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RESEARCH ARTICLE

Leftward oculomotor prismatic training induces a rightward bias in normal subjects

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Abstract Wedge prisms shifting the visual field laterally create a mismatch between the straight ahead position signalled by vision and that encoded by extraretinal and head-on-trunk proprioceptive information. Short-term adaptation to left-deviating prisms in normal subjects results in a visuomotor attentional bias towards the right-hand side (aftereffect). Prismatic adaptation (PA) is usually induced through a training consisting in repeated ballistic movements of the dominant arm towards visual targets, while participants are wearing prismatic goggles. The present study demonstrates that an original oculomotor PA procedure with leftward deviating prisms—without pointing movements and only consisting in repeated gaze shifts towards visual targets—can induce a rightward bias in normal subjects as assessed by visual straight ahead and line bisection tasks (Experiments 1 and 2). We show that oculomotor PA induces a bias in line bisection similar to that reported after visuomotor PA (Experiment 2). We suggest that a conflict between retinal, extraretinal and proprioceptive information about the straight ahead location causes the observed effects. In follow-up experiments 3, 4, and 5, we demonstrate that neither eye deviation without prisms nor shift of the visual field without eye deviation induces PA biases. We propose that an optimal integration model of visual and proprioceptive inputs can best account for the observed results.

Keywords Prismatic adaptation · Oculomotor prismatic training · Visual straight ahead · Line bisection from memory · Optimal integration model · Maximum Likelihood Estimation (MLE)

Introduction

Prismatic adaptation (PA) has been thoroughly studied since the early sixties (Harris 1963; Hay et al. 1965; Craske 1967). PA can be obtained by laterally shifting the visual field through prismatic wedges while participants execute pointing movements to visual targets. The optical deviation results in the subjective displacement of the visual field in the direction of the prismatic shift (Hay and Pick 1966) and, when aiming at a target under visual guidance, induces contralateral compensatory pointing movements necessary to adapt to the visual shift (PA). Following PA, when prisms are removed, a deviation of attention and behaviour is observed in the direction opposite to that of prismatic visual shift (i.e. aftereffects). By exploiting this re-orienting of attention, PA has been widely employed to treat the symptoms of unilateral neglect (Bisiach et al. 1997; Rossetti et al. 1998; Rabuffetti et al. 2013), a neurological condition frequently exhibited by stroke patients with diffuse or focal right-hemisphere damage which results in the systematic neglect of the left portion of the visual and imagined world (Bisiach 1997).

Classic PA is a visuomotor procedure consisting in a number of quick ballistic movements performed with the dominant arm directed to visual targets, while participants are wearing prismatic wedges. Learning from their initial

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pointing errors ipsilateral to prism deviation, participants quickly recalibrate the trajectory of their movements successfully aiming for the target. When prisms are removed, they show a pointing error contralateral to prism deviation (the so-called aftereffect), which disappears after a few trials (Chapman et al. 2010; Fortis et al. 2011). This effect can be measured through different experimental tasks, such as open loop straight ahead pointing (SSA), visual straight ahead (VSA), line bisection, pre-bisected line length estimation (Colent et al. 2000; Berberovic and Mattingley 2003; Girardi et al. 2004; Schintu et al. 2014), double-step saccades tasks (Bultitude et al. 2013), and computerized reaction-time tests of spatial attention (Striemer et al. 2006). When initial prismatic deviation is directed leftwards, it is effective in transitorily inducing neglect-like behaviours in healthy participants (Michel et al. 2003; Jacquin-Courtois et al. 2013). Overall, these data show that a simple sensory-motor manipulation misaligning visual and sensorimotor sources of information about the location of the straight ahead modulates spatial attention and the egocentric reference frame.

A question that has not yet been fully answered by researchers concerns the neurocognitive mechanisms involved in PA and its aftereffects. In particular, it is not clear the role of visual-motor feedback from pointing errors during prismatic adaptation. The results of our experiments suggest that such a feedback is not the only source of information from which prismatic effects arise. A number of previous studies also support this suggestion; e.g. Hay and Pick (1966) showed that simple observation of one's own body parts through prismatic lenses is sufficient to induce adaptation: as a consequence of the visual-proprioceptive conflict induced by prismatic goggles, body parts appear visually displaced in the direction of the optical deviation relative to their actual position, causing observable biases in behaviour. Hay et al. (1965) proposed that the simple observation of the displaced body part, e.g. the arm, produces an immediate effect on proprioception such that the arm tends to be felt where it is seen, instead of where it actually is (i.e. visual capture of proprioception). This, in turn, causes post-adaption arm movements deviated in the direction opposite to that of prismatic deviation (aftereffect). However, it should not be considered as a general principle that visual information takes the lead over proprioceptive information in case of visual-proprioceptive sensory conflicts. Van Beers and colleagues (van Beers et al. 1999, 2002), for example, have convincingly demonstrated that "feeling" can be more important than "seeing" in sensorimotor adaptation, depending on task demands.

Here, we propose that PA aftereffects do not arise uniquely from visuomotor feedback coming from subjects' pointing errors, but emerge also as a consequence of the conflicting sensory information relative to the straight ahead arising from the (deviated) eye position in the orbits and the (non-deviated) head-on-trunk proprioceptive input. We propose that, in order to minimize uncertainty of the final estimate, the CNS combines by means of a Maximum Likelihood Estimation principle retinal and extraretinal input coming from the eyes' deviated position in the orbits with the non-deviated egocentric reference frame information built upon the head-on-trunk proprioceptive input, giving more weight to this latter because it is considered as a more reliable input in this situation. According to this view (van Beers et al. 1999, 2002; Ernst and Banks 2002), the CNS dynamically combines multiple sensory inputs minimizing the variance of the final output, by assigning more weight—or salience—to the less noisy sensory input. Hence, even in the absence of limb movements, vision of one's own body and visuomotor feedback from pointing errors, the visuomotor system actively attempts to compensate for the visual-proprioceptive conflict induced by prismatic shift of the visual field giving more weight to the less noisy proprioceptive input than to the more noisy visual one (i.e. proprioceptive capture of vision).

To test this hypothesis, we manipulated presence/absence of prismatic displacement of the visual field and presence/absence of sustained eye deviation as sources of information available during an original PA procedure solely based on gaze shifts to visual targets (i.e. oculomotor prismatic training—OPT). If the integration between retinal input and proprioceptive information arising from the head-on-trunk proprioceptive information significantly contributes to the development of aftereffects, then eliminating arm movements and body observation from PA should not prevent their emergence after prism removal. On the contrary, if own body observation and visual feedback from pointing errors are necessary factors, then we should not observe any aftereffect following oculomotor PA.

In a series of five experiments, we first showed that prism-related effects in bisection and visual straight ahead tasks can be induced in healthy participants by means of a single session of OPT (Experiments 1 and 2). Capitalizing on these results, we then investigated the possible sources of information responsible for the observed effects: i.e. retinal, concerning the visual information about the displacement of the visual field (Experiment 3 was specifically aimed at assessing the role of peripheral visual information in inducing PA effects), and/or extraretinal, regarding the deviation of the eyes in the orbits induced by the prismatic shift, combined with the proprioceptive input from the head-on-trunk reference frame (Experiments 4 and 5). We expected that OPT effects only emerged in the presence of conflicting retinal and extraretinal/proprioceptive information signalling the straight ahead position, as a consequence of an automatic sensory-motor integration process carried out by the central nervous system to compensate for the mismatch between visual and proprioceptive information.

Materials and methods

Participants

Sixty healthy participants participated in the study, which comprises five different experiments. 24 participants (15 women) aged 22–38 years (26.6 ± 5.6; mean ± SD; years of education 17.5 ± 1.1) participated in Experiments 1 and 2. 12 participants (5 women) aged 26–33 years (25.1 ± 3.5; mean ± SD; years of education 17.3 ± 1.1) participated in Experiment 3. 12 participants (8 women) aged 21–30 years (24.3 ± 2.5; mean ± SD; years of education 17.0 ± 1.0) participated in Experiment 4. 12 participants (7 women) aged 21–31 years (23.5 ± 2.7; mean ± SD; years of education 16.8 ± 1.1) participated in Experiment 5. Mean age and educational level were comparable among groups (*p* values comprised between 0.6 and 0.7 at paired samples *t* tests). All participants gave their written informed consent to participate to the study. The study conformed to the standards required by the Declaration of Helsinki and was approved by the local ethics committee.

Subjects' sample size of Experiments 1 and 2 was determined on the basis of a power analysis on Michel et al. (2003) data on manual line bisection task. We collected 12 subjects and we performed an a priori power analysis to measure the effect size obtained in line bisection task following OPT, to set the required sample size to achieve a similar power as in Michel et al. 2003 (i.e. 0.8). The power analysis (alfa = 0.05; effect size calculated on 12 subjects = 0.6; set power = 0.8) set a sample size of 24 subjects. Therefore, we decided to increase sample size in Experiments 1 and 2 accordingly.

Experimental procedures

Experiment 1: effect of OPT on visual straight ahead (VSA)

PA was induced by simply asking participants to move their eyes towards target stimuli printed on a sheet of paper upon verbal command of the experimenter while wearing prismatic goggles shifting the visual field 11° to the left. Our aim was to assess whether eliminating overtly executed arm movements and, hence, visual feedback from pointing errors and body observation would eliminate the aftereffects normally occurring following traditional visuomotor PA. Our predictions were as follows: (1) if visual feedback from pointing errors and body observation have a major role in determining the effects of PA, one would expect to find no aftereffects following PA; (2) conversely, if the feedback from pointing errors and body observation are not necessary factors and other sources of visual information are sufficient to build prismatic aftereffects (i.e. retinal information about the shifted visual field, extra-retinal information from the deviation of the eyes in the orbits, proprioceptive information about the head-on trunk alignment), one would expect to find a rightward bias in straight ahead estimation and line bisection. This would indicate that residual aftereffects survive the elimination of pointing movements and body observation during PA.

Phase 1: pre-training visual straight ahead (baseline condition). Participants were asked to stand against a wall in a fixed location (each foot position was marked on the floor and head position was marked on the wall) and to look straight ahead at a white projection screen (2 × 2 m) hanging on the opposite wall. The screen was at a distance of 3 m from the participants. The experimenter operated a laser pointer directed to the screen, producing a green light dot with a diameter of 2 mm. The laser pointer was fixed on to a tripod and was manually rotated so as to produce a rectilinear movement of the green dot along the horizontal axis of the screen at a variable height matching individual eye level and at a speed of approximately 25 cm/s.

Participants were asked to stay still and to stop the green light dot by saying "stop" when it reached their trunk vertical midline, i.e. the virtual line that divides the body along its vertical axis into two identical halves. Trunk midline estimation was repeated ten times: trials were randomized such that on five instances the green dot movement followed a left-to-right direction, and on five instances a right-to-left direction, always initiating from the border of the screen. Following every estimation, the experimenter manually marked the position of the green light dot on screen by means of a pencil. The participant was allowed to repeat a trial if she/he was not confident about her/his midline estimation.

Phase 2: oculomotor prismatic training (OPT). Immediately after the baseline condition, participants underwent a PA procedure consisting in repeated fixations of a number of dots printed on a sheet of paper while wearing a pair of prismatic lenses. Participants were asked to sit at a desk with their trunk midline aligned with a target dot marked on the desk edge closer to the participant. An A3 sheet of paper was then placed upon the desk with four black dots printed on it, sequentially numbered from 1 to 4 (numbers were printed above each dot in Arial 29 style). The dots were evenly spaced along the horizontal side of the paper (inter-dots spacing was 11.8 cm), at a distance of 50 cm from the participant's chest. Each dot measured 0.5 cm in diameter (Fig. 1). A black cross (fixation cross) was printed at the centre of the sheet of paper and was aligned with the target marked on the desk, so that the fixation cross lined up with participants' trunk midline. The two black dots

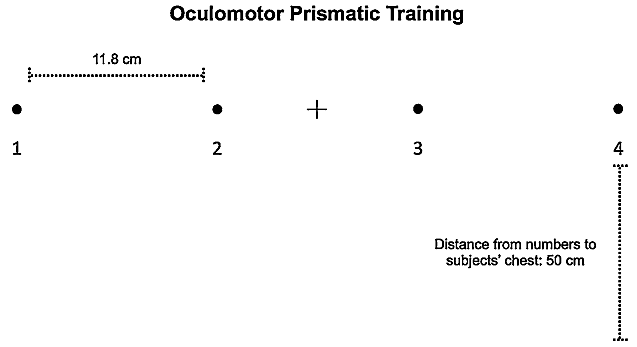

Fig. 1 Workspace employed for the OPT. OPT consisted in moving the eyes towards the 4 target stimuli printed on a landscape oriented A3 sheet of paper. The stimuli are 4 black equidistant *dots* (diameter 0.5 cm), centred with respect to the *vertical side* of the paper. The *black cross* (*fixation cross*), printed at the centre of the A3 paper, was aligned with participants'*midline*. The distance between number line and participants' chest was 50 cm

aside to the central fixation cross were distanced 5.8 cm from the cross itself. Before starting the PA procedure, participants were asked to check whether the fixation cross was actually aligned with their trunk midline. Then, they closed their eyes and they were put on a pair of prismatic goggles equipped with 20 dioptre prismatic lenses. The lenses where oriented so as to shift the visual field 11° to the left. Immediately before initiation, participants opened their eyes and were explicitly asked not to move their heads and arms during the procedure. By means of an analogical chronographer, every 3 s the experimenter said aloud the number of a dot (from 1 to 4), which the participant had to gaze at, without moving the head. Participants had to shift their gaze, i.e. voluntary move their eyes, from the fixation cross to the dot indicated by the experimenter and then return to the central fixation cross. Each dot was gazed at ten times (40 gaze shifts in total) in a pseudo-randomized order (each number was not repeated more than twice in a row) and different sequences were presented to the participants, in order to avoid sequence-related effects on training. OPT was limited to a single session and lasted approximately 3 min.

To be certain that participants were actually paying attention while performing the task, every ten trials the experimenter asked the participant to close the eyes for a few seconds and the A3 paper was changed with a new one, slightly different from the original one for irrelevant features of the stimuli (colour of the fixation cross or diameter of the dots). At the end, participants were asked to report any observed difference. All participants resulted able to perform the task.

After the completion of the task, participants were asked to close their eyes until the beginning of the next experimental condition (Phase 3).

Phase 3: post-training assessment of after effects on visual straight ahead. With their eyes closed, participants were moved to the same location within the experimental room as in Phase 1, and, after opening their eyes, they were asked to undergo the same straight ahead estimation task performed in Phase 1 to assess presence of possible effects of OPT on VSA.

Experiment 2: line bisection from memory

The rationale was the same as for Experiment 1, but here we aimed at exploring the presence of possible effects of OPT in a visuomotor task. Furthermore, in a separate session, we directly compared the effect of OPT with the effect of classical visuomotor prismatic training (VPT).

As experimental task, we chose line bisection from memory because of its simplicity and the possibility to remove visual feedback during task execution by requesting participants to close their eyes (letting participants to keep their eyes open would allow online correction of possible aftereffects induced by PA). Predictions were the same as for Experiment 1: (1) if the visuomotor feedback component of PA is necessary to induce effects in the spatial domain, the absence of such a component in OPT should result in no effects in line bisection from memory, i.e. absence or significant reduction of a rightward bisection bias; (2) conversely, if retinal and non-retinal factors (retinal shift of the visual field and eye position within the orbit, respectively) play a role in inducing the aftereffects of PA, a rightward bias in bisection should be apparent both following OPT and VPT.

Session 1: OPT

Phase 1: pre-training line bisection. Participants sat at a desk and had to repeatedly bisect from memory a 20 cm horizontal line, printed in the centre of an A4 paper (landscape oriented) and placed at a distance of 50 cm from the participants' chest. The sheet of paper was slightly misaligned relative to the participants' trunk midline—2 cm rightwards or leftwards—to prevent them from using the trunk vertical axis as a reference for segment bisection.

Participants were instructed to bisect a 20 cm long line printed on a sheet, placed in front of them. They were asked to close their eyes, then the experimenter placed the paper in the correct position and asked them to open the eyes, look at the paper for 2 s, close the eyes again and mark the line centre with a pencil. Participants were not given any feedback on their performance. The task was repeated ten times.

Phase 2: oculomotor prismatic training. The training procedure was identical to that performed in *Experiment 1*.

Phase 3: post-training line bisection from memory. Same task as in Phase 1.

Session 2: VPT

Phase 1: same as Session 1.

Phase 2: *visuomotor prismatic training*. VPT consisted in repeated ballistic pointing movements performed with the right arm towards the same targets employed in OPT (Fig. 1), while wearing the same prismatic lenses employed for OPT. To prevent subjects from seeing the initial part of their movement, a wooden shield was placed between the participants' chest and the worksheet, above their hands. Every 3 s the experimenter said aloud the number of a dot, which the participant had to point at. Each dot was pointed at 10 times (40 pointing movements in total) in a randomized order. A VPT session lasted approximately 3 min.

Phase 3: same task as *Session 1*.

Experiment 3: effect of OPT on visual straight ahead with laterally shielded goggles

This experiment replicated Experiment 1, except that prismatic lenses were shielded all-around by means of a thick layer of black tissue, thus blocking the participants' view of the extreme periphery of the visual field along the horizontal and vertical meridians.Whereas in the previous experiments employing unshielded goggles the periphery of the visual field was not optically deviated by the lenses, this procedure ensured that the entire visual field accessible to the participant's view was optically deviated. This manipulation was aimed at assessing the role, if any, of peripheral visual information, not affected by prismatic shift, in inducing the aftereffects of PA. Indeed, it is possible that the information arising from the periphery of the visual field, non-shifted by prisms, combined with visual information coming from the centre of the visual field, shifted by prisms, represents a sufficient retinal input to induce PA. The following two outcomes can be predicted: (1) if the non-deviated visual information arising from the peripheral visual field is a necessary component of the process leading to prismatic aftereffects, by suppressing this source of information one should expect to eliminate any aftereffect of PA (i.e. no rightward bias in straight ahead estimation); (2) conversely, if this information plays a minor role, or no role, a similar, or slightly reduced, effect should be evident on straight ahead estimation as the one observed following PA with unshielded goggles (Experiment 1).

Experiment 4: effect of OPT on visual straight ahead with workspace shifted 11° contralaterally to prismatic deviation and laterally shielded goggles

This experiment replicated Experiment 3, except that the workspace was located 11° rightward during PA, contrasting the leftward prismatic shift, without the participant being aware of the displacement. The workspace shift was obtained by positioning the A3 paper used for PA 9.7 cm [distance*tang(visual angle subtended by the workspace)] to the right of the participant's trunk midline, so as to appear exactly at the centre of the visual field (because it precisely counteracted the leftward deviation induced by prismatic lenses). The aim of this manipulation was to assess the role of the deviation of the eyes in the orbit in generating the effects of prismatic adaptation. Predictions were as follows: (1) if the displacement of the eyes in the orbit is a necessary source of information for inducing the effects of PA, moving the workspace contralaterally to prismatic shift by the same amount (11°) should result in the suppression of any effect (i.e. the rightward bias in straight ahead estimation) because the resulting eyes position in the orbit would be central; (2) conversely, if eyes position in the orbit is not a necessary source of information, a similar rightward bias as in experiments 1 and 3 on straight ahead estimation should be apparent.

Experiment 5: effect of oculomotor training executed without prismatic goggles, but with workspace shifted 11° leftward

This experiment replicated Experiment 1, except that it was performed without prismatic goggles but with the workspace shifted 11° leftward, in order to reproduce the same visual shift induced by prismatic lenses, although eliminating the misalignment between retinal and proprioceptive information induced by prisms. Experiment 5 was performed to control for the possible role of sustained eye deviation alone in the emergence of the observed biases in straight ahead estimations following PA. Ebenholtz (1976) suggested that a sustained lateral displacement of gaze direction (performed for 10 min) may fully reproduce the straight ahead bias obtained after the exposure to prismatic lenses (i.e. eye-muscle potentiation hypothesis).

The workspace was, therefore, positioned 9.7 cm [distance*tang(visual angle subtended by the workspace)] to the left of the participant's trunk midline. Subjects performed the same training as in Experiment 1 (duration 3 min).

Prediction are as follows: (1) If sustained gaze deviation is a sufficient factor for the emergence of the effects of PA, then a shift in straight ahead estimations after the training should be observed, as compared to baseline, similar to the one observed in Experiments 1 and 3; (2) Conversely, if sustained gaze deviation is unrelated to the effects observed following PA, then we should not find any significant difference in post-training measurements as compared to baseline values.

Statistical analyses

Paired samples *t* tests were used to explore the effect of OPT in each experiment, comparing baseline estimations with post-PA measurements.

In Experiment 2, we compared the effects of OPT and VPT through a two-way repeated measure Anova, with two within subject factors: Time (two levels: pre and post PA), and PA (two levels: OPT and VPT).

Results

Experiment 1: effect of OPT on visual straight ahead. Individual participants' straight ahead perceptual judgements after OPT are presented in Fig. 2. After OPT, participants' estimations resulted to be significantly biased toward the right-hand side relative to baseline values [(grand average deviation toward the right-hand side: 2.35 cm ± 4.8; mean ± SD; paired sample *t* test: $T_{23} = 2.398$, $p = 0.025$; $d_z = 0.490$; error expressed in degrees of visual angle: tan $\alpha = (2.35\ \text{cm}_{\text{error}}/300\ \text{cm}_{\text{subj distance}})$; arctan $\alpha = 0.458°$)].

Experiment 2: line bisection from memory. Individual participants' bisections following OPT and VPT are presented in Fig. 3a, b, respectively. Similarly to Experiment 1, following OPT line bisections resulted to be significantly biased toward the right-hand side relative to baseline values [(grand average deviation toward the right-hand side: 0.63 cm ± 1.1; mean ± SD; paired sample *t* test: $T_{23} = 2.697$, $p = 0.013$; $d_z = 0.572$; error expressed in degrees of visual angle: tan $\alpha = (0.63\text{cm}_{\text{error}}/50\text{cm}_{\text{subj distance}})$; arctan $\alpha = 0.722°$)].

Following VPT, line bisections also resulted to be significantly biased toward the right-hand side [(grand average deviation toward the right-hand side: 1.27 cm ± 1.3; mean ± SD; paired sample *t* test: $T_{23} = 5.362$, $p < 0.001$; $d_z = 0.976$; error expressed in degrees of visual angle: tan $\alpha = (1.27\text{cm}_{\text{error}}/50\text{cm}_{\text{subj distance}})$; arctan $\alpha = 1.454°$)].

To compare directly the effect of OPT and VPT, we performed a two-way repeated measure Anova. We found a main effect of Time ($F = 41.406$; $p < 0.001$; partial eta-square 0.643), with bisection errors significantly biased toward the right-hand side following both OPT and VPT. We did not find a main effect of PA ($F = 2.785$; $p = 0.109$), nor a significant interaction Time*PA ($F = 2.793$; $p = 0.108$). These findings suggest that OPT and VPT similarly affect the line bisection task.

Experiment 3: effect of OPT on visual straight ahead with laterally shielded goggles. Individual participants' straight ahead values after OPT are presented in Fig. 4. After OPT, participants' estimations remained significantly biased toward the right-hand side relative to baseline values [(grand average deviation toward the right-hand side: 3.43 cm ± 5.1; mean ± SD; paired sample *t* test: $T_{11} = 2.346$, $p = 0.039$; $d_z = 0.672$; error expressed

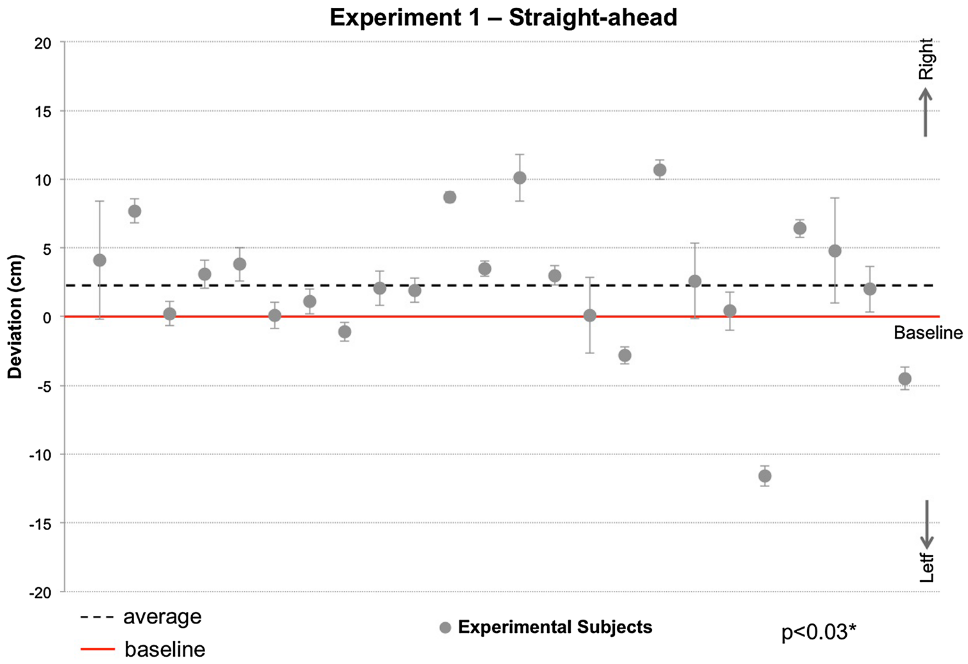

Fig. 2 Experiment 1: straight ahead estimation. Individual participants' straight ahead perceptual judgements after OPT are presented. Data are normalized according to each participant subjective *straight ahead* (*Baseline*, in *red*). *Grey dots* represent the difference (in cm) between the baseline and subjective straight ahead judgements collected after PT. *Y axis: positive values* indicate *rightward shifts, negative valuesleftward shifts*. Average deviation is shown by the *dashed black line. Vertical bars* represent standard errors

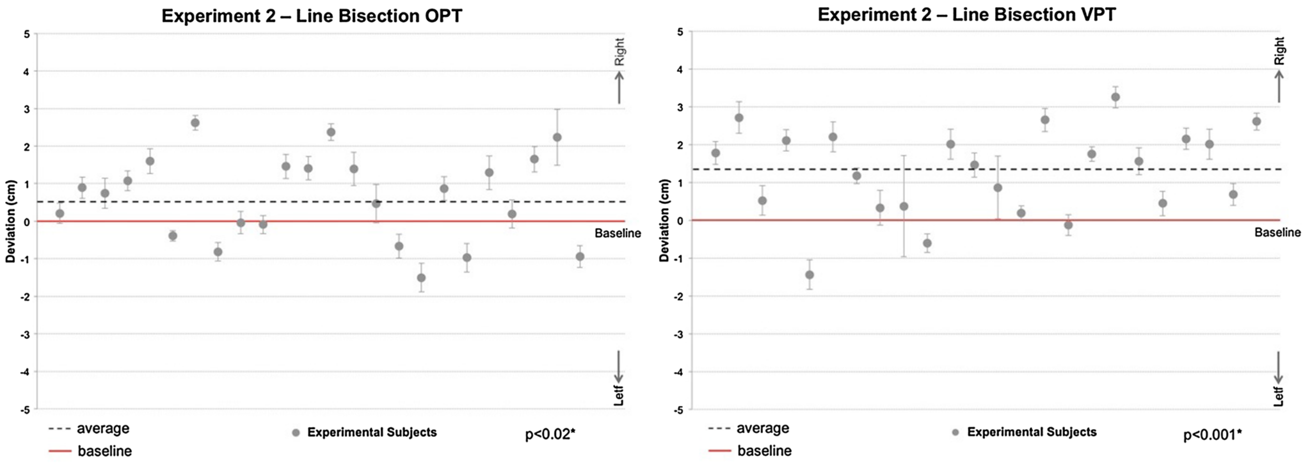

Fig. 3 **a, b** Experiment 2: line bisection. Individual participants' line bisection errors after PA are presented. Data are normalized according to each participant subjective line bisection measure before PA (*Baseline*, in *red*). *Grey dots* represent the difference (in cm) between baseline bisection performance and performance after PT. *Y axis*: positive values indicate a *rightward deviation*, negative values a *leftward deviation*. Average deviation is shown by the *dashed black line. Vertical bars* represent standard errors. *Panel 3a* (*left*) represents line bisection errors after OPT. *Panel 3b* (*right*) represents line bisection errors after VPT

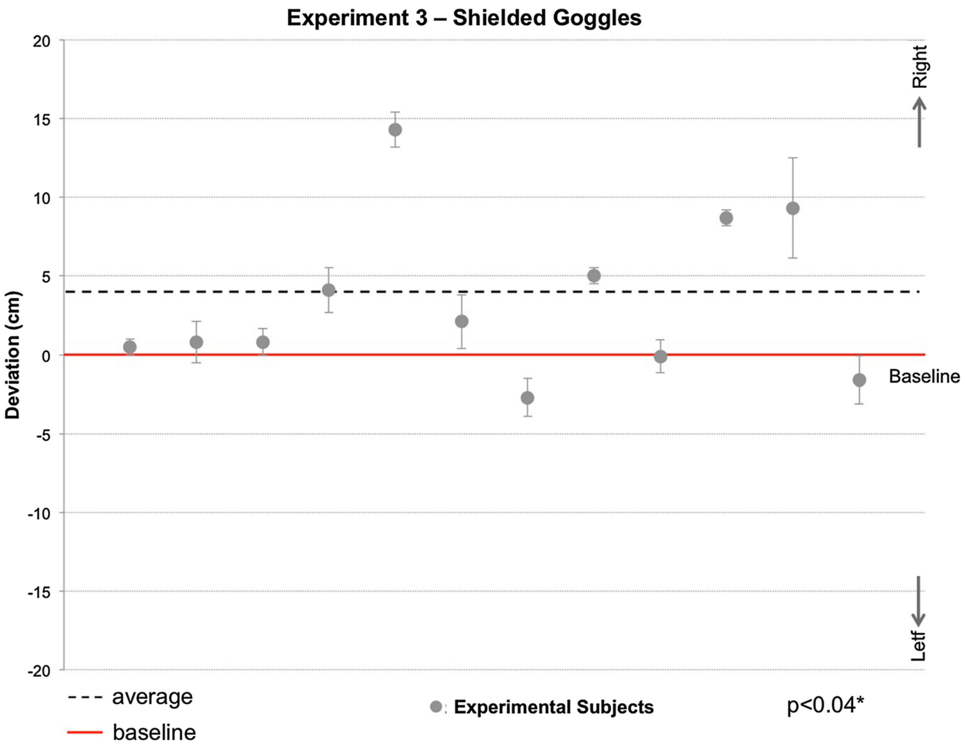

Fig. 4 Experiment 3: straight ahead estimation performed with laterally shielded goggles. Individual participants' straight ahead estimations after OPT performed with shielded goggles are presented. Data are normalized according to each participant subjective *straight ahead* (*Baseline*, in *red*). *Grey dots* represent the difference (in cm) between the baseline and subjective straight ahead judgements collected after PT. *Y axis*: positive values indicate *rightward shifts*, negative values *leftward shifts*. Average deviation is shown by the *dashed black line. Vertical bars* represent standard errors

in degrees of visual angle: tan $\alpha = (3.43\ \mathrm{cm}_{\mathrm{error}}/300\ \mathrm{cm}_{\mathrm{subj\ distance}})$; arctan $\alpha = 0.655°$)].

Experiment 4: effect of OPT on visual straight ahead with workspace shifted 11° contralaterally to prismatic deviation and laterally shielded goggles. Individual participants' straight ahead judgements after OPT are presented in Fig. 5. Interestingly, we did not find any significant modulation of participants' estimations after OPT [(grand average deviation toward the right-hand side: 1.51 cm ± 4.3; mean ± SD; paired sample t test: $T_{11} = 1.211$, $p = 0.251$; tan $\alpha = (1.51\ \mathrm{cm}_{\mathrm{error}}/300\ \mathrm{cm}_{\mathrm{subj\ distance}})$; arctan $\alpha = 0.286°$)].

Experiment 5: effect of oculomotor training, executed without prismatic goggles, but with workspace shifted 11° leftward. Individual participants' straight ahead judgements after oculomotor training are presented in Fig. 6.

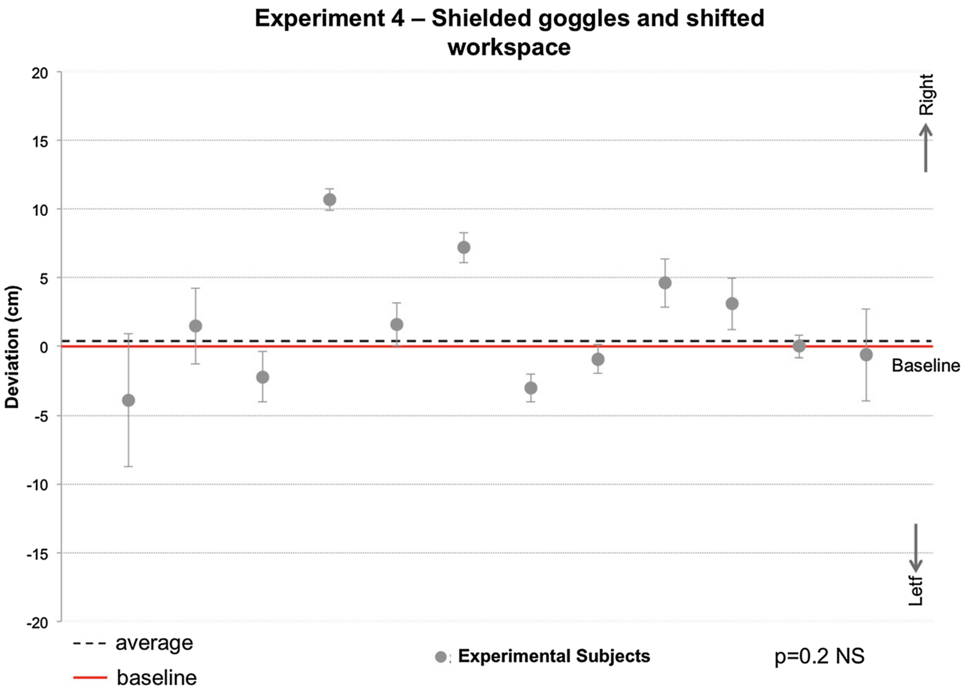

Fig. 5 Experiment 4: straight ahead estimation performed with laterally shielded goggles and shifted workspace. Individual participants' straight ahead estimations after OPT are presented. OPT was performed with shielded goggles and with the workspace shifted 11° toward the right-hand side. Data are normalized according to each participant subjective *straight ahead* (*Baseline*, in *red*). *Grey dots* represent the difference (in cm) between the baseline and subjective straight ahead judgements collected after PT. *Y axis*: positive values indicate *rightward shifts*, negative values *leftward shifts*. Average deviation is shown by the *dashed black line*. *Vertical bars* represent standard errors

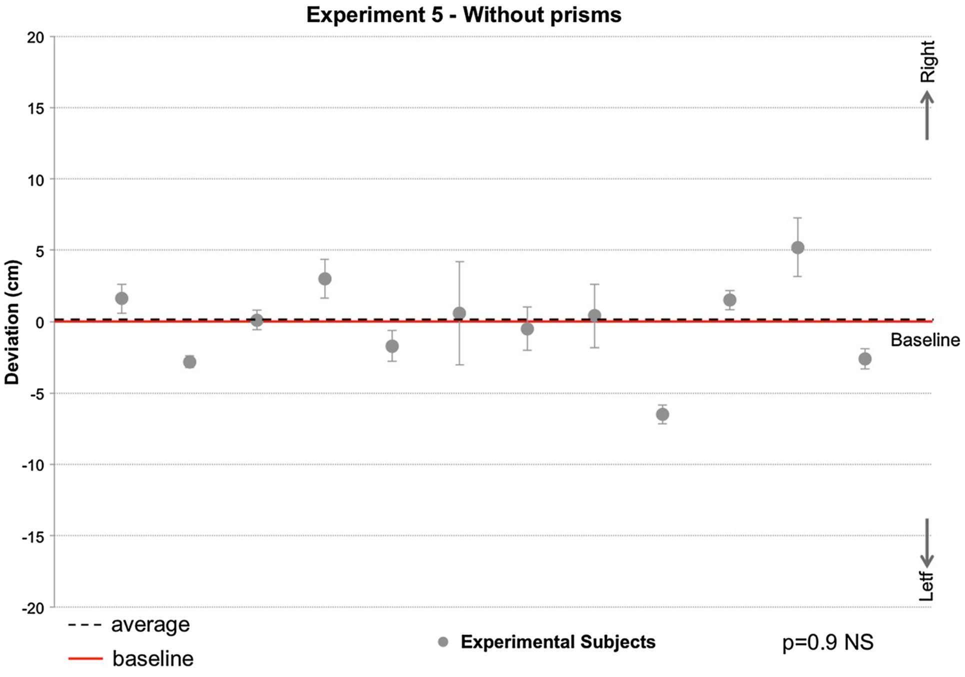

Fig. 6 Experiment 5: effect of oculomotor training, executed without prismatic goggles, but with workspace shifted 11° *leftward*. Individual participants' straight ahead estimations after oculomotor training without prisms are presented. Oculomotor training was performed without prismatic goggles and with the workspace shifted 11° toward the left-hand side. Data are normalized according to each participant's subjective straight ahead (*Baseline*, in *red*). *Grey dots* represent the difference (in cm) between baseline and subjective straight ahead judgements collected after training. *Y axis*: positive values indicate *rightward shifts*, negative values *leftward shifts*. Average deviation is shown by the *dashed black line*. *Vertical bars* represent standard errors

We did not find any significant modulation of participants' estimations after oculomotor training performed without prismatic goggles [(grand average deviation toward the right-hand side: −0.14 cm ± 3.0; mean ± SD; paired sample t test: $T_{11} = 0.162$, $p = 0.874$; tan $\alpha = (0.14\ \mathrm{cm}_{\mathrm{error}}/300\ \mathrm{cm}_{\mathrm{subj\ distance}})$; arctan $\alpha = 0.026°$)].

Discussion

In the present study, 48 participants performed a single ~3 min. session of PA repeatedly gazing at visual targets while wearing prismatic goggles displacing the visual field 11° to the left. Vision of one's own body was prevented. In Experiments 1 and 2, we demonstrated that OPT is effective in inducing a rightward bias both in perceptual (VSA: performed without any overtly executed movement) and in visuomotor tasks (line bisection from memory—Figs. 2, 3a, respectively). This latter result is particularly interesting, as it suggests that the effects of PA also apply to stored spatial representations, such as those activated during the bisection task from memory. In Experiment 2, we directly compared the effect of OPT and VPT, suggesting that, at least in the case of the line bisection task, the two procedures induce similar aftereffects.

Altogether, these findings indicate that a single session of OPT can induce PA across different visual-motor tasks, inducing a remapping of spatial representation similar to the one observed following VPT, even though the direction of the biases elicited by VPT and OPT may differ in different experimental tasks, possibly depending on the amount of visual and motor components involved (see *2. A possible explanatory model of OPT aftereffects*).

In Experiments 3, 4 and 5, we investigated the possible sources of the above-mentioned aftereffects.

In Experiment 3, where the goggles were shielded all around, we eliminated the possible visuovisual conflict between the deviated central portions of the visual field and the non-deviated peripheral ones; still, significant aftereffects were observed in a straight ahead visual task.

Critically, in Experiment 4, by shifting the workspace 11° contralaterally to visual field prismatic deviation, the workspace appeared co-aligned with the eyes at primary orbital position and with the head-on-trunk orientation, i.e. with the straight ahead position. Importantly, in this case we did not find any significant effect following PA (Fig. 5). Through this manipulation, we maintained the optical deviation of the visual field but counteracted the deviation of the eyes in the orbits, as well as the mismatch between the straight ahead signalled by the head-on-trunk reference system and the straight ahead arising from retinal information. In other words, participants (who aligned the worksheet centre with their sagittal midline before wearing prismatic goggles) no longer perceived a mismatch between the position of the fixation cross and their straight ahead. This condition served to assess the specific role of eye position in the emergence of the effects of OPT.

In Experiment 5, by shifting the workspace 11° leftward without prisms on, we reproduced the visual displacement of the worksheet but in absence of the prisms-induced visual field shift. By this means, we eliminated the optical deviation induced by prisms but we maintained the sustained eyes deviation in the orbits. This manipulation was performed to assess the possible role of eye-muscle potentiation in the emergence of the observed effects, as suggested by the results of the study by Ebenholtz (1976). It is worth noting that, following this manipulation, we did not find any significant effect of eye deviation (Fig. 6), contrary to what happens in the presence of prisms-induced eye (and visual field) deviation. This negative result is probably due to the shorter duration of sustained eyes' deviation relative to Ebenholtz's study, which is not sufficient to induce eye-muscle potentiation.

Altogether, the present results suggest that prismatic aftereffects are related to a conflict among retinal and proprioceptive inputs in signalling the straight ahead position (i.e. visual field deviation and eye rotation in the orbits plus head-on-trunk input, respectively) resulting in a misalignment between retinal and extra-retinal reference frames. Indeed, when only one reference system is put out of register (e.g. the retinal input, as in Experiment 4, or the extraretinal/proprioceptive input, as in Experiment 5), no biases are apparent in the straight ahead estimation task, suggesting that the system, in this case, is still capable of compensating for the biased input.

It remains to be established how the nervous system accomplishes the rightward remapping of visual-motor space following OPT, i.e. in the absence of error feedback signals from overtly executed pointing movements. We propose that two different mechanisms could account for such a remapping: (1) the automatic rotation of the eyes rightwards while wearing leftward-deviating prisms (Rock et al. 1966), partially counteracting the leftward visual field displacement; (2) the optimal integration of visual and proprioceptive information according to the principle of minimizing uncertainty, or noise, for localization of body parts and/or external stimuli and for action execution (van Beers et al. 1999, 2002).

1. The role of eye position in the orbits

Rock et al. (1966) showed that the visuomotor system compensates automatically and immediately for the displacement induced by prisms (20 dioptres/11° shift of the visual field), even when subjects are prevented from viewing their own body and movements, so that objects appear to lie in a direction closer to their true position than to that produced by the refraction of the prisms. The correction compensated for about 1/3 of the optical displacement of the visual axis, but occurred only when the entire visual scene was illuminated, perhaps because such a condition enhances the mismatch between apparent visual straight ahead and felt eye position. This immediate compensation of prismatic displacement is made by means of a (relative) rightward deviation of the eyes by 7° (Rock et al. 1966). In our experiment, we have shown that counteracting the leftward eye deviation during PA by shifting the visual workspace 11° rightward, contralaterally to prismatic deviation, so that the eyes are positioned (and possibly felt to be) physically straight ahead, eliminates any significant bias in straight ahead estimation following prisms removal

(Experiment 4). This result suggests that the proprioceptive input conveyed by the eye deviated position in the orbit while wearing prisms is a necessary condition for the development of aftereffects in the direction opposite to that of prismatic deviation.

An immediate correction mechanism in the direction opposite to that of prismatic shift, similar to the oculomotor one reported by Rock et al. (1966), has also been described for straight ahead estimation while wearing prismatic lenses: Harris (1963) reported that straight ahead objects tend to be judged closer to the veridical straight ahead than they appear, in spite of the optical displacement.

Although there is not yet a convincing explanation for these automatic corrective adjustments of eye position and of the straight ahead reference contralateral to prismatic shift of the visual field, such findings are suggestive of fast automatic compensatory mechanisms that the CNS activates to partially counteract the unexpected shift of the visual field. This fast adaptive mechanism could be related to the aftereffects observed once prisms are removed. In our study, we have indirect evidence of a rightward deviation of the gaze following PT. Indeed, in our straight ahead visual estimation task following OPT, participants stopped the moving LED rightwards of their straight ahead baseline value (Figs. 2, 4), which is indicative of a rightward deviation of the gaze relative to pre-training values. As supporting evidence, it is worth noting that a gaze deviation following PA has repeatedly been reported. Studies on SN patients demonstrated that, following PA, eye movements are significantly shifted toward the same direction of prismatic aftereffects (Ferber et al. 2003; Serino et al. 2006). Importantly, a recent study confirmed the presence of the same phenomenon also in healthy subjects. Bultitude et al. (2013) investigated the effects of PA on double step saccadic movements in normal subjects. They showed that, following PA to left deviating prisms, saccades were deviated rightwards (i.e. in the same direction of PA aftereffects) in the right hemispace. The authors demonstrated that VPT was able to induce both low-level changes in ocular movements, as well as a higher-level visuospatial remapping in healthy subjects.

2. A possible explanatory model of OPT aftereffects

The reported evidence that the CNS partially compensates for the visual displacement induced by left-deviating prisms through immediate partial eye rotation in the direction opposite to that of prismatic shift, however, leaves unanswered the question of why, following prisms removal, the visuomotor system errs rightwards in estimating the straight ahead location, even though visual input is no longer distorted (see however Girardi et al. 2004 and Newport et al. 2009 who found that, after VPT or a sustained eye deviation leftwards, VSA is biased toward the same direction of prismatic displacement). The model proposed by van Beers et al. (1999) and van Beers et al. (2002) offers a possible explanation for this effect. According to this model, the central nervous system dynamically adjusts the relative weight attributed to visual and proprioceptive inputs by taking into account the precision of the incoming sensory information, or, else said, giving more weight to the source the CNS estimates to best reduce final error. As a result, uncertainty in localization of body parts and of sensory stimuli in space is minimized. How the CNS may obtain the knowledge to do so is still object of debate. According to van Beers et al. (1999), there seem to be at least two possible ways: (1) the precision of each sensory modality has been learned through experience; (2) it may be derived from online sensory signals (with the possible partial contribution of attentional orienting towards a single sensory modality). In the case of the visual-proprioceptive conflict generated by wearing prisms during our oculomotor PA procedure, the straight ahead location signalled by the head-on-trunk alignment is considered by the CNS as a more reliable source of information than the retinal and extraretinal input. Head-on-trunk alignment is prioritized because it is unaffected by prismatic deviation of the visual field, whereas both retinal and extraretinal information are altered by prismatic shift and, therefore, more uncertain. Hence, less weight is given to the online information that the straight ahead position lies where the eyes are pointing once the prisms are removed, and more weight is assigned to the (stored) information arising from the proprioceptive reference system (i.e. that the correct straight ahead position is to the right of where the eyes are pointing). This process could lead to the rightward errors in our perceptual straight ahead task once prisms are removed. However, a further question remains open. What method does the CNS use to integrate multiple sensory inputs? A possible answer comes from the work of Ernst and Banks (2002), which has convincingly demonstrated that the CNS can dynamically combine multiple sensory inputs using a Maximum Likelihood Estimation principle to minimize the variance of the final output. In the case of OPT, the signal originating from the visual system carries more noisy information (i.e. with higher variance) about the straight ahead location: retinal information signals that the central target—the fixation cross—is centred on the fovea, whereas the eyes, which are deviated leftwards, simultaneously signal that the fixation cross is off-centre to the left. At the same time, the head-on-trunk proprioceptive input—not manipulated during PA—has lesser variance and signals that the straight ahead location has not changed its original position, remaining to the right of the position signalled by eye deviation. Hence, following prisms removal, straight ahead would result from the integration of the conflicting information arising from the former position of the eyes in the orbits, signalling a location of the straight ahead approximately 5° to the left of the objective straight ahead (Rock et al. 1966), the actual position of the eyes, and the head on trunk reference frame, possibly signalling a position 5° to the right of actual fixation. Given the final result of a rightward bias in straight ahead localization of only 0.458°, on average (see Experiment 1), this suggests that the system is quite effective in resolving the sensory conflict, mainly relying on the actual position of the eyes in the orbits in combination with the head-on-trunk signal.

The above-described sensory integration model can also explain the difference (although not significant) in the dimension of the aftereffect observed when comparing OPT and VPT. According to the model, the variances assigned to visual and proprioceptive inputs are likely to be different when subjects perform OPT or VPT. Indeed, the feedback coming from the observation of pointing movements during VPT is likely to reduce the variance of the visual input, inducing the so-called visual capture of proprioception effect, i.e. a proprioceptive shift, so that the adapted arm starts to be felt where it is seen, rather than where it actually is (Hay et al. 1965). This effect indicates that, contrary to what happens after OPT, where less variance is attributed to the less noisy proprioceptive input (i.e. proprioceptive capture of vision), after VPT the CNS attributes more weight to the less noisy visual input (visual capture of proprioception). Therefore, following the Maximum Likelihood Estimation principle, opposite to what we observe after OPT, following VPT the VSA should reveal a leftward bias, i.e. in the same direction of visual displacement. Indeed, this prediction is confirmed by some experimental results (Girardi et al. 2004). Overall, according to the model, OPT and VPT should induce similar effects in experimental tasks where proprioceptive and visual inputs similarly contribute to task execution and a ballistic movement toward a visual target is involved. Conversely, when one of the two inputs dominates over the other, we expect that OPT and VPT produce significantly different outputs.

A number of relevant questions remain to be answered and need further investigation. For example, it is not possible with our research paradigm to assess the role of attentional factors in inducing the observed rightward bias in bisection and straight ahead tasks following prisms removal. Is this bias dependent upon a rightward deviation of the gaze, or is it attentional in nature and responsible for the rightward gaze deviation?

In conclusion, we demonstrated that a single session of OPT is effective in inducing neglect-like behaviour in healthy participants in the absence of error feedback signals arising from pointing movements (which are absent in the OPT procedure) or visual capture of proprioception (vision of the body is prevented during our OPT procedure). We interpret these results as suggesting that the combination of retinal and extraretinal (eye position and head-on-trunk proprioceptive input) information is the crucial source for the nervous system for the emergence of the effects following OPT.

Finally, these findings are also relevant for their possible clinical applications. In Ronga et al. (*in press*), we successfully tested OPT on neglect patients: our results show a significant amelioration of neglect in straight ahead, bisection and drawing from memory tasks.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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