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Prism adaptation differently affects motor-intentional and perceptual-attentional biases in healthy individuals

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ABSTRACT

Prism adaptation (PA) has been shown to affect performance on a variety of spatial tasks in healthy individuals and neglect patients. However, little is still known about the mechanisms through which PA affects spatial cognition. In the present study we tested the effect of PA on the perceptual-attentional "where" and motor-intentional "aiming" spatial systems in healthy individuals. Eighty-four participants performed a line bisection task presented on a computer screen under normal or right-left reversed viewing conditions, which allows for the fractionation of "where" and "aiming" bias components (Schwartz et al., 1997). The task was performed before and after a short period of visuomotor adaptation either to left- or right-shifting prisms, or control goggles fitted with plain glass lenses. Participants demonstrated initial leftward "where" and "aiming" biases, consistent with previous research. Adaptation to left-shifting prisms reduced the leftward motor-intentional "aiming" bias. By contrast, the "aiming" bias was unaffected by adaptation to the right-shifting prisms or control goggles. The leftward "where" bias was also reduced, but this reduction was independent of the direction of the prismatic shift. These results mirror recent findings in neglect patients, who showed a selective amelioration of right motor-intentional "aiming" bias after right prism exposure (Fortis et al., 2009; C.L. Striemer & J. Danckert, 2010). Thus, these findings indicate that prism adaptation primarily affects the motor-intentional "aiming" system in both healthy individuals and neglect patients, and further suggest that improvement in neglect patients after PA may be related to changes in the aiming spatial system.

1. Introduction

The human brain has a remarkable ability to quickly learn and adapt to environmental changes. One such change – perturbation of the visual field – has been studied using wedge prisms for the last two centuries (Stratton, 1896). Exposure to lateral shifting prisms induces an optical deviation that causes objects to appear laterally deviated from their actual location. The classic procedure of prism adaptation (PA) consists of repeated active movements toward visual targets while subjects wear prismatic goggles (Kornheiser, 1976; Redding & Wallace, 1997). When subjects first point to an object, they initially perform a pointing error in the same direction as the optical deviation (e.g., rightward deviation for rightward shifting prisms). *Adaptation* to the lateral shift induced by prisms is demonstrated by a gradual correction of the pointing errors in subsequent movements and it is accompanied by contralateral pointing errors once prisms are removed, termed the *aftereffect* (e.g., leftward deviation for rightward shifting prisms). Importantly, recent work has demonstrated that prism adaptation may have therapeutic implications, improving left spatial neglect on both laboratory and functional tasks (Keane, Turner, Sherrington, & Beard, 2006; Pisella, Rode, Farne, Tilikete, & Rossetti, 2006; Rossetti et al., 1998; for a review see Rode, Klos, Courtois-Jacquin, Rossetti, & Pisella, 2006). Here we explored the potential mechanism of the therapeutic effects of prism adaptation in a group of healthy young adults.

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1.1. Spatial neglect and prism adaptation

Spatial neglect is a complex and heterogeneous disorder more frequently following right- than left-hemisphere brain damage that causes a failure to report, respond or orient toward stimuli presented in the space opposite the brain lesion (Driver & Mattingley, 1998; Halligan, Fink, Marshall, & Vallar, 2003; Heilman, Watson, & Valenstein, 1979; Ringman, Saver, Woolson, Clarke, & Adams, 2004; Vallar, 1998). It can affect different cognitive mechanisms mediating attention, intention, and/or space representation. Errors in neglect patients, for example, may be primarily due to perceptual-attentional "where" bias, demonstrated in reduced perceptual resources, or unawareness of stimuli in contralesional space (Barrett, Beversdorf, Crucian, & Heilman, 1998; Barrett, Crucian, Beversdorf, & Heilman, 2001; Rapcsak, Verfaellie, Fleet, & Heilman, 1989). Others may exhibit deficits primarily in motor-intentional "aiming" systems with specific impairments in the planning and execution of actions toward the contralesional hemispace, even in the absence of primary motor deficit (Heilman, 2004). "Aiming" impairments have been demonstrated in limb, body, or even eye movements (Barrett, Crucian, Schwartz, & Heilman, 1999; De Renzi, Colombo, Faglioni, & Gibertoni, 1982; Ringman, Saver, Woolson, & Adams, 2005). In many cases, both "where" perceptual-attentional and "aiming" motor-intentional deficits may be observed in spatial neglect patients, but these deficits may also be observed in relative isolation (Barrett & Burkholder, 2006; Danckert & Ferber, 2006; Kerkhoff, 2001; Mapstone et al., 2003). Spatial neglect, by definition, causes functional disabilities affecting everyday life (Barrett et al., 2006), and is also associated with poor rehabilitation outcomes, and loss of independence (Denes, Semenza, Stoppa, & Lis, 1982; Katz, Hartman-Maeir, Ring, & Soroker, 1999; Paolucci, Antonucci, Grasso, & Pizzamiglio, 2001). Improvement in neglect symptoms following prism exposure has been reported in visuospatial tasks (e.g., cancellation, drawing, line bisection; Rossetti et al., 1998), as well as mental imagery tasks (Rode, Rossetti, & Boisson, 2001; Rossetti et al., 2004) and may extend to different sensory modalities such as tactile (Maravita et al., 2003) and auditory extinction (Jacquin-Courtois et al., 2010). PA shows clear effects on motor performance such as postural imbalance or actions that require motor activation such as wheelchair navigation (Jacquin-Courtois, Rode, Pisella, Boisson, & Rossetti, 2008; Michel, Rossetti, Rode, & Tilikete, 2003; Shiraishi, Yamakawa, Itou, Muraki, & Asada, 2008; Tilikete et al., 2001). However, not all neglect-related symptoms, nor treated patients, improve (e.g., Dijkerman et al., 2003; Ferber, Danckert, Joanisse, Goltz, & Goodale, 2003; Ferber & Murray, 2005; Morris et al., 2004; Rousseaux, Bernati, Saj, & Kozlowski, 2006; Sarri, Greenwood, Kalra, & Driver, 2010; Sarri, Kalra, Greenwood, & Driver, 2006). Indeed, the mechanism through which PA ameliorates spatial neglect still remains unclear. Recent studies in neglect patients have hypothesized a specific effect of prism adaptation on the "aiming" component of spatial mapping as shown by a selective improvement in the motor bias, but not the perceptual bias, of a line bisection task (Fortis, Kornitzer, Goedert, & Barrett, 2009; C.L. Striemer & J. Danckert, 2010). We wished to learn whether a primary effect of PA on spatial "aiming" could be observed in a group of healthy young subjects. Some studies have detected an asymmetric effect of adaptation to left- and right-shifting prisms in healthy young adults mirroring that of neglect patients, with healthy young adults showing greater generalization of aftereffects after exposure to left-, as opposed to right-shifting prisms (Berberovic & Mattingley, 2003; Loftus, Nicholls, Mattingley, & Bradshaw, 2008; Loftus, Vijayakumar, & Nicholls, 2009; Michel et al., 2003, but see Michel, Vernet, Courtine, Ballay, & Pozzo, 2008; Morton & Bastian, 2004). Although these effects may be mediated in part by the a priori leftward baseline bias of young healthy individuals on visuomotor tasks (Goedert, Leblanc, Tsai, & Barrett, 2010), they are similar to PA effects in neglect patients who have an a priori rightward baseline bias on visuomotor tasks, and show adaptation to right-, but not left-, shifting prisms (Rossetti et al., 1998). If the "aiming" hypothesis of the therapeutic effects of PA were correct, we would expect to see dissociable effects of left- and right-shifting prisms on motor-intentional aiming performance in healthy young adults.

1.2. Decoupling motor-intentional and perceptual-attentional influences on performance

Our investigation focused on how PA may alter the spatial distribution of perceptual-attention versus motor-intention in a line bisection task. One means to separate the perceptual and motor contributions of a visually guided movement is by asking subjects to perform a visuo-motor task in which the viewed perception of their movement is dissociated from the direction of their action. This method has been used to decouple "where" and "aiming" components in visuo-motor tasks with video (Adair, Na, Schwartz, & Heilman, 1998; Barrett & Burkholder, 2006; Barrett et al., 1999, 2001; Coslett, Bowers, Fitzpatrick, Haws, & Heilman, 1990; Na et al., 1998; Schwartz, Adair, Na, Williamson, & Heilman, 1997), mirrors (Tegner & Levander, 1991), and an epidiascope (Nico, 1996). All of these methods reverse the orientation of visually viewed hand movement relative to the direction of actual hand movement in the workspace. In the paradigm of Schwartz et al. (1997), participants performed a line bisection task while viewing their hand and the line via a TV screen, rather than directly. The image presented on the screen was either natural or horizontally reversed with respect to the workspace where the participant bisected lines. In the natural condition, the visual feedback of the movement projected on the screen was congruent with the movement performed, so that rightward hand movements appeared rightward on the screen, and leftward hand movements appeared leftward. However, in the reversed condition, the display was horizontally reversed so that visual feedback of rightward movements appeared leftward, and vice versa. If a participant errs toward the same side (for example, moving toward the left side of the workspace) under both natural and reversed viewing conditions, it suggests that the participant's bias is relatively insensitive to visual feedback and thus may be an output-related motor-intentional or "aiming" bias. If a participant's error changes direction between the natural and reversed viewing conditions (e.g., the participant made leftward responses under natural viewing, but rightward responses under the reversed viewing), it suggests that the bias is dependent on visual input, and thus may be a perceptual-attentional or "where" spatial bias (Schwartz et al., 1997). In their sample of young to middle-aged adults, Schwartz et al. reported that the majority of the participants' line bisection errors were "where" in nature. Directly comparing performance in natural and reversed viewing conditions (Na et al., 1998; Schwartz et al., 1997) determines whether spatial errors are *primarily* "where" or "aiming" in nature. However, both "where" and "aiming" systems would be expected to work together to produce a visually guided action, and the procedure of Schwartz et al. (1997) does not separately and simultaneously quantify "where" versus "aiming" spatial bias. We used a paradigm similar to that of Schwartz et al. to decouple "where" and "aiming" spatial bias, but simultaneously quantified these biases after Barrett and Burkholder (2006) using Eqs. (1) and (2) below:

$$\text{Natural Error} = \text{Aiming Component} + \text{Where Component} \quad (1)$$

$$\text{Reversed Error} = \text{Aiming Component} - \text{Where Component} \quad (2)$$

In the natural condition, both "where" and "aiming" components are aligned, contributing additively to performance in the same direction (Eq. (1)). However, in the reversed condition, the "where" component is reversed 180° and thus changes its sign (Eq. (2)).

Because "where" and "aiming" functions are intimately linked in adaptive behaviour, the reversed condition imposes unnatural task demands by definition. We previously presented evidence confirming the validity of "where" and "aiming" spatial bias components fractionated by this method, by demonstrating response of healthy individuals to perceptual-attentional and motor-intentional cueing conditions (Garza, Eslinger, & Barrett, 2008). As predicted, visual distraction selectively affected perceptual-attentional "where", but not motor-intentional "aiming" bias. Conversely, motor cueing selectively affected motor-intentional "aiming", but not "where" bias components. Our team also demonstrated validity of the natural/reversed line bisection procedure in neglect patients receiving interventions expected to affect primarily "where" versus "aiming" bias (Barrett & Burkholder, 2006; Barrett et al., 1999, 2001).

In the present work, we evaluated whether PA would primarily affect "aiming" spatial bias by studying the effects of PA on "where" and "aiming" spatial errors in a video line bisection task, using a modified version of the Schwartz et al. (1997) paradigm in which participants bisected lines using a computer.

1.3. Current study

Participants were exposed to right- or leftward-shifting prisms or control goggles fitted with plain glass lenses. We used the computerized line bisection task to decouple the perceptual-attentional "where" and motor-intentional "aiming" components of their line bisection errors. Consistent with previous findings, we expected that adaptation to a leftward shifting prism would affect the motor-intentional "aiming" component of the computerized line bisection task, whereas no change was expected for the right-shifting group.

2. Methods

2.1. Participants

Eighty-four right-handed participants (35 males, 49 females, mean age: 19 years; SD: 2.11; range 18–31), naive to the purpose of the study, were enrolled from the Department of Psychology of Seton Hall University, South Orange, NJ and gave their informed consent prior to participating in the study. Twenty-eight participants were exposed to right-shifting prisms (13 male, mean age: 19 years, SD: 1.15, range 18–23), 28 to left-shifting prisms (11 male, mean age: 20 years, SD: 3.18, range 18–31), and 28 to control goggles fitted with plain glass lenses (11 male, mean age: 19 years, SD: 1.36, range 18–25). All participants were right handed and had normal or corrected to normal vision.

2.2. Prism adaptation procedure

Participants completed the following tasks in this order: (1) a pre-exposure evaluation; (2) exposure condition to either rightward or leftward lateral shift, or to control goggles fitted with plain glass lenses, and (3) a post-exposure evaluation identical to the pre-adaptation one. During prism adaptation with right - or left-lateral shift, participants wore Bernell™ Deluxe Prism Training Glasses fitted with optical wedge prisms shifting participants' vision 12.4° laterally. During adaptation with control goggles, and during pre- and post-adaptation evaluation, participants wore Bernell™ frames fitted with plain glass lenses. The glasses were inserted into a light-proof goggle that prevented participants from seeing any undistorted portion of the peripheral visual field.

2.2.1. Exposure condition

Participants sat at a table with their right hand positioned on top of the table near the center of their body. This served as a starting point for all movements. A narrow shelf (19 cm high × 14 cm wide) occluded the participant's view of the early part of any arm movements and a black cloth attached from the participant's neck to the shelf blocked the view of the starting position of the arm. The adaptation procedure consisted of a line bisection task. The arm's movement remained occluded to vision for most of its path and became available in the last part of the trajectory. Depending on the length of the individual participants' arms, participants could see the distal third of their handpath (approximately 20–22 cm including the hand, wrist, and early part of the arm). Participants were asked to mark the perceived center of a horizontal line by performing one quick out-and-back motion. They were also instructed to not correct the movement trajectory in the last part, when the hand became visible. After each movement, the participant returned her hand to the starting position at body center. Sixty horizontal lines (240 mm length, 2.0 mm thick) were presented one at a time on sheets of standard letter size paper. The lines were placed in the right, center, or left position relative to the participant's midsagittal plane. The right/left position deviated from center by 21 cm. The lines were presented twenty times in each position in a pseudorandom order, such that each group of 6 trials included two instances of the three positions (right, center, and left). The exposure phase lasted about 10 min. The difference between the deviation on the initial and last six trials was used to index the extent to which participants were able to correct the lateral deviation induced by the prismatic displacement.

2.2.2. Pre- and post-exposure evaluation

During the pre- and post-exposure evaluation, two aftereffect measurements (visual-proprioceptive and proprioceptive tests), and a computerized line bisection fractionation task were administered.

2.2.2.1. Proprioceptive test. Participants were blindfolded and used their right index finger to point straight ahead 5 times to indicate the subjectively estimated position of their body midline. After each movement, the experimenter prompted them to return to the starting position in the middle of their chest. A transparent panel (1.0 m long, 0.5 m high) marked with a ruler was placed at the distance of 55 cm, aligned with the center of participants' body (Mark & Heilman, 1990), allowing the experimenter to record the deviation of the finger position from the true objective body midline. Rightward errors were recorded as positive and leftward errors as negative (in degrees).

2.2.2.2. Visual-proprioceptive test. Participants sat at a table in front of a wooden box (35 cm high, 100 cm width, and 28 cm deep). A black cloth attached from the participant's neck to the upper side of the box blocked the initial view of arm movements and the shelf prohibited participants from viewing the remainder of their pointing movement. With eyes open, participants performed six pointing movements toward a visual target (pen) presented by the experimenter at the distal edge of the top face of the box. The target was presented two times in each of three positions (straight-ahead, 21° rightwards, and 21° leftwards), in a pseudorandom order. After each movement, the experimenter prompted participants to return to the starting position in the middle of their chest. The distal side of the box was closed by a transparent panel marked with a ruler visible only from the experimenter's side, such that pointing error could be recorded. Pointing errors were measured in degrees of distance between the finger and the target: a positive score denoted a rightward displacement with respect to the position of the target, a negative score a leftward error.

2.2.2.3. Computerized line bisection task. Participants were seated at a table in front of a computer screen (set to 640 × 480 pixel resolution). The screen was positioned at the distance of 50 cm and aligned with the center of the participant's body. The participants' task was to mark the center of twenty horizontal lines (265 mm length, 3 mm thick). Each line was presented alone and displayed at the center of the screen at participants' eye level. Between each line bisection trial a random-dot visual mask appeared for 500 ms. Participants used a computer mouse to click on the location that they believed to be the center of the line. The right arm and hand movement was occluded from view via a wooden box covering the arm and hand (25 cm high, 80 cm wide, and 25 cm deep) and via a black cloth attached from the participants' neck to the proximal side of the box. During the first half of the trials (10 lines, natural condition), the movement of the mouse and the pointer on the video screen was congruent: rightward movement of the mouse moved the pointer rightward and leftward movement, leftward. In the other half of the trials (10 lines, reversed condition) the right-left video feedback of the pointer movement was reversed. Thus, in the reversed condition, rightward movement of the mouse moved the pointer leftward on the video screen and vice versa.

The deviation from the objective midpoint of the line presented in the natural and reversed conditions was scored by transforming from pixels to the nearest mm: a positive value denoted a rightward error, a negative value, a leftward error. Using Eqs. (1) and (2) and their algebraic equivalents, we fractioned individual participants' error in the natural and reversed conditions into its "where" (Eq. (3)) and "aiming" (Eq. (4)) spatial bias components (Barrett & Burkholder, 2006; Barrett et al., 2001; Chen, Erdahl, & Barrett, 2009; Garza et al., 2008).

$$\text{Where Component} = \frac{\text{Natural Error} - \text{Reversed Error}}{2} \tag{3}$$

$$\text{Aiming Component} = \frac{\text{Natural Error} + \text{Reversed Error}}{2} \tag{4}$$

3. Results

We adopted an alpha (α) of 0.05. We followed up all significant interactions with orthogonal, single degree-of-freedom, simple main effects tests after Keppel and Wickens (2004, p. 520) and used a Bonferroni-corrected alpha when making multiple means comparisons with t tests. Where appropriate, we reported the partial eta-squared (η_p^2) measure of effect size.

3.1. Pre-test/baseline

Separate one-way ANOVAs with group (right- and left-shifting prisms, and control goggles) as a factor revealed that the groups were similar at baseline for all tests: proprioceptive test, $F(2,81) = 0.57$, $p = 0.566$, $\eta_p^2 = 0.01$; visual-proprioceptive test, $F(2,81) = 0.16$, $p = 0.851$, $\eta_p^2 = 0.01$; natural, $F(2,81) = 2.12$, $p = 0.124$, $\eta_p^2 = 0.05$, and reversed, $F(2,81) = 1.10$, $p = 0.332$, $\eta_p^2 = 0.03$, computerized line bisection tasks; "where", $F(2,81) = 1.71$, $p = 0.209$, $\eta_p^2 = 0.04$, and "aiming", $F(2, 81) = 1.40$, $p = 0.260$, $\eta_p^2 = 0.03$, fractionated bias components.

We performed separate single-sample t tests versus zero on the measures to determine the accuracy of performance at baseline using the Bonferroni-corrected α of 0.01. For the proprioceptive and visual-proprioceptive tests, participants' baseline performance was accurate ($ts < 1.3$, $ps \geq 0.200$). Consistent with the leftward bias of healthy young participants observed in previous studies, the natural line bisection performance ($M = -2.69$, SD = 3.6), and the fractionated "where" ($M = -2.16$, SD = 3.6) and "aiming" biases ($M = -0.52$, SD = 1.4) were significantly leftward biased at baseline ($ts \geq 3.4$ and $ps \leq 0.001$, for all tests; all errors in mm).

3.2. Prism exposure

The difference between the initial and last six trials of the exposure condition was examined to assess whether participants were able to correct the lateral deviation induced by the prisms. As can be seen in Table 1, participants exposed to right- or left-shifting prisms showed an initial line bisection error deviated in the direction of the lateral shift induced by prisms, but this error was reduced at the end of adaptation. A 3 × 2 mixed ANOVA with Prisms (left, right or control) and Time (first six trials, last six trials) as factors revealed a main effect of Prisms, $F(2,81) = 28.9$, $p < 0.001$, $\eta_p^2 = 0.42$ and a Prisms by Time interaction, $F(2,81) = 23.4$, $p < 0.001$, $\eta_p^2 = 0.37$. Simple main effects tests on the effect of Time at each level of Prism revealed that both the left-shifting, $F(1,81) = 25.1$, $p < 0.001$, $\eta_p^2 = 0.24$, and right-shifting, $F(1,81) = 20.5$, $p < 0.001$, $\eta_p^2 = 0.20$, prism groups reduced their prism-induced error between the first and last six trials of adaptation. The leftward deviation of the control group, however, did not significantly change between the first and last trials of the exposure condition, $F(1,81) = 2.9$, $p = 0.092$, $\eta_p^2 = 0.04$.

Table 1
Adaptation effect. Mean deviation of the initial and last six trials of the exposure condition across the three groups: right- and left-shifting prisms, and control plain goggle. Values represent the deviation (expressed in mm) from the objective center of the line: positive values indicate rightward deviation, and negative values indicate leftward deviation. Shift represents the difference between the first and last six trials of the exposure condition. Values in parentheses are standard deviations. Asterisks denote a significant reduction ($ps < 0.001$) in error from the first to the last six trials.

	Initial 6 trials	Last 6 trials	Error reduction
Right-shifting prism	3.71	0.96	2.75*
	(4.95)	(4.64)	(2.86)
Left-shifting prism	−6.57	−3.52	3.04*
	(3.56)	(3.17)	(3.88)
Control goggle	−1.93	−0.89	1.04
	(3.67)	(3.54)	(2.84)

3.3. Pre–post test differences

Analyses of pre- versus pos-test differences were performed using mixed ANOVAs with Prisms (left, right and control) and Pre/Post (pre, post) as factors. Furthermore, because the effects of prisms may wear off as a participant performs multiple post-test assessments, all analyses of pre–post differences were initially carried out with the inclusion of Test-order (first, second, or third) as a factor. For the proprioceptive, visual-proprioceptive, natural line bisection, and "aiming" bias there were no main effects nor interactions involving Test-order (all $ps > 0.09$). Thus, for simplicity of reporting, the order factor was dropped from these analyses. Effects of order on "where" bias and reversed line bisection are discussed below.

3.3.1. Proprioceptive test

Pointing movement deviations in the proprioceptive and visual-proprioceptive tests before and after exposure to the prism were examined to assess whether participants adapted to the prisms. As can be seen in Fig. 1a, accurate pre-prism proprioceptive pointing performance moved in the direction opposite the prism shift after training with the prism. Analyses revealed a significant main effect of Prisms, $F(2,81) = 3.89$, $p = 0.02$, $\eta_p^2 = 0.09$, and a Prisms by Pre/Post interaction, $F(2,81) = 5.85$, $p = 0.004$, $\eta_p^2 = 0.13$. Simple main effects tests of pre–post differences at each level of Prism revealed that proprioceptive straight-ahead was shifted significantly rightward after left prism adaptation, $F(1,81) = 4.4$, $p = .039$, $\eta_p^2 = 0.05$, and

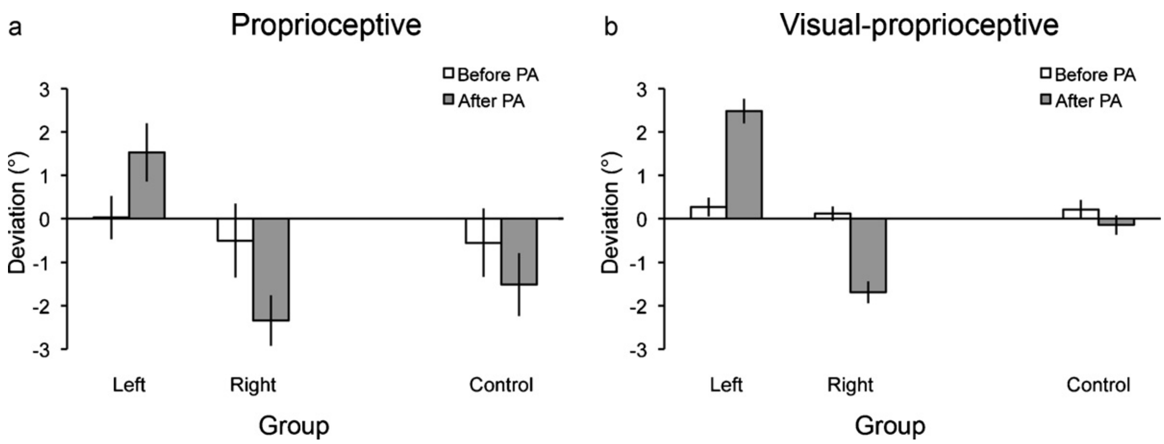

Fig. 1. (a) Proprioceptive test and (b) visual-proprioceptive test. Values represent the pointing errors (°, error bars are 1 SEM): in the proprioceptive test from the true objective body midline; in the visual-proprioceptive test from the visual target. Results refer to the average of the group of participants before (grey column) and after (black column) exposure to left-shifting prisms (left panel), right-shifting prisms (middle panel), or control plain goggles (right panel). Positive/negative scores indicate rightward/leftward errors.

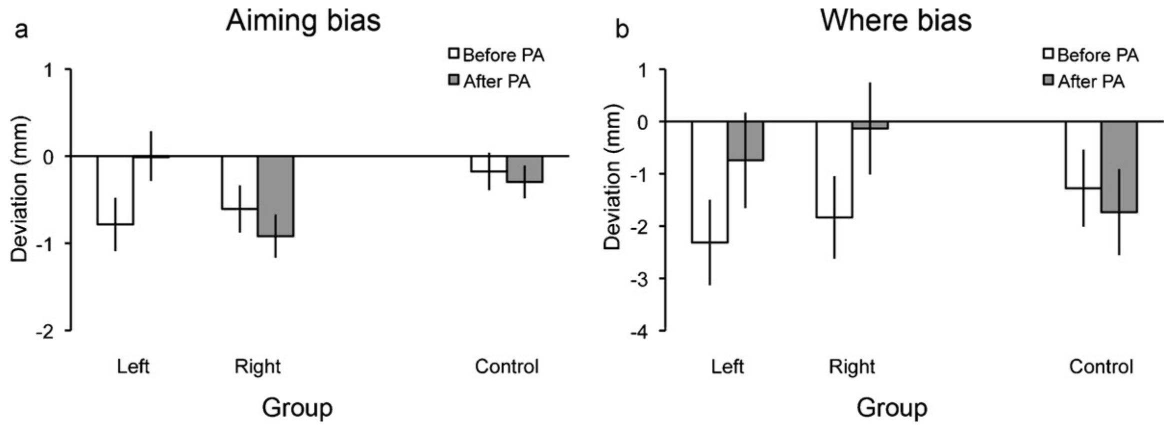

Fig. 2. (a) Motor-intentional "aiming" bias and (b) perceptual-attentional "where" bias. "Where" and "aiming" biases were derived from the fragmentation of the natural and reversed line bisection errors (mm, positive/negative scores indicate rightward/leftward errors, error bars are 1 SEM). Results refer to the average of the group of participants before (grey column) and after (black column) exposure to left-shifting prisms (left panel), right-shifting prisms (middle panel), or control plain goggles (right panel). Note that for the "where" bias, these averages exclude participants who performed the computerized line bisection last.

significantly leftward after right prism adaptation, $F(1,81) = 6.6$, $p = 0.012$, $\eta_p^2 = 0.08$. However, there was no significant change in proprioceptive straight-ahead for the control group, $F(1,81) = 1.8$, $p = 0.184$, $\eta_p^2 = 0.02$.

3.3.2. *Visual-proprioceptive test*

Pre–post performance on the visual-proprioceptive test is depicted in Fig. 1b. As can be seen in the figure, both left and right-shifting prisms induced aftereffects in the direction opposite the prism shift. Analyses revealed a significant main effect of Prisms, $F(2,81) = 30.85$, $p < 0.001$, $\eta_p^2 = 0.45$, and a Prisms by Pre/Post interaction, $F(2,81) = 69.39$, $p < 0.001$, $\eta_p^2 = 0.62$. Simple main effects tests revealed that for the right-prism group, the initial pre-exposure error in the pointing movements was more left-deviated in the post-exposure condition, $F(1,81) = 51.2$, $p < 0.001$, $\eta_p^2 = 0.39$. Similarly, for the left-prism group, the initial pre-exposure error was more rightward deviated in the post-exposure condition, $F(1,81) = 77.4$, $p < .002$, $\eta_p^2 = 0.49$. The amount of error in the pointing movements of the control group did not change from pre to post, $F(1,81) = 1.9$, $p = 0.167$, $\eta_p^2 = 0.02$.

Taken together, these results demonstrate that both right- and left-shifting prisms induced contralateral aftereffects in the proprioceptive and visual-proprioceptive tests, showing that participants adapted to the lateral displacement induced by both prisms. Inspection of the effect sizes suggests these effects were of similar magnitude for the left and right prisms (0.49 and 0.39 on the visual-proprioceptive and 0.05 and 0.08 on the proprioceptive for the left and right groups, respectively).

3.3.3. *Fractionated "where" and "aiming" components of computerized line bisection*

The fractionated "where" and "aiming" biases were our measures of primary interest as these represent a quantification of motor-intentional and perceptual-attentional errors assessed while a person is performing a visually guided action. Participants' average "aiming" bias is depicted in Fig. 2a. Consistent with our hypothesis, we observed a significant interaction between Prisms and Pre/Post for the "aiming" bias, $F(2,81) = 5.35$, $p = 0.007$, $\eta_p^2 = 0.12$, and no other effects $ps \geq 0.23$. Simple main effects tests of Pre/Post at each level of Prism revealed a significant rightward shift only for the left prism group, $F(1,81) = 9.6$, $p = 0.003$, $\eta_p^2 = 0.11$. By contrast, no pre–post difference was found for the right-shifting prism, $F(1,81) = 1.5$, $p = 0.222$, $\eta_p^2 = 0.02$, and control groups, $F < 1$, $\eta_p^2 = 0.00$. Thus, a motor-intentional "aiming" bias was significantly affected only in the group exposed to left-shifting prisms.

Preliminary analyses of the "where" bias including the factor of Test-order revealed a Pre/Post by Prism by Test-order interaction, $F(4,75) = 4.4$, $p = 0.003$, $\eta_p^2 = 0.19$. Inspection of the means revealed that for both left and right-shifting prisms, a general rightward pre–post shift was observable for those performing the computerized line bisection task first or second, but was absent in those who performed the task last. For the left prism, there was a mean rightward shift of 1.53, 1.62, and 0.09 mm for those performing the task first, second and third, respectively. For the right prism there was a mean rightward shift of 0.68 and 2.73 for those performing the task first and second, but a mean leftward shift of 0.50 for those performing the task third. Due to this order effect, remaining analyses of the "where" bias were performed on the subset of participants who performed the task either first or second ($N = 43$),[1] as the effects of the prism may have worn off for participants performing the task last.

The "where" bias for those who performed the task first or second appears in Fig. 2b. Analyses revealed a significant main effect of Pre/Post, $F(1,40) = 12.69$, $p = 0.001$, $\eta_p^2 = 0.24$ and a significant Pre/Post by Prisms interaction, $F(2,40) = 7.5$, $p = 0.002$, $\eta_p^2 = 0.27$. Simple main effects tests of Pre/Post at each level of Prism revealed a significant rightward shift for both the left, $F(1,40) = 10.9$, $p = 0.002$, $\eta_p^2 = 0.21$, and right prism groups, $F(1,40) = 13.6$, $p = 0.001$, $\eta_p^2 = 0.26$. There was no pre–post difference observed in the control group, $F(1,40) = 1.1$, $p = 0.294$, $\eta_p^2 = 0.03$.

3.3.4. *Computerized line bisection performance in natural and reversed condition*

Performance in the natural and reversed line bisection conditions, by themselves, do not indicate the extent of participants' "where" and "aiming" biases, but they do give a picture of the resultant performance when these biases are working together, as is the case in a visually guided movement. Table 2 contains the mean error for the natural and reversed conditions before and after prism exposure. Analysis of the natural condition revealed a main effect of Pre/Post, $F(1,81) = 5.31$, $p = 0.024$, $\eta_p^2 = 0.06$, and a Prisms by Pre/Post interaction, $F(2,81) = 3.04$, $p = 0.050$, $\eta_p^2 = 0.07$. Simple main effects tests revealed a significant rightward deviation after exposure to left-shifting prisms, $F(1,81) = 11.0$, $p = 0.001$, $\eta_p^2 = 0.12$. By contrast, there was no significant change in the line bisection performance of the right-shifting prism, $F < 1$, $\eta_p^2 = 0.01$, and control groups, $F < 1$, $\eta_p^2 = 0.00$. Thus, only the left-shifting prisms

[1] An error in assignment to the conditions led to 43 participants performing the line bisection task last and 43 participants performing it either first or second.

Table 2
Computerized line bisection. Mean error in the natural and reversed conditions of the computerized line bisection task pre and post prism exposure. Values represent the mean deviation (expressed in mm) from the objective center of the line: positive values indicate rightward deviation, and negative values indicate leftward deviation. Shift represents the difference between the pre and post exposure errors. Standard deviations appear in parentheses. Note that for the reversed condition, these averages exclude participants who performed the computerized line bisection last. Asterisks denote significant pre–post shifts in performance (ps < 0.01).

		Pre	Post	Shift
Line bisection natural condition	Right-shifting prism	−3.75 (−3.62)	−3.46 (−3.99)	0.29 (−2.55)
	Left-shifting prism	−2.51 (−3.84)	−0.97 (−4.84)	1.54* (−2.19)
	Control goggle	−1.79 (−3.24)	−1.77 (−3.64)	0.03 (−2.61)
Line bisection reversed condition	Right-shifting prism	1.18 (−3.99)	−0.9 (−4.22)	−2.08* (−3.3)
	Left-shifting prism	1.76 (−3.18)	0.83 (−3.23)	−0.93 (−1.56)
	Control goggle	1.09 (−2.97)	1.42 (−3.39)	0.33 (−1.8)

significantly affected the line bisection performance under natural viewing conditions.

Preliminary analysis of the performance in the reversed condition revealed a Prisms by Pre/Post by Test-order interaction, $F(4,75) = 4.1$, $p = 0.005$, $\eta_p^2 = 0.18$. Inspection of the means revealed that for both left and right-shifting prisms, a general leftward pre–post shift was observable for those performing the computerized line bisection task first or second, but this shift deviated rightward for those who performed the task last. For the left prism, there were mean leftward shifts of 0.998 and 0.84 for those performing the task first and second, and a 0.858 mean rightward shift for those performing it third. Similarly for the right prism, there were mean leftward shifts of 0.585 and 3.572 for those performing the task first and second, but a mean rightward shift of 0.260 for those performing the task third. Thus, the effects of the prisms on reversed line bisection performance seems to wear off for those who performed the computerized line bisection task last. Limiting the analyses of the reversed line bisection condition to those who performed the computerized bisection task either first or second, revealed a main effect of Pre/Post, $F(1,40) = 6.2$, $p = 0.017$, $\eta_p^2 = 0.18$ and a Pre/Post by Prisms interaction, $F(2,40) = 4.0$, $p = 0.027$, $\eta_p^2 = 0.17$. Simple main effects tests revealed a significant leftward pre–post shift in reversed bisection errors for the right prism group, $F(1,40) = 11.0$, $p = 0.002$, $\eta_p^2 = 0.22$ and no significant pre–post change in the errors of the left prism, $F(1,40) = 2.0$, $p = 0.162$, $\eta_p^2 = 0.05$ and control groups, $F < 1$, $\eta_p^2 = 0.01$.

3.3.5. Correlation analysis

To test whether the change in the "aiming" motor-intentional bias was related to the degree of adaptation, we computed Pearsons' correlations between the mean lateral deviation (post exposure–pre exposure) in the aiming bias and the proprioceptive and visual-proprioceptive measures of participants exposed to left-shifting prisms. Neither the correlation between the deviation in the "aiming" bias and the visual-proprioceptive shift ($r = -0.24$, $p = 0.22$), nor the correlation between the deviation in the "aiming" bias and the proprioceptive shift ($r = 0.05$, $p = 0.80$) approached significance.

4. Discussion

We sought to test the "aiming" hypothesis of the therapeutic effect of PA on left spatial neglect (Fortis et al., 2009) by examining decoupled perceptual-attentional "where" and motor-intentional "aiming" contributions to line bisection performance in a group of healthy young individuals. Consistent with previously observed dissociations in the healthy young (Berberovic & Mattingley, 2003; Colent, Pisella, Bernieri, Rode, & Rossetti, 2000; Loftus et al., 2008, 2009; Michel et al., 2003) we predicted that left-shifting, but not right-shifting prisms would induce a change in motor-intentional "aiming" bias. Our results support the idea that, at least in the current circumstances, PA primarily affects motor-intentional "aiming" spatial systems. Exposure to left-shifting prisms decreased the leftward "aiming" bias after PA, as demonstrated by a more central bisection performance in the post-exposure condition. However, no changes in the "aiming" bias were found after exposure to right-shifting prisms and control goggles, indicating that the effect of left-shifting prisms was not due to increased familiarity with the task. In contrast to the effects of PA on the "aiming" bias, the effect of PA on the "where" bias was not prism-specific: Participants who adapted to both left- and right-shifting prisms showed a more rightward deviated "where" bias after prism exposure.

4.1. Effects of PA on motor bias: implications for neglect

The present findings confirm an important role for motor-intentional "aiming" spatial systems in PA, and may elucidate the mechanisms through which PA affects spatial neglect. Our results are consistent with results of recent studies in small groups of neglect patients. For example, in a previous study, we found a selective improvement in the "aiming" bias of neglect patients who underwent a similar paradigm of computerized line bisection under natural and reversed conditions (Fortis et al., 2009; Fortis et al., Submitted for publication). C.L. Striemer and J. Danckert (2010) similarly showed that neglect patients improved in a manual line bisection task (consisting of both motor-intentional and perceptual components), whereas the performance on a purely perceptual landmark test remained unchanged after rightward prism exposure. These results can account for the improvement recorded in neglect patients post-PA in tasks requiring visually guided motor behaviours involving eye and arm movements. Beneficial effects of PA have been reported on manual motor tasks performed under visual guidance (e.g., cancellation and drawing; for reviews see Luaute, Halligan, Rode, Jacquin-Courtois, & Boisson, 2006; C.L. Striemer & J.A. Danckert, 2010), oculomotor scanning (Angeli, Benassi, & Ladavas 2004) and oculomotor bias (Dijkerman et al., 2003; Ferber et al., 2003), and in tasks requiring a motor activation such as postural imbalance (Shiraishi et al., 2008; Tilikete et al., 2001), and wheelchair navigation (Jacquin-Courtois et al., 2008). An ameliorative effect of PA on a motor-intentional "aiming" component of spatial errors may also help to explain the beneficial effects in daily-life activities in neglect patients exposed to PA training (Fortis et al., Submitted for publication; Fortis et al., 2009; Fortis et al., 2010; Frassinetti, Angeli, Meneghello, Avanzi, & Ladavas, 2002; Serino, Angeli, Frassinetti, & Ladavas, 2006; Serino, Barbiani, Rinaldesi, & Ladavas, 2009; Serino, Bonifazi, Pierfederici, & Ladavas, 2007; Vangkilde & Habekost, 2010).

A specific neuroanatomic-behavioral mechanism for a PA effect was recently hypothesized in a review by C.L. Striemer and J.A. Danckert (2010). The authors suggested that adaptation to prisms may primarily influence the visuomotor circuits of the dorsal visual stream (specifically, in the superior parietal lobule and in the intraparietal sulcus) that mediate not only motor-related but also attentional processes (Corbetta & Shulman, 2002; Milner & Goodale, 2006). This interpretation supports a beneficial effect of prisms in covert attention tasks requiring a shift of visual attention without eye movements (Nijboer, McIntosh, Nys, Dijkerman, & Milner, 2008; Striemer & Danckert, 2007; Striemer, Sablatnig, & Danckert, 2006). On this account, PA might also influence perceptual processes indirectly through connections between dorsal and ventral stream areas, mediated by the inferior parietal lobe (IPL) and the superior temporal gyrus (STG). Indeed, some studies have also suggested a beneficial effect of PA on perceptual tasks (Berberovic, Pisella, Morris, & Mattingley, 2004; Saevarsson, Kristjansson, Hildebrandt, & Halsband, 2009; Sarri et al., 2006, 2010). Since the IPL and the STG are critical sites for neglect (Karnath, Ferber, & Himmelbach, 2001; Mort et al., 2003) a failure to alter perceptual biases in neglect patients may be partly a consequence of a loss of connections between dorsal and ventral stream areas. Finally, it is also possible that PA alters subcortical-cortical interactions with both perceptual-attentional and motor-intentional effects (Barrett & Burkholder, 2006; Lünenburger, Kleiser, Stuphorn, Miller, & Hoffmann, 2001; Ogourtsova, Korner-Bitensky, & Ptito, 2010).

4.2. Effects of PA on perceptual bias

Unexpectedly, both left- and right-shifting prisms reduced a leftward "where" bias, and this effect was only observed immediately after PA. A possible (post hoc) explanation for a non-specific effect of PA on "where" bias could be that prism exposure triggered a correction of the baseline leftward "where" bias in the post-exposure condition through visuo-motor learning. During the exposure condition participants learned to detect and correct the line bisection error induced by the prismatic shift. It is possible that the mechanisms acquired during the exposure condition were transferred to the computerized line bisection task, especially when the task was performed immediately after the adaptation phase. The initial leftward "where" bias of our participants was bigger in magnitude than the leftward "aiming" bias ($t\ (83) = -3.70$; $p < 0.001$), replicating previous findings of a primarily perceptual-attentional bias in healthy young participants (Barrett, Crosson, Crucian, & Heilman, 2002; Garza et al., 2008; Schwartz et al., 1997).

In our study, both groups exposed to prisms reduced their leftward "where" bias. Therefore, the visuo-motor learning process of the adaptation phase may have induced an increased ability to correct the "where" bias in the post-exposure condition. Berberovic and Mattingley (2003) similarly found that both left- and right-shifting prisms induced a post-PA rightward shift on estimates of visual center for stimuli appearing in extrapersonal space. The same kind of effect was also observed by Barrett and Burkholder (2006) when both right and left monocular patching reduced leftward "where" spatial errors in the peripersonal space. More research is needed to understand non-directionally specific PA effects on the magnitude of perceptual-attentional "where" errors.

4.3. Mechanisms of prism adaptation

Previous investigators have hypothesized that the process of adapting to a visual displacement may depend on realignment of spatial coordinate reference frames (Redding & Wallace, 2010; see Redding & Wallace, 2006 and Redding, Rossetti, & Wallace, 2005 for reviews). The lateral visual shift induced by prisms generates discordance between visual and proprioceptive feedback that could initiate a re-alignment process during the visuomotor training. The presence of aftereffects when prisms are removed has been proposed to result from this transformation. A recent study in neglect patients showed a positive correlation between the re-alignment in the proprioceptive test and improvement in a standard cancellation test following PA (Sarri et al., 2008). To test whether the re-alignment process predicted the influence of prisms on the "aiming" component we performed a correlation analysis between the shift in the "aiming" component and the shift in the aftereffect measures. Our data showed that the effect on the motor behaviour was independent of the degree of adaptation: there was no correlation between the deviation in the motor-intentional "aiming" bias and the deviation in the visual-proprioceptive test ($p = 0.21$), nor in the proprioceptive test ($p = 0.80$). This result suggests that the influence of prisms on the "aiming" component was not directly attributable to the proprioceptive shift induced by prisms. Therefore, it is possible that adaptation to prisms induces realignment of sensory-motor reference frames and affects cognitive spatial functions through independent mechanisms. Indeed, clinical evidence has shown that the presence and severity of neglect deficits is dissociated from the rightward deviation of the egocentric reference frame (see Chokron, 2003 for a comprehensive review). As Chokron, Dupierrix, Tabert, & Bartolomeo (2007) recently suggested, the therapeutic effect of PA could be seen as resulting from the learning of new sensori-motor processes. Our result suggests that the new sensorimotor association may be driven by the change in the motor component following PA.

4.4. Asymmetrical effect of prism adaptation

It has been extensively described that healthy individuals show a systematic leftward bias when performing a line bisection task (Bowers & Heilman, 1980; Jewell & McCourt, 2000; McCourt & Jewell, 1999; McCourt, 2001). In accordance with previous findings, we found an initial leftward bias from the veridical true center of the line (natural condition). Similarly, a leftward perceptual "where" bias and a leftward motor-intentional "aiming" bias were also recorded when the two components where decoupled, replicating previous findings of leftward motor and perceptual biases in the line bisection task in healthy individuals. An a priori leftward bias has also been observed in the performance of numerous tasks in healthy individuals (Longo & Lourenco, 2007; McGeorge, Beschin, Colnaghi, Rusconi, & Della Sala, 2007; Nicholls, Bradshaw, & Mattingley, 1999; Nicholls & Loftus, 2007). Thus, in contrast with neglect patients, who show a rightward spatial bias, healthy individuals appear to show a subtle but systematic leftward spatial bias. In our study we showed a selective reduction of the leftward bias observed in the natural condition of the computerized line bisection task as well as of the motor-intentional "aiming" bias. This effect was recorded only after exposure to left-shifting prisms, whereas the same two tasks were not affected by right-shifting prisms. Previous research in healthy individuals provided evidence for similar lateralized effects of PA after left- but not right-shifting prisms (Berberovic & Mattingley, 2003; Colent et al., 2000; Loftus et al., 2008, 2009; Micheal et al., 2003; Micheal et al., 2008; Nicholls & Loftus, 2007). In all these tasks a consistent initial leftward bias was reduced after exposure to left-shifting prisms, whereas exposure to right-shifting prisms did not affect the performance.

A selective lateralized effect of PA has also been demonstrated in neglect patients by improvement of the rightward bias after right- but not left-shifting prisms (Rossetti et al., 1998, 2004). A possible explanation of the similarity of these results in healthy individuals and neglect patients is that PA may influence cognitive functions for which the baseline performance is biased (Goedert et al., 2010; Striemer et al., 2006; Bultitude & Woods, 2010). For example, Bultitude, Rafal, and List (2009) provided evidence that PA can reverse hierarchical perceptual processing, depending on the bias at the baseline level. Neglect patients, who typically show a local processing bias, acquired a more global processing bias after exposure to rightward shifting prisms. On the contrary, neurologically healthy individuals, who typically show a global processing bias, acquired a more local processing bias after exposure to left-shifting prisms (Bultitude & Woods, 2010). This interpretation could also account for the result we recorded in the reversed condition of the computerized line bisection task, in which the visual feedback was right-left horizontally inverted. In this task the initial bias from the veridical center of the line was deviated rightward, mirroring the initial leftward bias recorded in the natural condition. As suggested from the baseline bias interpretation, we recorded a selective lateralized effect of PA: the bias was reduced in the group of subjects who performed the task immediately after exposure to right-shifting prisms, whereas exposure to left-shifting prisms did not affect the performance.

4.5. Line bisection adaptation procedure: adaptation and aftereffect

In the present study we used a line bisection task during the exposure condition (see also Goedert et al., 2010). A commonly used adaptation task is based on repetitive pointing movements toward visual targets (see Redding & Wallace, 2006 for a review), although several other visuo-motor adaptation tasks have also been employed (e.g., ball and dart throwing tasks, walking tasks, and ecological activities; Fernandez-Ruiz & Diaz, 1999; Fernandez-Ruiz, Hall, Vergara, & Diiaz, 2000; Fernandez-Ruiz et al., 2003; Fortis et al., 2010; Martin, Keating, Goodkin, Bastian, & Thach, 1996a; Martin, Keating, Goodkin, Bastian, & Thach, 1996b; Micheal et al., 2008; Morton & Bastian, 2004; Shiraishi et al., 2008; see also the review of Kornheiser, 1976 for older works). The pointing adaptation task has also been the most frequently used task for the rehabilitation of neglect patients (Frassinetti et al., 2002; Humphreys, Watelet, & Riddoch, 2006Humprheys et al., 2006; Nijboer, Nys, van der Smagt, van der Stigchel, & Dijkerman, 2010; Rossetti et al., 1998; Serino et al., 2006, 2007, 2009). However, it is not easy for therapists to create an objective record of patients' performance while using the pointing adaptation task. In the absence of specialized equipment, recording of error during adaptation relies on the human examiner's visual assessment of the patient's deviation. On the contrary, when patients bisect lines on standard paper, a record of their adaptation error is created. Given the potential usefulness of recording adaptation errors (Serino et al., 2006) and the ease of the method, we introduced the line bisection task during the exposure condition of the present study. Our results showed that, similar to the typical effects of a pointing task, the line bisection task induced adaptation to prisms as well as symmetrical aftereffects.

Despite the presence of adaptation to prisms, we acknowledge that direct comparisons of findings involving diverse visuo-motor adaptation procedures (e.g., line bisection vs pointing task) should be carefully drawn. For example, the amplitude of the aftereffects recorded in the current study was smaller than previously reported in studies involving a pointing adaptation task (Redding & Wallace, 2006). Participants were exposed to prisms inducing a 12.4° of lateral visual shift. The magnitude of the shift of the two aftereffects tests ranged from 12% to 18% of the prismatic displacement, whereas the magnitude reported after pointing adaptation tasks has been stated to be around 30% of the prismatic displacement. Thus, it is possible that the line bisection task may have a reduced effectiveness in inducing sensorimotor aftereffects compared to the more traditional pointing task.

Another consideration is the visibility of the body part being monitored during the visuo-motor task in the adaptation phase. Previous studies have indeed demonstrated that minor changes in the adaptation procedure (i.e. exactly how much of the arm a person can see) can differentially influence the effectiveness of PA (see Ladavas, Bonifazi, Catena, & Serino, 2011; Redding & Wallace, 1990, 1997, 2010). For example, concurrent exposure conditions, in which simultaneous visual and proprioceptive feedback of the pointing movement is available, have shown to induce mostly proprioceptive aftereffects. On the contrary, terminal exposure conditions, in which the vision of the limb is available only at the terminus of the pointing movement, induce mostly visual aftereffects. In our study, the amount of lateral deviation induced in the proprioceptive test was similar in magnitude to the lateral deviation induced in the visual-proprioceptive test. This result suggests that our procedure produced a predominant change in the felt position of the arm, whereas the felt eye position was less affected. It will be interesting in future investigations to test if changes in the exposure procedure would differently affect our measures. Specifically, a delayed visual feedback exposure condition, which would produce a largely change in the felt eye position, may induce differently changes in the "where" and "aiming" spatial components.

However, different adaptation tasks do not necessarily result in a different effect of prisms on cognitive spatial functions. In a recent study in neglect patients Fortis et al. (2010) directly compared the effect of two adaptation tasks that differed in terms of movements performed and visibility of the arm exposed. The first task was a typical pointing task (as in Frassinetti et al., 2002), consisting of pointing movements to visual targets in which only the finger was visible during the movement. The other task consisted of ecological visuo-motor activities involving manipulation of common objects. In this novel procedure (which was much preferred by the patients) the arm movement was visible for the whole path. Interestingly, both tasks equally ameliorated visuo-spatial disabilities of neglect patients suggesting that despite differences in the adaptation procedures, the two adaptation tasks affected spatial biases of neglect patients in a similar way. This result indicates that diverse adaptation procedures may affect cognitive spatial mechanisms in similar ways, opening up promising new possibilities for the rehabilitation of neglect.

4.6. Prism adaptation and the reversed line bisection task

In our experiment, the prism adaptation task required participants to learn a new visuomotor transformation, but the reversed line bisection also introduces a visuomotor transformation. Interestingly, it was only this task (and one of the measures derived from this task—the "where" bias) that showed an effect of the order in which participants' performed the post-exposure tasks. We observed reliable effects of the prisms only in participants who performed the reversed line bisection task first or second, and not in those performing it after both the visual and visual-proprioceptive tests. This order effect suggests that the visuomotor transformation induced by the prisms could only "hold up" under the additional visuomotor transformation of the reversed line bisection when that task was performed very soon after the prism exposure. Furthermore, the failure to find effects of task order on the visual and visual-proprioceptive tests suggests that performing the reversed line bisection task first did not eliminate the visuomotor transformation induced by the prism: We observed significant changes pre to post for both prisms in both of these measures.

4.7. Conclusion

The present study demonstrated specific effects of PA on motor-intentional "aiming" spatial bias. A primary PA effect on "aiming" components of spatial errors in both neurological healthy participants and neglect patients (Fortis et al., 2009) has major implications for the feasibility of PA as a therapy for stroke survivors with left neglect. These results imply that some neglect patients (perhaps those primarily disabled as a result of "aiming" spatial errors) may be better candidates for PA training. This may partly explain heterogeneity of response to PA in prior therapeutic PA studies for spatial neglect. Our finding also confirms an asymmetrical effect of PA in healthy individuals where left- but not right-shifting prisms affect the congruent line bisection performance. This result supports the theory that PA may influence cognitive functions for which the baseline performance is biased due to either brain damage as in neglect patients or to a normal cognitive phenomena as in neurologically healthy individuals.

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