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Prism adaptation changes the subjective proprioceptive localization of the hands

Federica Scarpina[1,2,*], Stefan Van der Stigchel[2], Tanja Cornelia Wilhelmina Nijboer[2,3,4] and Hendrik Christiaan Dijkerman[2,4]

[1]Department of Brain and Behavioural Sciences, University of Pavia, Italy
[2]Experimental Psychology, Helmholtz Institute, Utrecht University, Utrecht, the Netherlands
[3]Rudolf Magnus Institute of Neuroscience and Centre of Excellence for Rehabilitation Medicine, University Medical Centre Utrecht and Rehabilitation Centre De Hoogstraat, Utrecht, the Netherlands
[4]Department of Neurology, University Medical Center, Utrecht, the Netherlands

Prism adaptation involves a proprioceptive, a visual and a motor component. As the existing paradigms are not able to distinguish between these three components, the contribution of the proprioceptive component remains unclear. In the current study, a proprioceptive judgement task, in the absence of motor responses, was used to investigate how prism adaptation would specifically influences the felt position of the hands in healthy participants. The task was administered before and after adaptation to left and right displacing prisms using either the left or the right hand during the adaptation procedure. The results appeared to suggest that the prisms induced a drift in the felt position of the hands, although the after-effect depended on the combination of the pointing hand and the visual deviation induced by prisms. The results are interpreted as in line with the hypothesis of an asymmetrical neural architecture of somatosensory processing. Moreover, the passive proprioception of the hand position revealed different effects of proprioceptive re-alignment compared to active pointing straight ahead: different mechanisms about how visuo-proprioceptive discrepancy is resolved were hypothesized.

Prism adaptation is a procedure in which participants perform visuo-manual pointing towards targets while looking through wedge prisms that optically displace the visual field. It is recognized to be a multi-component process (Newport & Schenk, 2012; Redding, Rossetti, & Wallace, 2005), involving three different adaptive components: first, a *proprioceptive* component, which reflects the position of the limb relative to the body; second, a *visual* component, which reflects the recalibration of the direction of gaze; and finally, a *motor* component, which reflects the re-organization of the muscle commands and the postural adjustment (Prior, Laboissière, Plantier, Prablan, & Roumes, 2011; Redding & Wallace, 2006; Redding *et al.*, 2005). At present, the role of these different components during adaptation and their reciprocal interactions are still

*Correspondence should be addressed to Federica Scarpina, Psychology Laboratory, Istituto Auxologico Italiano – IRCCS Ospedale S. Giuseppe, Via Cadorna, Piancavallo (Oggebbio – VCO) 90 - 28824, Italy (email: f.scarpina@auxologico.it).

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unclear (Newport & Schenk, 2012). In the current study, we focused exclusively on the proprioceptive component of prism adaptation. More specifically, we investigated how prism adaptation influences the felt position of the hands independent of motor adaptation.

The proprioceptive shift induced by prism adaptation is generally explored using a *straight-ahead pointing task* in which participants have to indicate the subjectively estimated position of their body midline by pointing in straight-ahead direction with the eyes closed (Chokron, Colliot, Atzeni, Bartolomeo, & Ohlmann, 2004; Harris, 1963; Redding & Wallace, 1992; Redding *et al.*, 2005; Wilkinson, 1971). In this task, the prism after-effect is reported to be in an opposite direction to the displacement of the glasses (i.e., rightwards after leftward deviating prisms; vice versa for rightward deviating prisms; Girardi, McIntosh, Michel, Vallar, & Rossetti, 2004; Hatada, Rossetti, & Miall, 2006; Fortis, Goedert, & Barrett, 2011; Newport & Schenk, 2012). The absence of the visual feedback is suggested to result in a straight-ahead pointing movement which is based exclusively on the proprioceptive reference frame. Indeed, judgement of the straight-ahead requires proprioceptive information about the position of the head and the body but also the motor (efferent) signals related to the arm during pointing (Redding & Wallace, 2006, 2008, 2009). In the current study, we sought to investigate a more limited proprioceptive judgement, specifically the localization of the finger, in a task in which the motor response was absent. This task was borrowed from a rubber hand illusion study (Kammers, de Vignemont, Verhagen, & Dijkerman, 2009) in which participants have to verbally indicate when a laterally moving visual external target is aligned with the felt position of the unseen hand. This paradigm requires a perceptual judgement about the perceived proprioceptive position of the index finger, without active movements that could provide an update of the proprioceptive information, which is presumed to reduce the proprioceptive displacement induced by prism adaptation in the present study or by rubber hand illusion in Kammers *et al.* (2009).

Thus, we aimed to test directly the effect of adaptation to a visual deviation on proprioception, independent of the other components involved in adaptation. Healthy participants' judgements about the felt position of the hands was tested before and after adaptation to prisms in a task in which a motor component was absent and no visual input about the hand was available.

In the current study the *exposure* was *concurrent*, meaning that the starting position of the adaptation movement is occluded from the participants' sight and the active pointing hand is visible for almost all its path. During the concurrent exposure, both visual and proprioceptive inputs were available for the process of spatial realignment, but the mismatch between the two sources of sensory input was most likely to be attributed to errors in the proprioceptive input (Newport & Schenk, 2012). Therefore, the consequence of the concurrent exposure as used in our study was that the proprioceptive component was enhanced in the process of realignment (Newport & Schenk, 2012; Redding & Wallace, 2006, 2010).

Moreover, we varied the visual deviation of the prisms. Different effects have generally been reported for adaptation to right and left glasses in healthy participants (Colent, Pisella, Bernieri, Rode, & Rossetti, 2000; Michel *et al.*, 2003; Redding & Wallace, 2008, 2009): Left shifting prisms produce a rightward perceptual after-effect, simulating the typical behavioral pattern of neglect, whereas right prisms generally do not induce perceptual effects in healthy individuals (Colent *et al.*, 2000; Berberovic & Mattingley, 2003; Michel *et al.*, 2003; Loftus, Vijayakumar, & Nicholls, 2009; Fortis *et al.*, 2011).

Finally we varied the adapted hand (right and left) between participants, to test possible differences in relation to the hand that was used during the adaptation procedure. In fact, Redding and Wallace (2008, 2009) suggested different prism adaptation after-effects whether the dominant or non-dominant hand is exposed, as a neurological and functional imbalance between the right and the left hemispheres applies to the control of orienting movements and to the representation of body parts (Redding & Wallace, 2008, 2009).

Method

Participants

Forty-eight right-handed healthy participants took part in this study (see Table 1 for demographical details). They had normal or corrected-to-normal visual acuity and received monetary compensation for their participation. The experiment was performed in compliance with the ethical principles according to the Declaration of Helsinki (World Medical Association, 1991).

Experimental set-up

The participants were asked to remove all jewellery from their hands and arms. They were seated comfortably at a chair behind a desk. On the desk, a wooden white framework ($75 \times 50 \times 25$ cm) was placed, with its centre aligned with the participants' body midline. The box was open on the side facing the participants and on the opposite side facing the experimenter. The experimenter was hiding behind the box and not visible to the participant's view. The participants placed their forearms in the framework with palms down, upon a laterally moving plane; the middle fingers were perpendicular to the shoulders and parallel to the body midline. No visual information about the position of the hands was provided during the task. A white cloth extended from the shoulders to the white framework to prevent any possible clue about the position of the hands by estimating the position of the shoulders.

The proprioceptive task

The participants were requested not to move their fingers or their hands during the task (see Figure 1A). The experimenter changed the horizontal location of the moving plane through the open side of the framework, defining five different horizontal locations of the hands: the central position, in which the centre of plane was aligned with the centre of the box; two positions on the right side and two positions on the left side of the central

Table 1. Demographic information of the participants. For *Age* and *Education*, mean and *SD* in years are reported

Group (adaptation procedure)	Number of participants	Age	Education
1 (left shift deviation; right hand)	12 (5 m; 7 f)	27 (3)	16 (2)
2 (left shift deviation; left hand)	12 (2 m; 10 f)	27 (4)	17 (1)
3 (right shift deviation; right hand)	12 (2 m, 10 f)	25 (3)	17.33 (1)
4 (right shift deviation; left hand)	12 (2 m, 10 f)	23 (1)	17 (0)

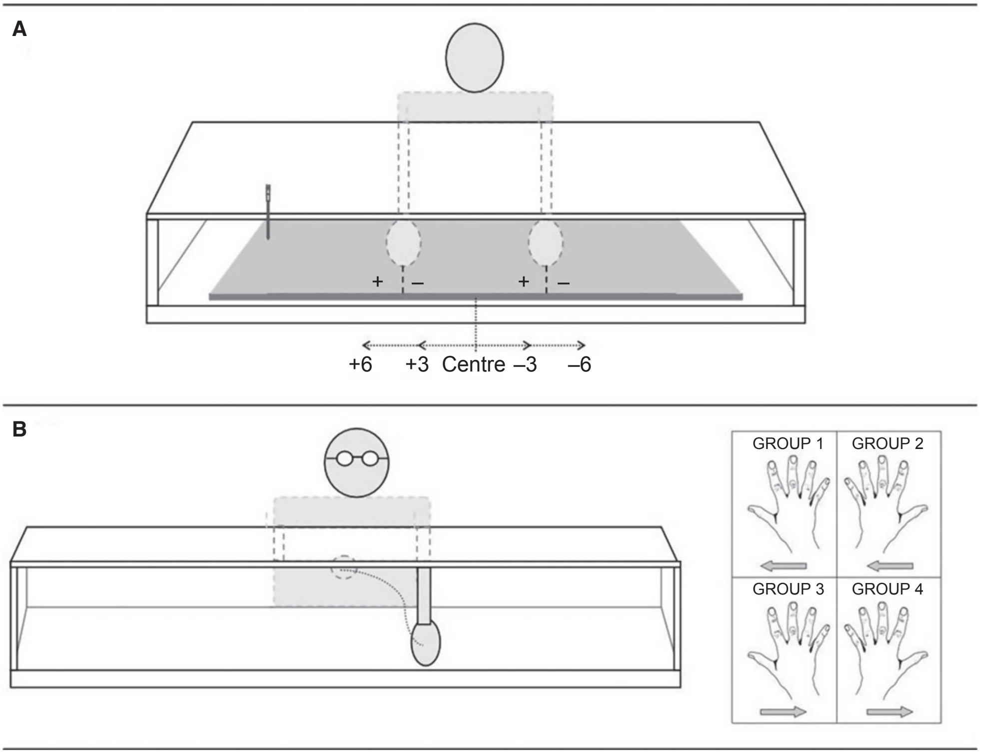

Figure 1. Experimental set-up and the schematic representation of the adaptation procedure. Part A shows the set-up during the proprioceptive task. Part B shows the set-up during the adaptation procedure and the different adaptation procedures: the adapted hand used to perform the pointing movements during the adaptation phase is indicated. The left arrow indicates 10° left prisms, while the right arrow indicates 10° right prism. The dotted lines represent the body parts that were not visible to the participants' view.

position, in which the plane was moved either six or three centimetres from the central position (see Figure 1A).

Each experimental trial started with a passive repositioning of the hands towards a horizontal location, while the participants kept their eyes closed (Figure 2A). After the change of the horizontal location of hands, the experimenter measured the real position of the probed middle finger through the open side of the framework (Figure 2B). The participants were subsequently informed which middle finger (the right or left hand) had to be estimated during the trial (i.e., the probed hand); they received the verbal command to open their eyes and to look at a target (i.e., a needle) being moved by the experimenter from the right or the left edge of the box towards the centre (Figure 2C). They were asked to mentally draw a vertical line from the location of the needle to the felt location of the centre of their own middle finger nail and to report verbally when they were aligned (Figure 2D). Finally, the participants closed their eyes to prepare for the next trial, while the experimenter measured the distance between the real position of the probed hand and the position of needle stopped by the participants through the open side of the framework (Figure 2E).

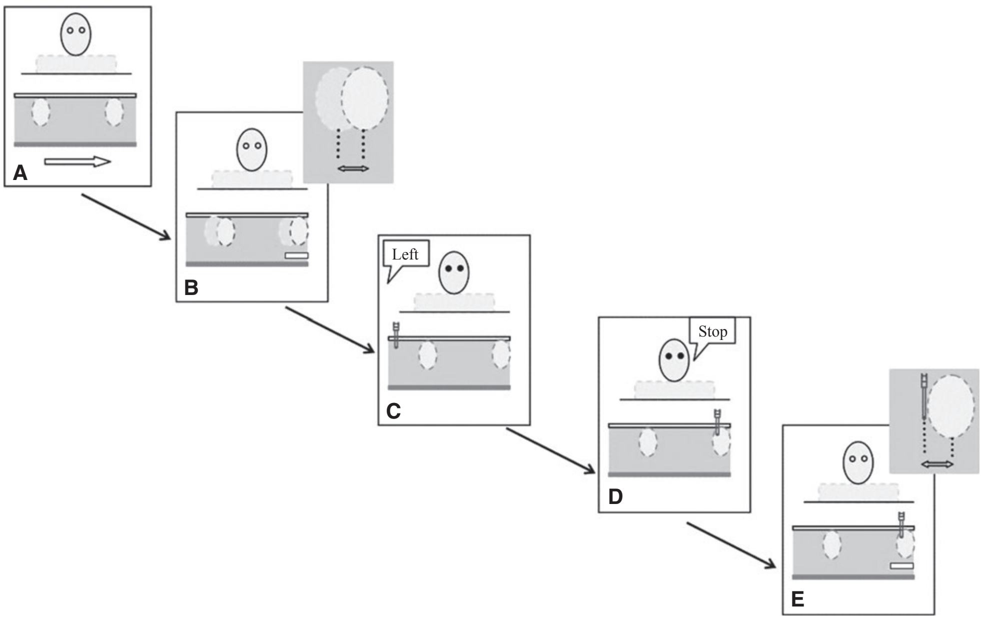

Figure 2. Timeline of one trial. Parts A, B, C, D, and E refer to the different steps of an experimental trial. The dark grey dotted lines represent the actual position of the hands during the trial, whereas the light grey dotted lines represent their previous position.

For each trial, the difference in millimetres between the real position of the middle finger, measured by the experimenter, and the position indicated by the participants was calculated: this value represented the deviation in proprioception judgement, namely *the error*. A *negative value* indicated a *leftward error*, a *positive value* a *rightward error*.

Each participant performed this task twice: once before and once after the prism adaptation procedure. Overall, 120 trials were administered in two sessions: 60 trials were performed before the adaptation procedure (pre-adaptation task) and 60 trials after (post-adaptation task). The probed hand (right or left), the starting side of the needle (right or left edge of box) and the position of the moving plane (6 or 3 cm towards left, the centre, 6 and 3 cm towards right) were presented in pseudo-random order across sessions: two of the same trials did not occur in successive order. On average, each session took about 30 min.

Prism adaptation procedures

To emphasize the proprioceptive component, the prism adaptation procedure had been modified from the standard adaptation procedure. While wearing the prism goggles, the participants were asked to perform 250 pointing movements from the chest (approximately from the sternum) with the index finger of one hand to the fingers of the other hand, at a fast but comfortable speed, following the experimenter's instructions. The starting position was occluded by a wooden frame: the arm's movement was not visible for the first part (about 1/3) of its path (namely the *concurrent exposure*, Redding & Wallace, 2010) (see Figure 1B). The participants were instructed to keep their eyes closed between the end of the adaptation session and the start of the post-adaptation experimental task to minimize de-adaptation.

The direction of prism deviation and the adapted hand were varied between groups. Twenty-four participants were exposed to 10° *leftward* deviating prisms: half of these participants pointed with their right hand (group 1) and the other half pointed with their left hand (group 2). The other 24 participants were exposed to 10° *rightward* deviating prisms: again, half of these participants pointed with their right hand (group 3) and half of these participants pointed with their left hand (group 4) (see Figure 1B).

The presence of the visuomotor adaptation was qualitatively checked after the post-adaptation experimental task, at the end of experiment. The participants were asked to perform pointing movements from the chest to the fingers of the hand target with the same hand used during the adaptation procedure until they were accurate: the presence of the adaptation was assumed if the first pointing movement error occurred in the opposite direction to the optical deviation. All participants showed an error in the first pointing movements: For groups 1 and 2, the deviation was rightwards; in contrast for groups 3 and 4, leftward deviation occurred.[1]

Statistical analyses

Overall, 1.09% of trials were excluded (for group 1: 18 trials for the pre- and 13 for the post-adaptation task; for group 2: eight trials for the pre- and five trials for the post-adaptation task; for group 3: seven trials for the pre- and six trials for the post-adaptation task; for group 4: three trials for the pre- and three trials for the post-adaptation task), because the participants judged the position of the wrong hand with respect to the instruction given, or moved the hands during the trial.

Moreover, trials in which the error was out of the range of two *SD* of group's mean were excluded from the analysis: overall, 0.45% of trials (for group 1: four trials for the pre- and seven trials for the post-adaptation task; for group 2: one trial for the pre- and three trials for the post-adaptation task; for group 3: two trials for the pre- and two trials for the post-adaptation task; for group 4: no trial for the pre- and one trial for the post-adaptation task).

The means of the different five positions were collapsed together for the left hand and right hand[2] and a mixed within-between design ANOVA was performed with the variable *Group* (group 1; group 2; group 3; group 4) as between-subjects factor and the variables of

[1] *As we used the judgement of the position of an external stimulus as reference for the proprioceptive position, a control experiment was performed to test whether the observed prism adaptation effects were related to the relocation of the external stimulus in space or to the proprioceptive relocation. Six participants were asked to judge three positions in peripersonal space by the movement of a needle, to investigate whether adaptation to prisms affected the localization of the target (i.e., the needle) with respect to an external reference point. The task was assessed in two different experimental sessions; in the first one, it was assessed before and after the adaptation procedure as presented in the paragraph* Prism Adaptation Procedures*; in the second one, the task was performed before and after a canonical adaptation procedure, in which the participants were requested to point towards visual targets from the starting point, both placed in peripersonal space. According to the results, the type of adaptation procedure did not affect the location of the external visual stimulus ($p = .79$; $\eta^2 = .015$) neither interacted with the probed position ($p > .75$; $\eta^2 = .055$) nor with the experimental session (if the task was performed before and after the adaptation procedure) ($p = .21$; $\eta^2 = .29$). The prism adaptation did not affect the relocation of the external visual stimulus: it can therefore be concluded that the drift in the proprioceptive task was solely due to the proprioceptive relocation of the hands and not to the relocation of the needle in space.*

[2] *A preliminary mixed within-between design ANOVA was performed with the between-subjects variable* Group *(group 1; group 2; group 3; group 4) as between-subjects factor and the within-subjects variables of* Probed hand *(left hand vs. right hand),* Session *(pre-adaptation task vs. post-adaptation task) and* Position *(6 or 3 cm towards the left, the centre, 6 and 3 cm towards the right). There was no main effect of the horizontal* Position *($p = .29$; $\eta^2 = .027$), neither interaction of* Position *with the variable* Probed hand *($p = .94$; $\eta^2 = .004$),* Session *($p = .97$; $\eta^2 = .002$) or* Group *($p = .74$; $\eta^2 = .046$): the proprioceptive judgement therefore was not affected by the horizontal position of the hands during the task.*

Probed hand (left hand vs. right hand) and *Session* (pre-adaptation task vs. post-adaptation task) as within-subjects factors.

Results

Proprioceptive judgement difference between the pre-adaptation- and the post-adaptation tasks (*Session)* were explored by ANOVA in relation to the four groups to explore any possible proprioceptive drift of the left and the right hands (*Probed hand*) as prism after-effect.

No significant main effect of *Group* ($F(3, 44) = 1.26$; $p = .29$; $\eta^2 = .08$) emerged, suggesting no difference among the four different prism adaptation conditions (group 1: $M = .33$, $SD = 4.08$; group 2: $M = -.51$, $SD = 3.98$; group 3: $M = .77$, $SD = 2.78$; group 4: $M = 0.66$, $SD = 3.8$). Moreover, no significant main effect of *Probed hand* (right hand: $M = .07$, $SD = 4.12$; left hand: $M = .55$, $SD = 3.24$) ($F(1, 44) = .29$; $p = .58$; $\eta^2 = .007$), no an interaction with *Group* (relative to the right hand, group 1: $M = -.07$, $SD = 1.27$; group 2: $M = -.53$, $SD = .65$; group 3: $M = .8$, $SD = .14$; group 4: $M = .1$, $SD = .57$. Relative to the left hand, group 1: $M = .74$, $SD = .34$; group 2: $M = -.49$, $SD = 1.26$; group 3: $M = .75$, $SD = .62$; group 4: $M = 1.22$, $SD = .2$) ($F(3, 44) = .10$; $p = .95$; $\eta^2 = .007$) emerged, meaning that the proprioceptive drift was in the same direction for both hands.

Interestingly, although no significant main effect of *Session* emerged (pre-adaptation task: $M = .37$, $SD = .25$; post-adaptation task: $M = 3.61$, $SD = 3.81$) ($F(1, 44) = .21$; $p = .64$; $\eta^2 = .005$), a significant interaction between *Session* and *Group* appeared ($F(3, 44) = 3.16$; $p = .034$; $\eta^2 = .177$). Bonferroni corrected *post-hoc* estimated marginal means comparisons indicated a significant difference between pre-adaptation condition ($M = .39$, $SD = 2.62$) and post-adaptation condition ($M = -1.38$, $SD = 3.01$) for group 2 ($p = .013$) for which the left hand was adapted and a left visual deviation was applied: the perceived position of both hands was drifted leftwards. No other comparison reached significance ($p > .29$; see Figure 3). Moreover, the *post-hoc* analyses indicated the absence of any difference among the means of four groups at the pre-adaptation task ($p > .936$): the performance at the proprioceptive judgement task was comparable among the four groups at the baseline.

A significant interaction between *Probed hand* and *Session* also emerged ($F(1, 44) = 5.45$; $p = .024$; $\eta^2 = .11$). Bonferroni corrected *post-hoc* estimated marginal means comparisons indicated a difference between the pre-adaptation condition ($M = .91$, $SD = 2.82$) and post-adaptation condition ($M = .19$, $SD = 3.61$) for the left hand as a trend ($p = .054$), while the difference between pre- ($M = -.16$, $SD = 4.22$) and post-adaptation ($M = .31$, $SD = 4.05$) for the right hand did not reach the significance ($p = .21$). This result might be explained by the presence of a proprioceptive drift of the perceived position of the left hand towards the subject's body midline due to the prolonged absence of visual input (Wann & Ibrahim, 1992); nevertheless, this explanation would be controversial as this effect was not found for the right hand.

Finally, the second-order interaction between *Probed Hand*, *Session* and *Group* was not significant ($F(3, 44) = .571$; $p = .63$ $\eta^2 = .037$).

These results suggested that only for group 2, prism adaptation affected the proprioceptive judgements of both hands; specifically, a leftward drift of right and left hands was observed as after-effect and it was in the same direction as the prism deviation. In the other groups, no after-effect was found.

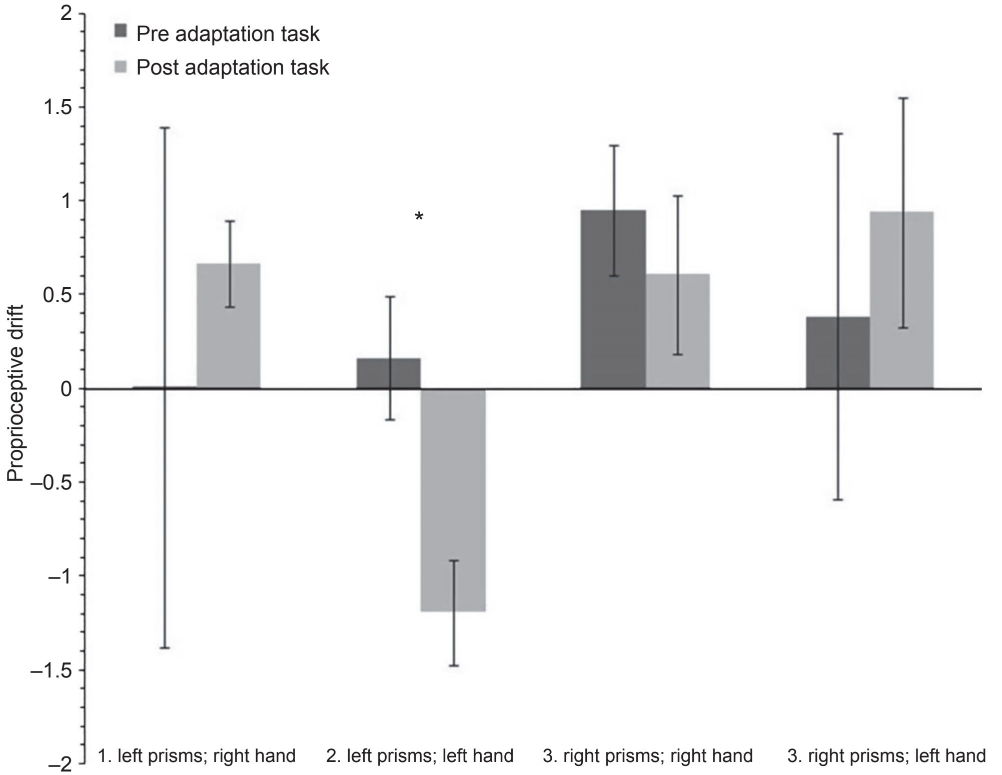

Figure 3. The results. For each adaptation group (1: left prisms, right hand; 2: left prisms, left hand 3: right prisms, right hand; 4: right prisms, left hand), mean of the proprioceptive drift in centimetres (*y*-axis) for pre-adaptation task (dark grey bars) and post-adaptation task (light grey bars) are reported. Positive values represent a drift in right direction; negative values a drift in the left direction. Error bars denote standard deviations with respect to mean. *Significant difference ($p < .05$).

Discussion

The aim of this study was to test any possible effect of prism adaptation on the felt position of the hands. To dissociate between proprioceptive and visual-motor effects of prism adaptation, a passive proprioceptive task was used to estimate where participants perceived their own hands after prism adaptation, in the absence of visual feedback about the hands. The proprioceptive component was emphasized in the process of re-alignment, as a consequence of the concurrent exposure (Newport & Schenk, 2012; Redding & Wallace, 2006, 2010).

Prism adaptation affected the healthy participants' performance in the judgement of the felt position of their hands differently depending on the direction of prism deviation and the hand used to perform the adapting pointing movements. In particular, adaptation movements with the left hand resulted in a horizontal drift of the proprioceptive judgements of both hands, only when a left visual deviation was induced by the prisms: the direction of the horizontal drift was similar for both hands and in the same direction as the prism deviation. Thus, no proprioceptive deviation was observed when the right hand was adapted to left shifting deviation or when the right prisms were used.

The results would be consistent with the hypothesis that particularly the right hemisphere is involved in proprioceptive drift after prism adaptation. Indeed, the right hemisphere is supposed to contain spatial maps of both left and right body space (Butler *et al.*, 2004; Weintraub & Mesulam, 1987). Thus, the right hemisphere was suggested to play a primary role not only in the construction of an internal representation of the body, in terms of ownership, emotional and motivational attitudes and metric perception of the spatial position body parts (Dijkerman & de Haan, 2007; Vallar & Ronchi, 2009) but also at the more basic level of the somatosensory domain, in particular concerning pain sensation and proprioception (Sterzi *et al.*, 1993; Vallar, 2007). This pattern of asymmetry could not be applied to the cortical control of reaching movements, which appears lateralized; the left hemisphere controlling the right hand pointing movements and the right hemisphere controlling the left ones (Redding & Wallace, 2009). As the right hemisphere controls the left hand, performing the pointing movements with the left hand allows preferential access to proprioceptive representations of both hands in the right hemisphere. This might explain why an after-effect was observed for the felt position of both hands. The present interpretation would be considered as partial, as the role and the reciprocal interaction of the different adaptive components during prism adaptation still need to be clarified (Newport & Schenk, 2012). Specifically, further investigations are required to understand the role of the right hemisphere in the prism adaptation and the after-effect on the proprioceptive component.

The direction of the after-effect that was observed after prism adaptation with the left hand as pointing hand was not in agreement with the pattern found in previous studies in which the straight-ahead pointing task was used (Berberovic & Mattingley, 2003; Fortis *et al.*, 2011; Girardi *et al.*, 2004; Redding & Wallace, 1992): We found a displacement in the same rather than the opposite direction to the glasses deviation. So, what causes this difference between the current study and previous studies? The visuo-proprioceptive discrepancy induced by the prism adaptation can, in our opinion, be resolved in two ways: By changing the vector of the *pointing movement* in the direction opposite to the prism shift, or by moving the *felt* starting position of the pointing hand in the direction of the prism shift (see Figure 4). Possibly, compensation for the reaching errors during prism adaptation is achieved through a combination of both processes. Previous studies, in which active straight-ahead pointing was used to assess the after-effect and the position of the finger at *the end* of the movement was measured (Berberovic & Mattingley, 2003; Bernier, Gauthier, & Blouin, 2007; Borchers, Hauser, & Himmelbach, 2011; Chokron *et al.*, 2004) have tested the former, that is the change in the direction of the pointing movement. The current study only assessed a possible drift of the *starting position* of the passive hand (i.e., before making a movement) in the direction of the prisms. The pattern of results for pointing with the left hand during the adaptation to left prisms is consistent with this idea; for both hands, a drift in felt position in the direction of the prism deviation was observed. As has previously been noted, this type of hand-prism combination is peculiar: It would involve preferential access to the right hemisphere, which contains spatial representations of left and right body parts and the cortical control of reaching movements of the left hand (Redding & Wallace, 2009). This pattern allows the intermanual transfer of the prism adaptation after-effect from the exposed left hand to the un-exposed right hand (Redding & Wallace, 2009).

To conclude, the results of the present exploratory study appeared to suggest a drift in the felt position of the hand after prism adaptation, which depends on the combination of the pointing hand and the prism direction. The observation of different after-effects would

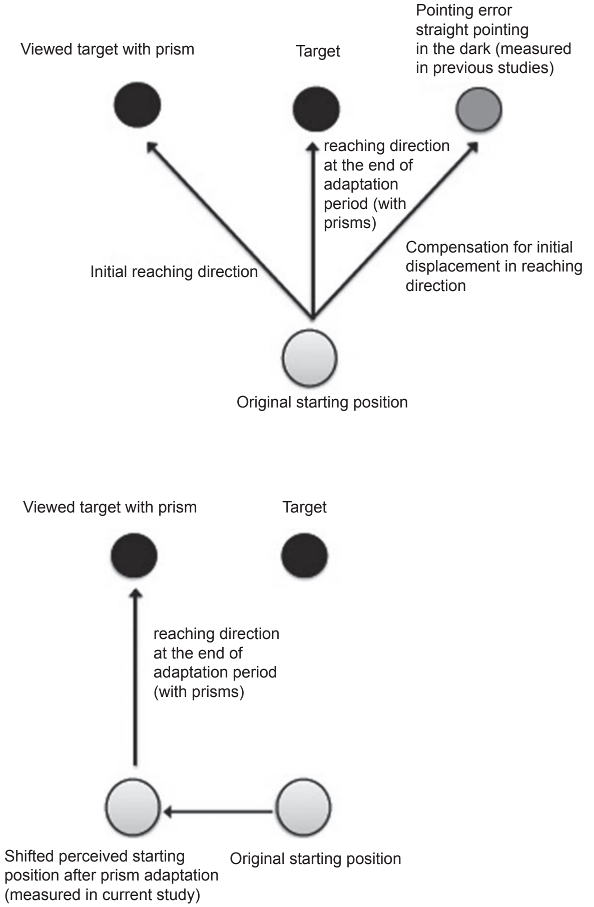

Figure 4. An outline of the proposed model. Two processes for the resolution of the visuo-proprioceptive discrepancy induced by the prism adaptation were hypothesized. In the upper part, the change of the vector of the pointing movement in the opposite direction to the visual deviation is represented as tested by the straight-ahead pointing task when the left prisms were used. In the lower part, the change in the felt starting position of pointing hand in the direction of the prism shift is represented as tested by the proprioceptive task in the current study: when the left prisms were used, the starting position is proprioceptively felt to the left of the original starting position at the end of the adaptive pointing movements.

be in line with the hypothesis of an asymmetrical architecture of spatial cortical representations, with a bilateral proprioceptive representation in the right hemisphere (Sterzi *et al.*, 1993; Vallar, 2007). Moreover, it showed that passive perception of finger position reveals different effects of proprioceptive re-alignment compared with active pointing straight ahead, allowing different mechanisms to be disentangled.

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