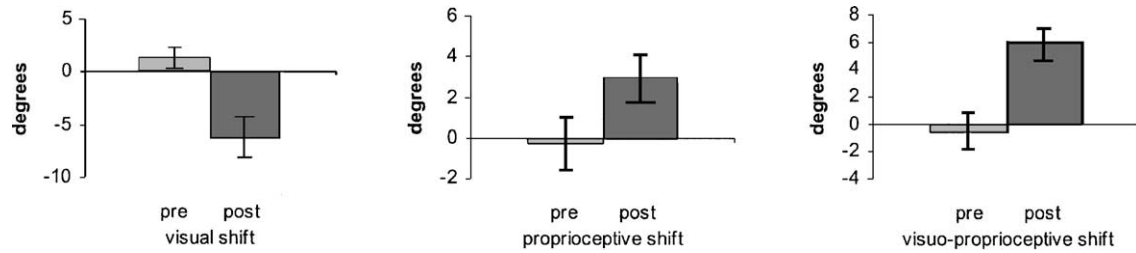


Fig. 4. Experiment 2. Subjective midline before (pre) and after (post) the prism adaptation procedure (values are expressed in degrees and the value 0 represents the true body midline): (a) visual; (b) proprioceptive; (c) visual-proprioceptive. In all cases, positive values indicate a rightward displacement from the midline and negative values indicate a leftward displacement.

being the result of a change at the level of the representation of space. In Experiment 2, we primarily wanted to test the hypothesis that adaptation to a leftward prismatic displacement would influence, in a similar manner, the performance of normal subjects on a task executed under visual guidance. As noted earlier, a positive effect would further support the hypothesis of central supramodal effects induced by prism adaptation.

3.1. Methods

3.1.1. Subjects

Twelve right-handed subjects (mean age: 29.9 years; S.D.: 7.73; range: 23–47) with no history of neurological or psychiatric illness participated in this study. Seven of these subjects had already participated in Experiment 1.

3.1.2. Visual circle centring task

Subjects were required to perform a visual circle centring task, adapted from the haptic task used in Experiment 1. A 30 cm diameter circular hole was cut into a rectangular sheet of thick grey paper (about 1 mm thick). This sheet was secured over a rectangular touch screen (resistive technology, accuracy 1 mm) so that the centre of the circular hole was at the centre of the touch screen. The screen was placed on a table in front of the subject, aligned with his/her body midline, at a distance of about 25–30 cm. On each trial, the subject's right hand was placed by the experimenter at one of two points on the circle circumference (left or right with respect to the subject). The subject was then asked to indicate the centre of the circle by touching it with the right index finger. The lateral and radial coordinates of each response were recorded by a computer connected to the touch screen. Rightward and distal errors were scored with positive values. Leftward and proximal errors were scored with negative values. Each subject performed 12 trials at each administration of the task: six trials with the hand starting on the left and six with the hand starting on the right, with the order of trials randomised. Subjects were free to move their head and trunk. Each subject performed the task twice: once before and once after adaptation to leftward displacing prisms.

3.1.3. Prism adaptation procedure and measures of sensorimotor adaptation

The prism adaptation procedure and the procedures for the measurement of sensorimotor adaptation were identical to those described for Experiment 1.

3.2. Results

3.2.1. Measures of sensorimotor adaptation

Fig. 4 shows the group mean estimate of subjective body midline location, prior to and after prism adaptation. The global pattern of results is similar to that obtained in Experiment 1 (see Fig. 2). For each measure separately, a paired *t*-test was used to compare pre- and post-prism performance. On this occasion, the leftward visual shift was significant ($t[11] = 4.56$; $P < 0.001$), the rightward proprioceptive shift was significant ($t[11] = -2.81$; $P < 0.025$), and the rightward total shift was highly significant ($t[11] = -7.39$; $P < 0.0001$).

3.2.2. Visual circle centring task

The mean results obtained in the visual centring task prior to and after adaptation, for lateral and radial errors, are shown in Fig. 5. A preliminary repeated measures ANOVA by adaptation condition (pre, post), starting position (left, right) and group (naive, non-naive) was conducted for lateral and radial errors separately. The factor of group was included to check for any differences in performance between those seven subjects who had participated in Experiment 1, and those five who had not. Neither ANOVA found a significant main effect ($F[1, 10] = 0.05$; $P > 0.8$ for lateral errors and $F[1, 10] = 1.09$; $P > 0.3$ for radial errors) or interaction involving the factor of group (group by starting position: $F[1, 10] = 1.63$; $P > 0.2$ for lateral errors and $F[1, 10] = 0.24$; $P > 0.6$ for radial errors; group by adaptation condition: $F[1, 10] = 2.97$; $P > 0.1$ for lateral errors and $F[1, 10] = 2.12$; $P > 0.1$ for radial errors), indicating that prior experience of Experiment 1 did not bias performance in Experiment 2. As far as the other factors and interactions are concerned, the following results were obtained.

For radial errors, no significant effects were observed. For lateral errors, the effect of adaptation condition was

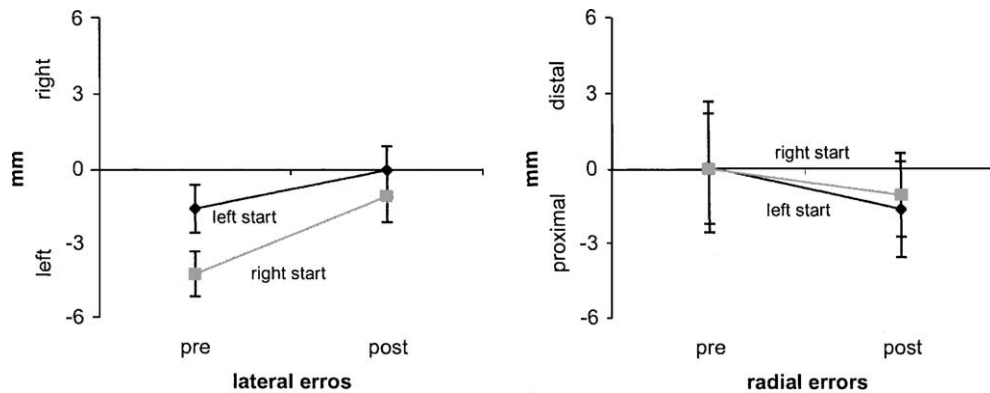


Fig. 5. Experiment 2. Results obtained on the visual circle centring task. The left panel shows the average lateral errors. The right panel shows the average radial errors. Values are expressed in mm and indicate the distance from the objective centre of the circle: rightward and distal errors are indicated with positive values; leftward and proximal errors are indicated with negative values.

significant ($F[1, 10] = 5.42$; $P < 0.05$), confirming the presence of a rightward shift of responses following prism adaptation, as observed in Experiment 1. The effect of starting position was also significant for lateral errors ($F[1, 10] = 9.55$; $P < 0.015$) and congruent with the findings of Experiment 1: when the hand started moving from the right, mean performance was more leftward than when the hand started from the left. However, in contrast with the results of Experiment 1, start position did not have a significant influence on radial errors. These main effects were modified by a significant interaction between adaptation condition and starting point ($F[1, 10] = 7.45$; $P < 0.025$). As Fig. 5 illustrates, the effects of prism adaptation were more evident for responses starting from the right than for responses starting from the left. This result is different from that observed in Experiment 1, where the same interaction was not significant (Fig. 6).

The significant interaction was then further explored by means of Sheffé's post hoc tests. This post hoc analysis confirmed the presence of a significant rightward shift of the performance, in the comparison between the pre- and post-test conditions, which was significant both when the movement of the hand started from the right ($P < 0.0001$) and from the left ($P < 0.025$). Furthermore, it showed the presence of a significant difference between the two pre-tests (left versus

right start: $P < 0.005$), but not between the two post-tests ($P > 0.3$). These results not only confirm the existence of an effect on the performance induced by prism adaptation, but also that the effects of prism adaptation were more evident for the condition where the hand started moving from the left rather than when the hand started moving from the right.

As for Experiment 1, single-sample *t*-tests against zero, collapsed across hand starting position, were conducted. For lateral errors, mean pre-adaptation performance (-5.04 mm) was significantly biased leftward ($t[11] = 3.89$; $P < 0.004$) (i.e. pseudoneglect), while mean post-adaptation performance (-1.14 mm) did not differ significantly from zero. For radial errors, neither pre- nor post-adaptation performance deviated significantly from zero.

3.2.3. Correlations between the measures of sensorimotor adaptation and the effect of prism adaptation on the visual circle centring task

Bivariate correlations were computed between the effects of prism adaptation on lateral and radial visual circle centring errors (mean post-adaptation performance minus mean pre-adaptation performance) and the three measures of sensorimotor adaptation. No significant correlations were observed (all $r < 0.26$).

3.2.4. Comparisons between Experiment 1 and Experiment 2

One suggestion advanced to explain the significant effect of hand starting position in Experiment 1 was that a natural tendency to overshoot errors was exacerbated by the lack of visual feedback in the haptic circle centring task. This predicts that the availability of visual feedback should reduce the influence of hand starting position. To test this hypothesis, an independent samples *t*-test between the haptic and the visual tasks was conducted on the difference in performance between responses starting from the left and from the right in the pre-adaptation condition. The magnitude of the difference in mean error associated with the hand

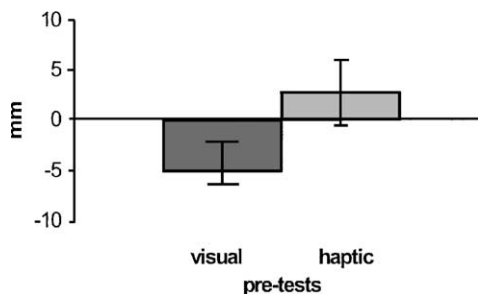


Fig. 6. Comparison between the performance obtained in the two experiments in the pre-test collapsed across hand start position.

start position was significantly larger for the haptic task (25.81 mm) than for the visual task (2.63 mm) ($t[21] = 4.2$; $P < 0.0005$).

A similar analysis was conducted to investigate whether the magnitude of the prism adaptation effect in the haptic task was significantly larger than that obtained in the visual task. An independent samples t -test between the haptic and visual tasks was conducted on the difference between the lateral errors before and after prism adaptation. This t -test found that the prism effect obtained in the haptic task was larger than that obtained in the visual task ($t[21] = 2.14$; $P < 0.05$).

3.3. Discussion

The main aim of Experiment 2 was to test the hypothesis that adaptation to a leftward visual displacement could induce a rightward shift of the performance of normal subjects on a visual version of the circle centring task employed in Experiment 1. The results confirmed the presence of such a shift, with the effects of prism adaptation again limited to the lateral dimension. Moreover, the shift in circle centring performance induced by prism exposure was again uncorrelated with all three measures of sensorimotor adaptation, indicating that the effect is unlikely to be due directly to the sensorimotor effects of the treatment. Rather, our results again imply that prism adaptation induces additional changes at a higher representational level, even in normal subjects. This outcome is in line with the data of Colent et al. (2000), Michel et al. (2003a) and Berberovic & Mattingley (2003), showing that prism adaptation can induce a rightward bias in visual line bisection tasks. Furthermore, as predicted, the effect of hand starting position was reduced in Experiment 2 relative to Experiment 1, both for lateral and radial errors, suggesting that this bias was due to the lack of visual feedback in the task employed in Experiment 1. Finally, as expected, the pseudoneglect phenomenon appeared in the visual task, confirming the hypothesis that the pre-test leftward bias may be attributed to a hyper-correction of a rightward bias again due attributable to the lack of visual control of the performance.

4. General discussion

We have presented two investigations of the effects of prism adaptation on the performance of normal subjects in spatial judgement tasks. Our main finding is that prism adaptation biased the performance of normal subjects both on a visual and on a haptic task and that neither effect depends directly on sensorimotor after-effects. Thus, adaptation to a visual displacement can induce an effect on the representation of space in normal subjects. This effect is qualitatively similar to that produced by unilateral neglect. It is worth recalling here that while the effects of prism adaptation on sensorimotor realignment processes are well established, it

is only recently that the possibility that this procedure can also affect higher levels of cognitive processing, both in patients and in normals, has become a matter of intensive research and theoretical debate. Our study was mainly designed to deepen the understanding of these latter kinds of effects and their relationship with the well-established sensorimotor after-effects.

4.1. Prism adaptation induces a rightward shift of performance both on a haptic and on a visual circle centring task

In Experiment 1, subjects were requested to locate the centre of a haptically explored circle before and after adaptation to 15° leftward displacing prisms. In Experiment 2, subjects performed a similar circle centring task, but this time in free vision and with no manual exploration of the circle circumference. In both experiments, a significant rightward shift of centring responses was induced by the adaptation procedure. These results are in line with existing data on the cognitive effects of sensorimotor adaptation and provide further data useful for the understanding of these effects in normals and presumably also in neglect patients. Of primary relevance, McIntosh et al. (2002) found a significant amelioration of left neglect following rightward prism adaptation in the haptic task employed in Experiment 1. Our results extend this phenomenon to normal subjects and thereby strengthen the evidence for a cross-modal effect of this procedure. The main distinction, of course, is that whilst adaptation to a rightward displacement ameliorates the symptoms of left neglect patients, adaptation to leftward displacement induces left neglect-like behaviour in normal subjects.

Our results are also in line with the known effects of prism adaptation on normal performance of several visual tasks commonly used for neglect assessment. Colent et al. (2000) and Michel et al. (2003a) showed that adaptation to a leftward prismatic displacement induced a small but significant rightward shift of performance on visual bisection tasks, simulating left neglect. One argument favouring the hypothesis that the effects observed were attributable to high-level cognitive changes, and not to sensorimotor mechanisms, was that these effects were evident on purely perceptual bisection tasks in which manual responses were not required. Moreover, it was also possible to induce a line position effect (i.e. the rightward bias was present only on the left and on the centre, but not on the right of the mid-sagittal plane) and a line length effect (i.e. the rightward bias was larger for longer lines), which are well-established features of neglect performance (see Michel et al., 2003a). In addition, Berberovic & Mattingley (2003) showed that leftward adaptation induced a significant rightward bias in normal subjects, both in peripersonal and extrapersonal space. The findings of the present study add significantly to this body of research by demonstrating that, although prism adaptation depends

upon a visual displacement, it can nonetheless affect performance of spatial tasks with no explicit visual component.

4.2. *The rightward shift of performance is produced at a central level of spatial information processing*

Prism exposure induces a uniform shift of the visual field, thereby manipulating the body-space interface in egocentric coordinates. Sensorimotor after-effects reflect changes in the coding of egocentric space and their presence is measured using straight-ahead pointing tasks (at least for the proprioceptive shift and the total shift) which are commonly considered to be pure egocentric tasks. By contrast, both the haptic and the visual tasks used in our experiments can be considered as object-centred tasks, since successful performance on these tasks depends upon an accurate representation of the stimulus object (circle). Accordingly, the observed effects of prism adaptation on these tasks may be interpreted as reflecting a change in allocentric (i.e. object-centred) spatial representation, consistent with the characterisation of these effects as occurring at a level of spatial representation more abstract than the coding of egocentric co-ordinates. In addition, the fact that the adaptation to a visual distortion induced an effect on a haptic task already supports the hypothesis of cross-modal central effects.

Beyond these purely theoretical considerations, we wanted to assess the degree to which the effects of prism adaptation on our spatial judgement tasks were related to the sensorimotor after-effects of the adaptation procedure. We predicted that, if the effects on the circle centring tasks were due to sensorimotor re-mappings, then a significant correlation should emerge with at least one of the sensorimotor after-effects measured. In fact, no significant correlations were found in either experiment. We therefore propose that the effects of prism adaptation on the haptic and visual centring tasks reflect changes in the cognitive representation of space and that they represent a simulation, not only of kinaesthetic and visual neglect behaviour, but also of the underlying cognitive impairments induced by the brain lesions of these patients. This view is compatible with the finding that leftward and rightward prism adaptation do not produce symmetrical cognitive after-effects although a symmetry is observed at the level of the direct sensorimotor consequences of the adaptation (Tilikete et al. 2001; Michel, Rossetti, Rode, & Tilikete, 2003b). Prism adaptation may be a procedure with which it is possible to induce effects similar to the ones obtainable by the application of right posterior parietal repetitive transcranial magnetic stimulation (rTMS), as shown recently by Fierro et al. (2000). It could therefore be interesting, in future investigations, to investigate the possibility of mutual interference and interaction between prism adaptation and rTMS. This kind of study might provide useful data for determining the cerebral areas mediating the effects seen in neglect patients and normal subjects, which is at the moment a matter of

speculation. In fact, even though the neural structures considered to be involved in prism adaptation have long been restricted to the cerebellum (see Jeannerod & Rossetti, 1993), it seems that the improvement of neglect symptoms may depend on more central cognitive mechanisms (see Rossetti et al., 1998; Rossetti & Rode, 2002), perhaps mediated by an indirect left parietal inhibition (Rode et al., 2003; Pisella, Michel, Gréa, Vighetto, & Rossetti, 2004).

Michel et al. (2003a; Experiment 3) compared the effects of active and passive prism adaptation on manual and perceptual visual line bisection tasks, showing that only active adaptation to the visual displacement had a cognitive effect, as is also the case for the sensorimotor after-effects (e.g. Held, 1965). These data, taken together with the absence of any significant correlation between the effects on the haptic and visual tasks and the measures of sensorimotor adaptation in the present study, suggest that while the induction of the sensorimotor and cognitive effects of prism adaptation may share some common processes, the sensorimotor and cognitive after-effects may nonetheless be dissociable. In addition, they support the hypothesis that prism adaptation may produce supramodal effects, at the cognitive or noetic level of space representation (Redding & Wallace, 1997). Finally, there is recent evidence, which shows that the acquisition of adaptation to a lateral visual displacement is preserved in patients with bilateral parietal damage (Pisella et al., 2004).

4.3. *Secondary findings*

In addition, three collateral aspects of our results warrant discussion here.

Pre-test performance: In our study, we found that the mean pre-test performance was different between the two tasks: whereas under visual guidance, subjects tended to make leftward errors (i.e. pseudoneglect; Bowers & Heilman, 1980), the same tendency was not present when visual feedback was not available. This result is in line with the claim that the pseudoneglect phenomenon is characteristic of normal performance of visual bisection tasks, but not of pure kinaesthetic tasks (e.g. Sampaio & Philip, 1991; Girardi, Daini, & Vallar, 2002), supporting an interpretation of the pseudoneglect phenomenon as due to cognitive processes distinct from those giving rise to rightward errors in unilateral neglect (Girardi et al., 2002; Girardi, 2002).

The effect of hand start position: In both experiments, performance was also influenced by the start position of the responding hand. One possible a priori expectation was that performance could have been subject to a cueing effect, with performance biased towards the cued side, as usually happens in neglect patients (e.g. Riddoch & Humphreys, 1983) and normal subjects performing visual line bisection (e.g. Nichelli, Rinaldi, & Cubelli, 1989; Milner, Brechmann, & Pagliarini, 1992). In our haptic task, the cueing effects would derive from the proprioceptive sensations coming from the arm. In the visual task, the hand start position would constitute a visual, as well as a proprioceptive cue, leading to

the possible prediction that cueing effects in the visual task should be more powerful than those in the haptic task. However, the results did not support the existence of any such cueing effects. First, although the side of start influenced responses, this effect was directionally opposite to that predicted by the cueing hypothesis. Second, the effect of hand start appeared to be larger for the haptic task than for the visual task, rather than vice-versa. Finally, an effect of the starting position of the hand was also observed in the radial dimension (for the haptic task), which cannot be easily interpreted as a cueing effect. Rather, a simpler post hoc explanation can account for all these findings. The overshooting of the intended target can be attributed to a natural imprecision in the use of sensory feedback to correct movements, which would be more evident when visual feedback is not available (Prablanc et al., 1979a,b). This would account for the fact that the effects of hand starting position were less evident in the visual task than in the haptic task. Therefore, as a main conclusion on this point, the biasing effect of hand start position may be conveniently attributed to sensorimotor mechanisms.

The interaction between effects due to prism adaptation and to the starting position of the hand movements. Two main effects were observed in these experiments. First, a representational effect was observed, consisting of a global rightward shift of the performance due to prism adaptation. Second, a sensorimotor effect was present, consisting of a tendency to overshoot the intended target. In the haptic task, these effects were independent, as shown by the lack of a significant interaction between them. By contrast, the interaction did reach significance in the visual task, with a larger effect of prism adaptation for the right hand start position than for the left. Tentatively, it could be proposed that prism adaptation had a partially different effect on two different components of the same supramodal representation.

Finally, we have suggested that the effect due to the starting position of the hand was larger on the haptic task because of the lack of visual feedback. One neural structure commonly involved in movement correction by sensory feedback, especially visual, is the cerebellum. Furthermore, several case studies have shown that the ability to adapt to a visual displacement can be disrupted by cerebellar lesions (review in Jeannerod & Rossetti, 1993). The cerebellum is richly interconnected with the parietal lobe (Glickstein, 1997; Schmahmann, 1998), the cerebral area classically associated with neglect (Vallar & Perani, 1986, 1987; Vallar, 1993, 2001; Halligan et al., 2003). One possible further inference that could follow these observations is that, since the effect of prism adaptation and the effect of hand movement direction interacted on the visual task and not on the haptic task, the cognitive processes which are involved in the performance in the visual task may be functionally (and perhaps also anatomically) closer to those sensorimotor processes involved in error movement correction and sensorimotor adaptation.

5. Conclusions

The main finding of this study is that prism adaptation can affect normal subjects' performance both of a haptic and a visual circle centring task, and that these effects are not directly attributable to changes in sensorimotor mechanisms, but reflect changes in central cognitive processes involved in the representation of space. We have therefore suggested that prism adaptation in normal subjects induces, and does not merely simulate, cognitive spatial biases that in neglect patients are caused by brain lesions. Now that it has been firmly established that prism adaptation can induce cognitive effects both in neglect patients and in normal subjects, and both in visual and haptic tasks, future investigations should investigate how this procedure can influence the heterogeneous components of the pathological and simulated symptoms of unilateral neglect.

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