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Effect of prism adaptation on thermoregulatory control in humans

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HIGHLIGHTS

- After visuo-motor adaptation to rightward displacing glasses, the participants' hands temperature decreased.
- After adaptation to neutral lenses and left shifting prisms, we found an increase of the temperature of both hands.
- The results suggest a relationships between body spatial representations and homeostatic control.

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ABSTRACT

The physiological regulation of skin temperature can be modulated not only by autonomic brain regions, but also by a network of higher-level cortical areas involved in the maintenance of a coherent representation of the body. In this study we assessed in healthy participants if the sensorimotor changes taking place during motor adaptation to the lateral displacement of the visual scene induced by wearing prismatic lenses (prism adaptation, PA), and the aftereffects, after prisms' removal, on the ability to process spatial coordinates, were associated with skin temperature regulation changes. We found a difference in thermoregulatory control as a function of the direction of the prism-induced displacement of the visual scene, and the subsequent sensorimotor adaptation. After PA to rightward displacing lenses, with leftward aftereffects (the same directional procedure efficaciously used for ameliorating left spatial neglect in right-brain-damaged patients) the hands' temperature decreased. Conversely, after adaptation to neutral lenses, and PA to leftward displacing lenses, with rightward aftereffects, the temperature of both hands increased. These results suggest a lateral asymmetry in the effects of PA on skin temperature regulation, and a relationship between body spatial representations and homeostatic control in humans.

1. Introduction

The relationship between the sense of body ownership and the physiological regulation of bodily functions has recently drawn the attention of those researchers interested in understanding how the human brain develops, represents, and maintains a bodily "self" [1–3]. In particular, the link between several physiological parameters (heartbeat, temperature regulation, skin conductance responses, pupil dilatation), different aspects of perception (tactile, thermal, proprioception, pain), and bodily consciousness has been investigated both in healthy participants, and in neurological patients showing autonomic dysfunctions, or abnormalities in cortical representations of the body, and the space around it [4–11].

One of the most recent approaches to the study of the relationship between brain mechanisms of bodily self-consciousness and the integrity of the body itself, has made use of perceptual illusions in both healthy participants and clinical populations. Within such paradigms, ambiguous multisensory information about the location and the appearance of one's own body (or body parts) has been used, with the purpose of altering the persons' sense of body ownership, and the regulatory control of their physiological functions [3,9,12]. In particular, the Rubber Hand Illusion has been used to test the hypothesis that hand skin temperature can be modulated by disrupting the sense of ownership over that limb. Specifically, when participants begin to perceive that an artificial limb is part of their own body, the temperature of their real hand (the one placed on the same side of the artificial limb) decreases

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[13,14; see also 15]. Importantly, the temperature's drop observed in the real 'disowned' hand is positively correlated with the vividness of the illusion [13]. In a complementary way, the strength of the Rubber Hand Illusion is increased when a real hand is artificially cooled, while warming the hand decreases the strength of the illusion [7]. In other recent studies, the induction of a Full Body Illusion, obtained by immersing participants in a virtual reality environment, was found to be effective in modulating the exteroceptive sensitivity of the palm of the hand to thermal changes [16], and to cause a widespread drop of the participants' skin temperature [17]. Correspondingly, the sight of the reflection of the participant's limb through a mirror, produced a limb-specific increase in skin temperature: this suggests that the vision of the body could result in an enhanced ownership over the seen limb, thus increasing temperature and homeostatic control, in a process opposite (and complementary) to that acting in the Rubber Hand Illusion [18].

Importantly, disorders of bodily awareness and of thermal regulation are correlated in a number of different neurological and psychiatric conditions, such as schizophrenia [19–22], autism [23,24], epilepsy [25,26], neuropathic pain [27], anorexia nervosa, and bulimia [28,29]. The Complex Regional Pain Syndrome (CRPS) is another clinical condition, whose features include a disruption of thermoregulation [8,30,31], and an altered representation of the body in a number of patients [32–39].

Interestingly, both patients affected by CRPS, and right-brain-damaged patients with left spatial neglect (a multi-componential disorder involving the ability to process spatial information contralateral to the side of the lesion, and/or to perform actions in that side of space [40]), share a number of symptoms [33,34,41–48]. In particular, CRPS patients exhibit a neglect-like, space-based, tactile processing deficit [30] (see also [49] for a study showing that also patients with chronic back pain may show spatial neglect-like symptoms under certain conditions of stimulus presentation). Specifically, in a temporal order judgment task, CRPS patients show a prioritization of vibrotactile stimuli presented on the unaffected hand, when arms are kept uncrossed, and a reversed prioritization when they are crossed over the body midline. These results suggest that the information processing deficits in CRPS patients may be related to body-centered (with reference to the patient's body midline) spatial, rather than to somatotopic (based on the somatosensory representation of the body in the primary somatosensory cortex, area S1) reference frames. CRPS patients show also a deficit in hand skin temperature regulation, with a cooling of the affected limb, related to the prioritization effect: the larger is the difference in temperature between the two hands, the earlier vibrotactile stimuli have to be delivered to the affected hand, in order to be perceived simultaneous to those delivered to the unaffected hand [30]. Interestingly, hand temperature of CRPS patients is modulated by manipulating the position of the hands in peri-personal space, namely: placing the unaffected hand in the "affected" side of space (the one where the affected hand is generally placed), in a position that crosses over the body midline, causes a decrement of hand temperature, suggesting a space-based (body-centered), rather than arm-based (somatotopic), modulation of skin temperature [8].

A further similarity between CRPS and neurological disorders of spatial cognition comes from a single case study. van Stralen and colleagues [50] induced the Rubber Hand Illusion (considered as an experimental measure of disownership of the real hand) on both hands of a right brain-damaged patient suffering from left somatoparaphrenia (a neuropsychological disorder, most often brought about by damage to the right cerebral hemisphere, and characterized by a delusion of disownership of left-sided body parts [51]), and recorded hand skin temperature before and after the induction of the illusion. A decrement in temperature after the induction of the illusion was found, but only in the left, disowned, hand. This result suggests that thermoregulatory control is related to the sense of body ownership, whose disruption may alter thermoregulation.

Visuo-tactile illusions have been so far a main method to investigate the relationships between spatial processing, body ownership, and thermoregulatory control. However, other tools (based on different neurocognitive mechanisms) may prove to be effective in temporarily altering body and peri-personal space representations. In particular, here we used a prism adaptation (PA) procedure in order to study the link between spatial processing and thermoregulation.

In the PA procedure, participants are asked to perform a series of pointing movements to visual targets, while wearing goggles designed to shift the visual scene laterally. Typically, first pointing movements are biased and deviated in the direction of the displacement of the visual scene brought about by the optical prisms (the so-called "direct effect" [52]). This sensorimotor discrepancy between the planned and the actual movement toward the target enhances a correction in subsequent movements, until the target is reached and the sensorimotor discrepancy reduced (adaptation). When prisms are removed, pointing movements are biased toward the opposite side of the prism-induced displacement (aftereffects). The resolution of the sensorimotor discordance induced by optical prisms displacing the visual scene requires a remapping of bodily and space coordinates into a new egocentric spatial frame of reference. The occurrence of sensorimotor aftereffects, that index successful adaptation, is assessed by measuring the egocentric straight ahead, both before (pre-), and after (post-) prismatic exposure. Straight ahead measures are obtained for the visual, the proprioceptive, and the visual-proprioceptive sensorimotor systems. Proprioceptive and visual-proprioceptive aftereffects are shifted in the opposite direction with respect to the displacement of the visual scene induced by exposure to optical prisms, while visual aftereffects are shifted in the same direction of it [52].

PA has been extensively used to investigate both neural plasticity in healthy participants, and the effect of spatial remapping in the rehabilitation of neuropsychological disorders [53–56] (see [57] for a comprehensive review on PA). PA has been used to treat also the symptoms of CRPS patients, achieving a substantial relief of pain, as well as the amelioration of other symptoms [35,58]. Prismatic lenses have been recently used in CRPS patients to test the hypothesis that its thermal manifestations depend on the perceived location of the hand relative to the body midline, rather than to its actual location. Prisms induced a displacement of the perceived position of the affected hand either towards the affected (ipsilateral), or towards the unaffected (contralateral), side of space, in the latter condition, illusorily crossing the body midline. The patients' pathological arm warmed up (with a reduction of the thermoregulatory dysfunction), when visually perceived in the unaffected, contralateral, side of space, and cooled down when perceived in the affected side, in both conditions regardless of its actual physical position [31]. Accordingly, those cortical mechanisms involved in processing the perceived position of the limbs in space, on the basis of visual and proprioceptive information, may also participate in modulating hands' temperature.

As far as the neural basis of the higher-order modulations of thermoregulatory control is concerned, the temporary interference over the activity of the posterior parietal cortices (PPC) by means of rTMS, reduces hand temperature in healthy participants [59]. The PPC, an area involved in the multisensory integration of stimuli in different sensory modalities [60,61], the maintenance of spatial and body representations [61–63], and the planning of goal-directed movements [64–66], might be also part of a network that exerts a top-down modulation on physiological functions related to body

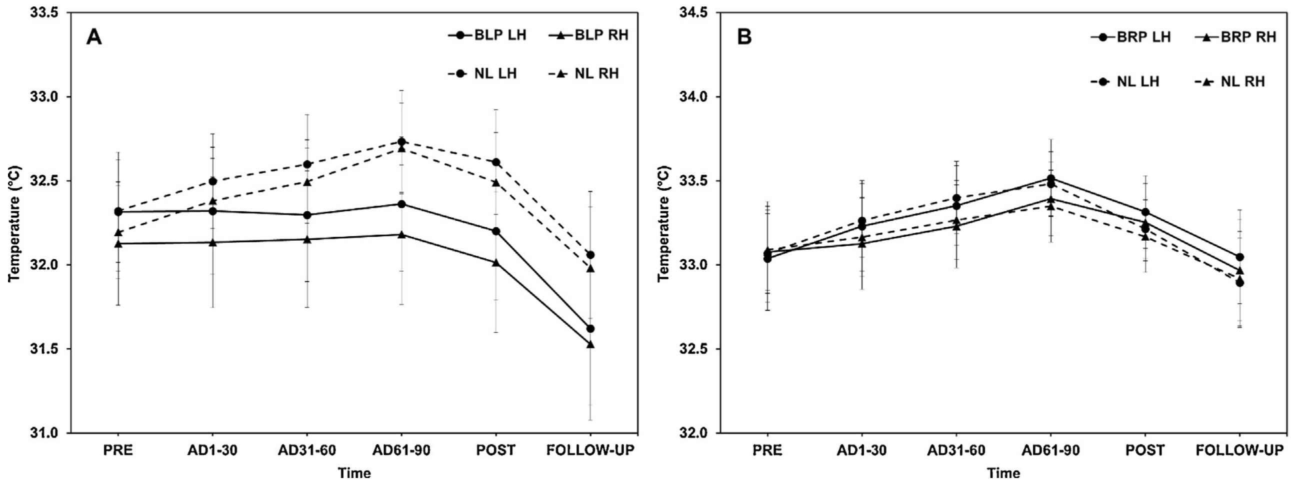

Fig. 1. Mean (SE) skin temperature (°C) of the hands. Circles indicate temperature values for the left hand (LH), and triangles for the right hand (RH), before (pre), during (AD1-30, AD31-60, AD61-90), and after (post and follow-up) the pointing adaptation tasks. Experiment #1 A: adaptation to base-left prisms (BLP, solid line) and to neutral lenses (NL, dashed line). Experiment #2 B: adaptation to base-right prisms (BRP, solid line) and neutral lenses (NL, dashed line).

ownership, such as thermoregulation. The PPC is also involved in mediating PA processes and aftereffects [67–74].

On the basis of these previous findings, we carried out two experiments to test the hypothesis that the sensorimotor effects of PA, and its aftereffects on bodily spatial reference frames, can be effective in modulating thermoregulatory control in healthy participants. In particular, in Experiment #1, we tested the primary hypothesis that sensorimotor adaptation to right-displacing prisms, the ones that exert ameliorating effects on manifestations of left spatial neglect, affecting spatial representation and attention [55], could also affect body temperature regulation. Such a finding would suggest a relationship between spatial processes and basic physiologic parameters, such as body temperature. Specifically, we expected a different pattern of temperature change after sensorimotor adaptation to right displacing prisms with respect to the control condition (i.e., sensorimotor adaptation to neutral, not displacing lenses).

In Experiment #2, we tested whether a change in body temperature is the result of an autonomic response to the visual-proprioceptive incongruence induced by the participants' exposure to a lateral shift of the visual field, or if it reflects a more specific function sustained by cortical areas implied in spatial remapping during PA to rightward displacing prisms. Were the first hypothesis correct, we should expect a different hands' skin temperature evolution following adaptation to left displacing prisms, compared to the control condition. Moreover, the temperature change should be in the same direction of that found using rightward displacing prism (Experiment #1). Otherwise, no significant differences between the left displacing and the control conditions should be found.

2. Materials and methods

2.1. Participants

Forty-eight healthy right-handed [75] students, recruited in the Department of Psychology of the University of Milano-Bicocca, took part in the study (24 for each experiment; Experiment #1: 12 females, mean age: 26 ± 3.54 years, range: 19–32; mean education: 16.54 ± 1.67 years, range: 13–18; Experiment #2: 12 females, mean age: 25.08 ± 3.12 years, range: 19–30; mean education: 16.21 ± 2.17 years, range: 13–22). Participants had normal

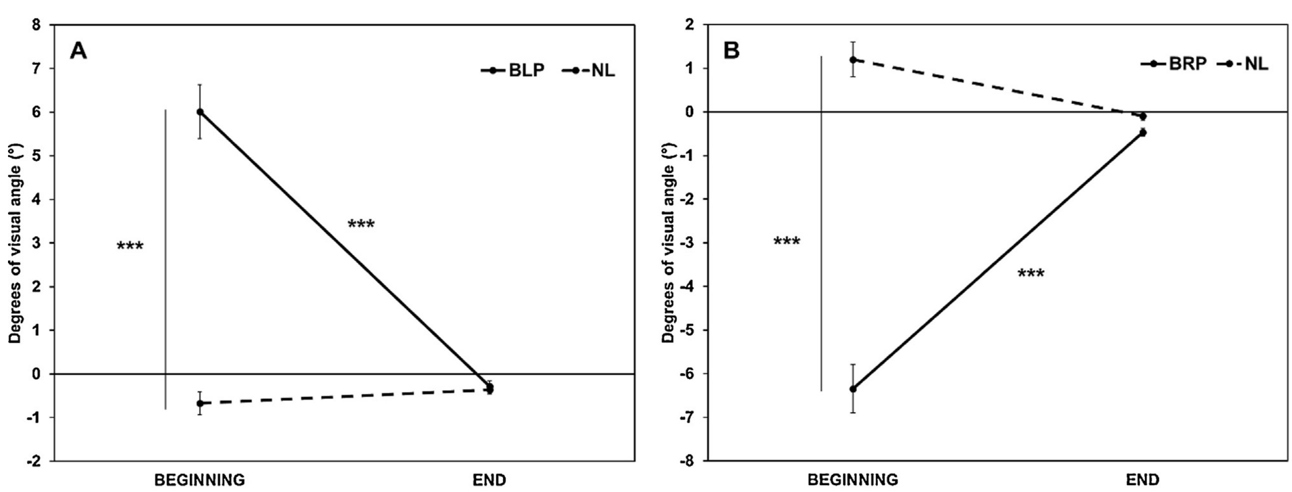

Fig. 2. Mean (SE) deviation of the first four pointing movements (beginning) and the last four pointing movements (end) of the right index finger from the visual target in the pointing adaptation task, in degrees of visual angle (°); positive values correspond to rightward deviations from the visual target, negative values to leftward deviations. Experiment #1 A: prism adaptation to base-left prisms (BLP, solid line), and to neutral lenses (NL, dashed line); Experiment #2 B: prism adaptation to base-right prisms (BRP, solid line), and to neutral lenses (NL, dashed line). $p < 0.001$***, <0.01**, <0.05*.

or corrected-to-normal vision, no history of diseases of the central or peripheral nervous system, epilepsy, migraine, ongoing flu, or other concurrent conditions that may alter body temperature (i.e., females were asked not to participate during the menstruation phase of their cycle).

The study was approved by the local Ethical Committee, and performed according to the ethical standards laid down in the 1991 Declaration of Helsinki. All participants gave informed consent, after a brief session that outlined the nature of the study. Students received credits for their participation.

2.2. Temperature measurement

Skin temperature was measured during the whole of the two sessions of each experiment by means of two wireless digital thermometers (Thermochron iButton® data loggers; model DS1922L, Maxim Integrated, San Jose, CA, USA) applied with two crossed strips of latex-free, hypoallergenic paper tape on the back of the participants' hands (3M™ Micropore™ Medical Tape). These thermometers are certified to measure human temperature with a resolution of 0.0625 °C, from −10 °C to +65 °C [76,77]. The thermometers sampled at a rate of 0.2 Hz (12 recordings per minute).

2.3. Prism adaptation task

In Experiment #1, in one session, participants were adapted to an 11.4° rightward visual shift induced by 20-diopter, base-left prism glasses (BLP; Optique Peter, Lyon, France). In the other session, they adapted to a normal vision condition using goggles with neutral lenses (NL; Optique Peter). In Experiment #2, in one session, participants were adapted to an 11.4° leftward visual displacement (20-diopter, base-right prism glasses, BRP; Bernell™ Deluxe Prism Training Glasses), and in the other session to the same neutral lenses used in Experiment #1. For both experiments, the order of sessions was counterbalanced between participants within the two experiments. Sensorimotor adaptation was achieved by the execution of 90 pointing movements by the index finger of the right upper limb towards a target (a red pen) presented in 2 different positions (+10° rightwards, and −10° leftwards, with respect to the body midline) in a pseudorandom fixed order [78]. The same order was maintained within the two days for all participants, who were asked to point with their right fingertip to the pen, with a fast and accurate movement, and then to return to the initial position (right finger on their sternum). The view of the pointing movement was occluded by means of a wooden box and a cape. This apparatus covered the participant's arms, with the sole exception of the finger, which became visible at the very last part of the movement [53]. This setting was adopted in order to prevent participants from using an online control of the arm movement, but still to provide a feedback of the final pointing error, induced by the prismatic displacement of the visual scene. During the procedure, the pointing error progressively reduced, until participants pointed to the actual target position. The task was the same in the neutral condition. Wearing neutral goggles is generally not associated with pointing errors. The pointing adaptation task lasted about 15–20 min, with a two minute break every 30 pointing movements, resulting in three blocks, each block including 30 pointing movements. The external side of the wooden box, the one facing the experimenter, was graduated in degrees of visual angle, so that the experimenter could measure the deviation from the target of each pointing movement with an accuracy of 1°, with rightward deviations from the pen being scored with positive values, leftward with negative values (see [54,78] for further details).

2.4. Proprioceptive straight-ahead test

In order to assess the presence of aftereffects due to PA [52], participants underwent the proprioceptive straight-ahead test before and after the PA session, and in the follow-up session of the experiment. Participants, with their eyes closed, were asked to point with their right index finger, placed on a graduated panel, towards the perceived position of their body midline. This procedure was repeated 10 times [78]. For each trial, the deviation of the finger position from the true body midline was measured in degrees of visual angle, with an accuracy of ±0.5°. Rightward deviations from the objective body midline were scored with positive values, leftward deviations with negative values.

2.5. Procedure

Each participant took part in two sessions, performed in two consecutive days; sessions were scheduled at the same time of the day for each participant, in order to prevent differences in body temperature due to the phase of the circadian rhythms [79–81]. During the whole session participants sat, in a comfortable position, with their arms leaning on a table, with the temperature of the room being recorded during each phase. Each block lasted about 90 min, and consisted of six sections: 1) thermometer stabilization and baseline, 2) pre-PA, 3) PA, 4) post-PA, 5) rest, and 6) follow-up. In each of these phases, the experimenter recorded the initial and the final time of each activity, using the computer clock, which was synchronized with the thermometers.

a Stabilization phase: The thermometers were activated and applied to the back of each participant's hands. Then the participant was asked to relax for a period of 20 min, in order for the thermometers to measure a stable baseline temperature of the hands. The mean of the samples recorded in the 5 min following this phase constituted the baseline temperature measure (T_{baseline}, see [59] for details).
b Pre-PA phase: (and post-PA phase). Each participant was firstly asked to perform the proprioceptive straight-ahead task, followed by 2 min of rest, and by 3 additional minutes of registration, that constituted the pre-test measure (T_{pre}).
c PA phase: Each participant performed the pointing task. The order of the PA sessions was counterbalanced across participants: half of the participants were adapted to prism lenses in the first day and to neutral lenses in the second day, the other half vice versa. In this phase, three temperature measures were computed, by averaging the temperature samples during the three PA blocks ($T_{\text{AD1–30}}$, $T_{\text{AD31–60}}$, $T_{\text{AD61–90}}$).
d Post-PA phase: (exactly the same as the pre-PA one). Temperature was measured for 3 min (T_{post}), and this was followed by the execution of the proprioceptive straight-ahead test to assess the aftereffects.
e Rest phase: Each participant just sat at the table for 20 min, avoiding any arm movements, to prevent any direct loss of adaptation [82].
f Follow-up phase: Participants performed the proprioceptive straight-ahead task again, to assess the possible persistence of the aftereffects, followed by other 3 min of temperature measurement ($T_{\text{follow-up}}$).

During the whole session the left hand was kept still, while the right hand executed the movements.

2.6. Preliminary data processing

We excluded from all the analysis data from participants having >50% of their temperature measurements (included $T_{baseline}$) more than 2SD lower than the mean of the entire group [7].

2.7. Analysis

2.7.1. Experiment #1

The statistical analyses were carried out with the software Statistica (StatSoft, Tulsa, OK, USA, version 6.0). The measures obtained by two participants were excluded from the analysis, according to our *a priori* policy (see Section 2.6). The analyses were thus carried on the remaining 22 participants.

2.7.1.1. Temperature. In order to assess the presence of temperature stability between the baseline and the pre-PA phase, a repeated-measures analysis of variance (ANOVA) was performed on the average of the samplings collected during the 5-min baseline period (mean of 60 registrations for each hand), and the pre-PA temperature 3-min samplings (mean of 36 registrations for each hand). The ANOVA was performed with the within-subjects main factors of "Type of Lenses", used later during the PA phase (BLP/NL), and "Time" ($T_{baseline}$, T_{pre}). Afterward, in order to assess the presence of differences in hand skin temperature due to the PA to BLP or to NL, a repeated-measures ANOVA was performed on the six temperature samplings following the baseline: one before (T_{pre}), three during (T_{AD1-30}, $T_{AD31-60}$, $T_{AD61-90}$), and two after PA (T_{post}, $T_{follow-up}$). Each measure was the mean of the overall samples of that registration period. That is, each T_{pre}, T_{post}, and $T_{follow-up}$ value was the average of the 36 samplings, during the three minutes registration. Since the execution time of each of the three pointing blocks could slightly vary across participants (with a total pointing task lasting between 15 and 20 min, including some minutes of rest between blocks), the number of samplings of the three temperature measures during PA varied. The ANOVA was performed with the within-subjects factors of "Type of Lenses" used during PA (BLP/NL), "Hand" (left/right), and "Time" (T_{pre}, T_{AD1-30}, $T_{AD31-60}$, $T_{AD61-90}$, T_{post}, $T_{follow-up}$).

2.7.1.2. Behavioral measures: PA and aftereffects measures. In order to establish the occurrence of PA (in terms of reduction of the initial pointing error), a repeated-measures ANOVA was performed on the mean deviations from the position of the target (degrees of visual angle) of the first four and the last four pointing movements during the PA phase. In this analysis, the within-subjects factors were "Type of Lenses" (BLP/NL) and "Pointing" (first four/last four pointing trials).

A repeated-measures ANOVA, with the within-subjects factors of "Type of Lenses" (BLP/NL), and "Time" (Pre/Post/Follow-up), was performed on the pointing deviations from the true objective body midline, in order to assess the presence and the magnitude of the aftereffects, caused by PA, on the proprioceptive straight-ahead task.

In all ANOVAs, significant effects and interactions were investigated with Tukey's HSD (Honestly Significant Difference) test *post hoc* multiple comparisons. Partial eta squared ($\eta_p{}^2$) of significant effects were also computed, in order to determine the effect sizes [83]. Significance was set at $\alpha = 0.05$.

2.7.2. Experiment #2

The measures obtained by two participants were excluded from the analysis, according to our *a priori* policy (Section 2.6). The analyses were thus carried on the remaining 22 participants. The same analyses adopted in Experiment #1 were performed on temperature and behavioral measures from Experiment #2; in this second experiment the two levels of the within-subjects factor of "Type of Lenses" used during PA were BRP and NL.

3. Results

3.1. Experiment 1

3.1.1. Temperature

The preliminary ANOVA assessing the temperature stability between $T_{baseline}$ and T_{pre} did not show any significant effect [Type of Lenses $F_{(1,21)} = 0.02$, $p = 0.889$; Time $F_{(1,21)} = 1.21$, $p = 0.284$] or interaction [Type of lenses by Time $F_{(1,21)} = 0.03$, $p = 0.861$], thus demonstrating the stability between the baseline and the pre-PA temperature values.

Fig. 1A (left panel) shows the hands' skin temperature evolution during time, across the two sessions (values are summarized in Table 1). For NL, some increase of temperature was apparent in the final PA phase, while for BLP temperature decreased after PA. The ANOVA showed that the main effect of Time [$F_{(5,105)} = 6.54$, $p < 0.001$, $\eta_p{}^2 = 0.24$] was significant, while those of Type of Lenses [$F_{(1,21)} = 2.78$, $p = 0.11$], and Hand [$F_{(1,21)} = 2.31$, $p = 0.143$] did not attain the significance level. The Type of Lenses by Time interaction [$F_{(5105)} = 2.34$, $p = 0.047$, $\eta_p{}^2 = 0.10$] was significant, while the Type of Lenses by Hand [$F_{(1,21)} = 0.53$, $p = 0.475$], and Hand by Time [$F_{(5,105)} = 0.42$, $p = 0.836$] interactions, as well as the Type of Lenses by Hand by Time [$F_{(5,105)} = 0.52$, $p = 0.76$] interaction, were not significant. Multiple comparisons exploring the Type of Lenses by Time interaction showed that, when participants adapted to NL, the hands' temperature in the last block of PA was significantly higher with respect to the pre-PA phase ($T_{AD61-90}$ *vs.* T_{pre} $p < 0.01$). During the follow-up (specifically, after 15 min of rest), temperature was lower than it was during ($T_{follow-up}$ *vs.* T_{AD1-30} $p < 0.05$, *vs.* $T_{AD31-60}$ and $T_{AD61-90}$ p-values < 0.001), and after the PA phase ($T_{follow-up}$ *vs.* T_{post} $p < 0.001$), but it did not differ from the initial temperature during the pre-PA phase ($T_{follow-up}$ *vs.* T_{pre} $p = 0.58$). The increase in temperature found during the adaptation task, when participants wore neutral lenses, might be considered a consequence of the metabolic heat production during the prolonged motor effort, followed by a return to baseline thermal values once such motor activity ended [84–86]. Interestingly, during the day in which participants adapted to BLP, no such increase in temperature during the PA task occurred (T_{AD1-30}, $T_{AD31-60}$, $T_{AD61-90}$, T_{post} *vs.* T_{pre} all p-values > 0.993). Moreover, the hands temperature measured during the follow-up resulted to be significantly lower than the temperature measured in all the other phases of the experiment ($T_{follow-up}$ *vs.* T_{pre}, T_{AD1-30}, $T_{AD31-60}$, $T_{AD61-90}$, T_{post}, all p-values < 0.001). The analysis also showed significant differences in temperature between the two types of lenses at the end of the PA phase ($T_{AD61-90}$ NL *vs.* $T_{AD61-90}$ BLP $p < 0.01$), after goggles removal (T_{post} NL *vs.* T_{post} BLP $p < 0.01$), and during the follow-up phase ($T_{follow-up}$ NL *vs.* $T_{follow-up}$ BLP $p < 0.01$). All of the comparisons showed a cooler temperature during and after the BLP PA, as compared to NL. No significant differences between right and left hand temperature were found. Notably, left hand temperature was affected as much as the right hand by the experimental manipulation even though the former remained still for the whole experimental session.

3.1.2. PA: pointing error reduction

Fig. 2A (left panel) shows the deviation of the first and last four pointing movements of the two PA phases, with the first pointing movements of PA to BLP being more deviated toward the right than the last pointing movements, that were more accurate; no such effects were found with NL. A repeated measures ANOVA showed that the main effects of Type of Lenses [$F_{(1,21)} = 82.20$, $p < 0.001$,

Table 1
Experiment #1. Mean (SE) skin temperature (°C) of the hands (average of left and right hand) before, during and after the prism adaptation tasks, by session (base-left prisms, neutral lenses).

Type of Lenses	T_{pre}	T_{AD1-30}	$T_{AD31-60}$	$T_{AD61-90}$	T_{post}	$T_{follow-up}$
BLP	32.22 ± 0.36	32.23 ± 0.38	32.23 ± 0.40	32.27 ± 0.40	32.11 ± 0.41	31.58 ± 0.45
NL	32.26 ± 0.29	32.44 ± 0.26	32.55 ± 0.27	32.71 ± 0.28	32.55 ± 0.30	32.02 ± 0.37

BLP Base Left Prisms, NL Neutral Lenses.

$\eta_p^2 = 0.80$], and Pointing [$F_{(1,21)} = 85.33$, $p < 0.001$, $\eta_p^2 = 0.80$], as well as their interaction [$F_{(1,21)} = 82$, $p < 0.001$, $\eta_p^2 = 0.80$] were significant. As shown by multiple comparisons, the first pointing movements of PA to BLP (6.01 ± 2.91°) were more deviated toward the right ($p < 0.001$) than the last pointing movements, which, in turn, were more accurate (−0.28 ± 0.59°). Adaptation to NL did not show such a significant difference ($p = 0.93$) between the first (−0.67 ± 1.21°), and the last pointing movements (−0.36 ± 0.43°). Moreover, the first pointing movements executed while wearing BLP were more shifted rightward than the first pointing movements while wearing NL (first pointing movements BLP 6.01 ± 2.91° *vs.* first pointing movements NL −0.67 ± 1.21°, $p < 0.001$). By contrast, the last pointing movements did not differ between the two conditions (last pointing movements BLP −0.28 ± 0.59° *vs.* last NL −0.36 ± 0.43°, $p = 0.999$). Accordingly, at the end of the pointing task, participants pointed correctly to the target, demonstrating the PA effect.

3.1.3. Aftereffects: proprioceptive straight-ahead

Fig. 3A (left panel) shows the participants' performance in the proprioceptive straight-ahead task before (Pre), after (Post), and later after (Follow-up) the two PA sessions. Exposure to NL was ineffective, while that to BLP brought about leftward aftereffects. The ANOVA showed that the main effects of Type of Lenses [$F_{(1,21)} = 1.21$, $p = 0.28$], and Time [$F_{(1,21)} = 2.26$, $p = 0.12$] were not significant. The Type of Lenses by Time interaction was significant [$F_{(2,42)} = 3.18$, $p = 0.05$, $\eta_p^2 = 0.13$]. Multiple comparisons showed that exposure to NL did not induce any shift of the subjective body midline, both immediately after exposure (M ± SD Pre −0.42 ± 2.62° *vs.* Post −0.45 ± 2.75°, $p = 0.999$), and in the follow-up (Pre *vs.* Follow-up −0.16 ± 2.01°, $p = 0.991$, Post *vs.* Follow-up $p = 0.983$). Exposure to BLP induced an immediate leftward shift in the proprioceptive straight-ahead (Pre 0.01 ± 2.16° *vs.* Post −1.57 ± 3.12°, $p < 0.01$); during the Follow-up the shift was no longer present, and the participants' performance did not differ from the Pre-PA and Post-PA phases (Pre *vs.* Follow-up −0.47 ± 2.35°, $p = 0.873$, Post *vs.* Follow-up, $p = 0.137$).

3.2. Experiment 2

3.2.1. Temperature

The preliminary ANOVA assessing the temperature stability between $T_{baseline}$ and T_{pre} did not show any significant effect [Type of Lenses $F_{(1,21)} = 0.09$, $p = 0.773$; Time $F_{(1,21)} = 0.98$, $p = 0.333$], or interaction [Type of lenses by Time $F_{(1,21)} = 1.37$, $p = 0.255$], thus demonstrating the stability between the baseline and the pre-PA temperature values.

Fig. 1B (right panel) shows the hands' skin temperature evolution during time, across the two sessions (values are summarized in Table 2). The main effect of Time [$F_{(5,105)} = 5.13$, $p < 0.001$, $\eta_p^2 = 0.20$] was significant, while those of Type of Lenses [$F_{(1,21)} = 0.02$, $p = 0.88$], and Hand [$F_{(1,21)} = 1.18$, $p = 0.29$] were not significant. The Hand by Time interaction [$F_{(5,105)} = 3.89$, $p = 0.003$, $\eta_p^2 = 0.16$] was significant. The Type of Lenses by Hand [$F_{(1,21)} = 0.05$, $p = 0.82$], Type of Lenses by Time [$F_{(5,105)} = 0.45$, $p = 0.81$], and Type of Lenses by Hand by Time [$F_{(5,105)} = 0.98$, $p = 0.43$] interactions were not significant. Multiple comparisons on the main effect of Time showed that hand temperature measured during the last block of PA significantly increased, as compared with those measured both in the pre-PA phase ($T_{AD61-90}$ *vs.* T_{pre}, $p = 0.01$), and during the follow-up ($T_{AD61-90}$ *vs.* $T_{follow-up}$, $p < 0.001$). Moreover, during the follow-up, hands' temperature did not differ from the initial temperature of the pre-PA phase ($T_{follow-up}$ *vs.* T_{pre} $p = 0.90$). This was the same pattern of temperature changes found in Experiment #1 during PA to NL. Notably, in Experiment #2, no significant main effect of the factor Type of Lenses, or interactions involving it, were found, indicating that PA to BRP generated the same effect in hands' temperature as the exposure to a non-deviating condition (i.e., adaptation to NL), as shown in Fig. 1B. As for the Time by Hand interaction, multiple comparisons showed a difference in temperature between hands during the adaptation task, where the right hand was cooler than the left hand, in the second and third PA blocks ($T_{AD31-60}$ left hand *vs.* $T_{AD31-60}$ right hand and $T_{AD61-90}$ left hand *vs.* $T_{AD61-90}$ right hand, both p-values < 0.01).

3.2.2. Adaptation: pointing error reduction

Fig. 2B (right panel) shows the deviation of the first four and the last four pointing movements of the two PA phases, with the first four pointing movements during PA to BRP being more deviated toward the left than the last four pointing movements. The last four pointing movements were more accurate. No such effect was found with NL. A repeated measures ANOVA showed that the main effects of Type of Lenses [$F_{(1,21)} = 103.45$, $p < 0.001$, $\eta_p^2 = 0.83$], Pointing [$F_{(1,21)} = 54.08$, $p < 0.001$, $\eta_p^2 = 0.72$], as well as and the interaction between Type of Lenses and Pointing [$F_{(1,21)} = 97.68$, $p < 0.001$, $\eta_p^2 = 0.82$] were significant. Multiple comparisons showed that the first four pointing movements during the PA to BRP (−6.34 ± 2.59°) were significantly more deviated towards the left ($p < 0.001$), than the last four pointing movements (−0.47 ± 0.42°). Adaptation to NL did not show such a difference ($p = 0.085$) between the first (1.20 ± 1.87°) and the last (0.09 ± 0.48°) pointing movements. Moreover, the first pointing movements, executed while wearing BRP, were significantly shifted more leftward, as compared to those executed while wearing NL (BRP −6.34 ± 2.59° *vs.* NL 1.20 ± 1.87°, $p < 0.001$). By contrast, the last pointing movements did not differ between the two conditions (BRP −0.47 ± 0.42° *vs.* NL −0.09 ± 0.48°, $p = 0.88$). This finding indicates that, at the end of the pointing task, participants pointed correctly to the target, showing that PA had been obtained.

3.2.3. Aftereffects: proprioceptive straight-ahead

Fig. 3B (right panel) shows the participants' performance in the proprioceptive straight-ahead task before (Pre), after (Post), and later after (Follow-up) the two PA sessions, with the first pointing movements of PA to BRP being more deviated toward the right than the last pointing movements, which were more accurate; no such effect was found with NL. The ANOVA showed that the main effect of Time [$F_{(2,42)} = 4.42$, $p < 0.02$, $\eta_p^2 = 0.17$] was significant, while that of Type of Lenses [$F_{(1,21)} = 3.02$, $p = 0.097$] did not attain the significance level. The Type of Lenses by Time interaction was significant [$F_{(2,42)} = 4.64$, $p = 0.015$, $\eta_p^2 = 0.18$]. Multiple comparisons showed that exposure to NL induced no shift of the subjective body midline, both immediately after exposure (M ± SD Pre −0.21 ± 3.07° *vs.* Post 0.21 ± 3.73°, $p = 0.92$), and in the follow-up (Pre *vs.* Follow-

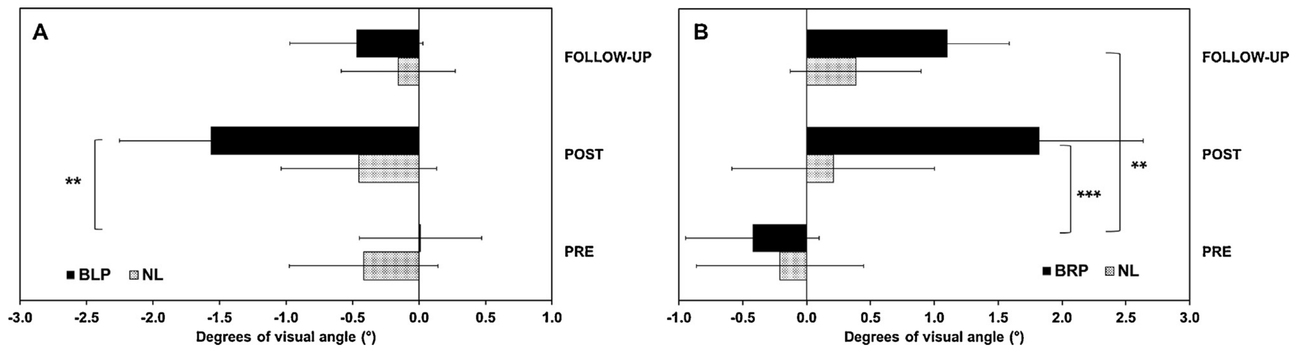

Fig. 3. Mean (SE) deviation from body midline in the proprioceptive straight-ahead pointing task before (pre), immediately after adaptation (post), and after the rest (follow-up), in degrees of visual angle (°); positive values correspond to rightward deviation from the objective body midline, negative values to leftward deviations. Experiment #1 A: prism adaptation to base-left prisms (BLP, solid black bars), and to neutral lenses (NL, dotted bars). Experiment #2 B: prism adaptation to base-right prisms (BRP, solid bars), and to neutral lenses (NL, dotted bars). $p < 0.001$***, <0.01**, <0.05*.

up $0.38 \pm 2.40°$, $p = 0.73$, Post *vs.* Follow-up $p = 0.998$). Exposure to BRP induced a rightward shift in the proprioceptive straight-ahead (Pre $-0.42 \pm 2.45°$ *vs.* Post $1.82 \pm 3.82°$, $p < 0.001$; Pre *vs.* Follow-up $1.10 \pm 2.27°$, $p = 0.01$). These findings are in line with previous evidence [87].

4. Discussion

The present study assessed the hypothesis that the visuo-spatial manipulation occurring during PA, and its consequent aftereffects on body-spatial representations, can be effective in modulating thermoregulatory control in healthy participants. Hands' temperature was measured before, during, and after PA to lenses shifting the visual scene laterally (base-left prisms, shifting to the right, with leftward aftereffects; base-right prisms, shifting to the left, with rightward aftereffects), and to a control condition, where no displacement of the visual scene was induced (neutral lenses, without sensorimotor aftereffects).

The two types of lenses worn by participants exert different effects on hands' temperature. Namely, adaptation to both leftward deviating prisms, and neutral glasses, result into an increase of hands' temperature, whereas adaptation to rightward deviating prisms does not. Particularly, the evolution of the hands' temperature during adaptation to neutral lenses (used as the control condition in both experiments), exhibits a gradual increase during the pointing motor task, and a subsequent coming back to baseline values 20 min after the end of it. This might reflect the natural increase in temperature caused by metabolic heat production during the prolonged motor effort done by participants [84–86]. Importantly, this evolution pattern was found in both experiments, and in different groups of participants.

The main finding of this study is that the hands' temperature evolution during the adaptation to displacing prismatic lenses, as compared to that occurring during the control conditions (neutral lenses), shows a difference related to the lateral direction of the prism-induced displacement of the visual scene. When participants adapt to rightward displacing prisms (Experiment #1) no increase of temperature occurs during the adaptation motor task, at variance from the control condition. Moreover, 20 min after the end of the pointing motor task, a drop in temperature follows. By contrast, an increase in hands' temperature (just as in the control condition), and a subsequent return to baseline values, was found in the condition in which participants wore leftward displacing prisms (Experiment #2).

So far, in the studies investigating the modulation of skin temperature [8,14,16,18], results have been explained in the light of the "body matrix". This neuro-functional model, proposed by Moseley, Gallace and Spence [3], comprises a network of brain regions that combines information from vision, proprioception, and touch, with the main function of maintaining the psychological and homeostatic integrity of the body. The body matrix also accommodates for changes in a person's body structure and orientation, by integrating multisensory inputs. Interestingly, Moseley and colleagues suggest that a peculiar characteristic of the body matrix, which differentiates it from other representations of peri-personal space, is that it is aligned with a body-centered frame of reference, rather than being centered over specific body parts. Moreover, they suggest that the connections between the PPC (which elaborates peri-personal and body-centered spatial information), and the autonomic centers in the insular cortex and their projections to the brainstem, might be the possible neural substrate by which body-centered spatial representations can modulate limb-specific blood flow, and, thus, thermoregulation.

The concept of body matrix has interesting similarities with the notion of the "noetic space" proposed by Redding and Wallace [88–90], mainly discussed with reference to the sensorimotor adjustments of coordinate frames during and after PA. The "noetic space", as put forward by Redding and Wallace [90], refers to a combined, higher-order, egocentric reference frame, which enables the connections and the alignment of different sensorimotor reference frames (e.g., the proprioceptive hand-head system, the visual eye-head system, and the coordination eye-hand system; the tactile and auditory sensorimotor reference frames) into a common egocentric reference frame. When the coherence of an aligned system of reference frames is perturbed, as it occurs during the pointing movement while looking through displacing prisms, the different sensory-motor reference frames signal different spatial egocentric information. The sensory-motor system needs therefore to be realigned within a common frame. Thus, the spatial realignment within the noetic frame, occurring during PA, consists in paramet-

Table 2
Experiment #2. Mean (SE) skin temperature (°C) of the hands before, during and after the pointing adaptation (average of values of the two prism adaptation sessions, base-right prisms and neutral lenses).

Hand	T_{pre}	T_{AD1-30}	$T_{AD31-60}$	$T_{AD61-90}$	T_{post}	$T_{follow-up}$
LEFT	33.05 ± 0.25	33.25 ± 0.23	33.38 ± 0.21	33.50 ± 0.19	33.26 ± 0.18	32.97 ± 0.25
RIGHT	33.08 ± 0.26	33.15 ± 0.24	33.25 ± 0.23	33.37 ± 0.20	33.21 ± 0.21	32.94 ± 0.28

ric transformations between the different component frames, so that they result in, and signal again, the same egocentric frame. Accordingly, the notion of a body-centered spatial representation is a feature shared by the body matrix and the noetic space models, that, similar in some respects, account for the spatial modulation of thermoregulatory control (the body matrix), and for the effects of PA (the noetic space). Moreover, both models would seem to find a relevant component of their neural underpinnings in the PPC [67–74]. Following on from the body matrix, the suggestion can be made that the remapping of the spatial frames of reference, occurring during PA to rightward displacing lenses, exerts some changes in a body-centered cortical representation of the body, resulting in alterations of homeostatic control.

As far as the asymmetry of the effect found is concerned (i.e., we find an increase in temperature during adaptation to the leftward prismatic displacement and during the neutral condition, and a decrease in temperature at the follow up after adaptation to rightward prismatic displacement), evidence from both brain-damaged patients and neurologically unimpaired participants regarding sensorimotor adaptation to right-displacing and left-displacing prisms should be considered. Although there is no complete agreement upon hemispheric asymmetries in somatosensory processes [91,92], there is evidence from clinical populations that somatosensory and spatial processing deficits are more frequent after right brain damage [93–95]. Moreover, disturbances in body representation and body ownership are more frequent after right brain damage [11,51,96].

Studies in right brain-damaged patients affected by left spatial neglect show that adaptation to the rightward prismatic displacement of the visual scene, positively modulates higher-level spatial processing, ameliorating the main manifestations of this disorder (defective exploration of the left side of peri-personal space, as assessed by target cancellation and copy drawing tasks; rightward bias in line bisection), and results in a reduction of sensorimotor postural disturbances, deficits of tactile perception, and visual extinction to double simultaneous stimulation [55,97–99]. Conversely, adaptation to leftward prismatic deviation [100] is ineffective in reducing the disproportionate rightward bias of right-brain-damaged patients with left neglect, and the other abovementioned manifestations of the syndrome, ameliorated by adaptation to rightward prismatic deviation [55]. It is worth noting that we found an effect on temperature just with rightward prismatic deviation, the direction that also ameliorates several manifestations of left spatial neglect. This result might suggest a link between temperature regulation and multisensory spatial representations.

Healthy participants adapt to both right-displacing and left-displacing prisms, with the same amount of sensorimotor aftereffects, biasing the participants' reaching and pointing performance in the opposite direction of the induced visual shift, namely: a leftward bias after rightward displacing, a rightward bias after leftward displacing prisms [55,101,102]. In one study [103] an asymmetric effect was found: adaptation using the left (but not the right) hand to leftward-displacing prisms brings about directional biases in the felt position of both hands, while rightward-displacing prisms are ineffective. In healthy participants, adaptation to rightward shifting prisms usually does not result in higher-order effects [102,104–107], over and above the typically symmetrical sensorimotor aftereffects after PA to right *vs.* left-prisms [55,101–102]. A different study [108] has shown an asymmetry of aftereffects in goal-oriented locomotion, with the rightward aftereffects being larger after PA to leftward deviation, than the leftward ones after PA to a rightward deviation; the asymmetry was related to higher-order "cognitive" factors, enhancing the rightward aftereffects. Adaptation to leftward shifting prisms also causes directional biases in lateral posture control [102], and in higher-order tasks such as perceptual line bisection [104], and decision about the darkness of horizontal stimuli in the "greyscale task" [105]; it impairs spatial remapping for left visual half-field targets, above and beyond the lower-level shifts of aftereffects [109], and also exerts global, non-lateral effects, such as enhancing local processing [106], and reducing global processing [107]. Interestingly, we found a drop in body temperature after adaptation to right deviating prisms. A few studies in healthy participants show effects of right-displacing prisms, as well as of left displacing prisms. Berberovic and Mattingley [101] found a rightward bias in perceptual judgments about the midpoint of horizontal lines ("landmark task" [110]), confined to extra-personal space, for right-displacing prisms, and similar directional effects in both the peri-personal and the extra-personal spaces for left-displacing prisms; based on these findings, they suggest an asymmetry in the effects of left-displacing and right-displacing prisms on spatial judgments. In a line bisection task, directionally opposite aftereffects of exposure to left and right displacing prisms in aged, but not in young, healthy participants, and a relation with preexisting biases, have been found [111].

Before drawing any conclusion on the differences between the results of the studies in healthy participants mentioned above, and the effects on temperature found in our experiments, it is worth noting that the present results might have been influenced by the motor component of the pointing adaptation task. In fact, one might suggest that during the adaptation to left-shifting prisms, the natural increase in temperature that results from the pointing adaptation while wearing neutral lenses (caused by metabolic heat production during the prolonged motor effort done by participants [84–86]), may have masked the effect of left-shifting prisms on thermoregulatory control. On the other hand, heat production during right-shifting prisms is not likely to be suppressed, thus weakened by the intrinsic effect of prisms. It is important to mention here that, due to the presence of this metabolic heat production effect we could not isolate the genuine effect of PA to a rightward shift from that due to the movement itself, nor can we exclude that also left-shifting prisms could affect body temperature (however, in the opposite direction to that of right-shifting prisms, which is, in any case, a decrease specifically related to the rightward, prism-induced, deviation). It might be interesting to investigate the possible effects of other manipulations that bring about directionally-specific improvements of manifestations of the neglect syndrome, such as vestibular, optokinetic, and transcutaneous stimulation (but that do not necessarily require body movements) on skin temperature in healthy participants [112–116].

To date, the modulation of skin temperature has been investigated by means of perceptual illusions such as the Rubber Hand Illusion [13,14], and the Full Body Illusion [17]. The drops in skin temperature reported in these studies are proposed to relate to the phenomenon of embodiment [117]. In particular, in order to explain the cooling of the participant's arm after the induction of the Rubber Hand Illusion, Moseley and colleagues [13] suggest that such effect is likely to be caused by an autonomic thermoregulatory response to hand disembodiment. Somehow similarly, the drop of temperature observed after a Full Body Illusion by Salomon and colleagues [17] has been related to an alteration of bodily self-consciousness, consequent to the induced self-identification and self-localization within a virtual body. Such an explanation is informed to some degree by the comorbidity of alterations of thermoregulatory control, and disrupted body ownership or body image, in a range of clinical populations (schizophrenia [20]; neuropathic pain [27]; eating disorders [28,29]; CRPS [30,32,35,36]; somatoparaphrenia [50]).

As far as the effects of prism adaptation on body representations in healthy participants are concerned, components related to the disownership of body parts, at least at an explicit level, cannot be determined in our study. In fact, both subjective (i.e., questionnaires used to investigate ownership, location and agency, as main subcomponents of embodiment) and objective (i.e., proprioceptive drift) measures are necessary in order to assess the presence of embodiment over the fake hand, and disownership over the real one [117]. To our knowledge, the effect of prism adaptation on the perceived location or ownership of body parts has never been investigated so far with direct subjective questionnaires. Also in our study, we only investigated the effect of prism adaptation on the proprioceptive straight-ahead task and thermoregulatory control. One might predict, however, that differential effects on body ownership and other aspects of bodily awareness might also occur according to the direction of a visual shift induced by prisms (though see [59] for the lack of effects on the sense of disownership after temporary interference by rTMS over activity of the posterior parietal cortex). Alternatively, given the intrinsic sensorimotor component of the PA paradigm, and the participants' awareness of a mismatch between the planned and the actual pointing movement during adaptation to the lateral displacement of the visual scene, the temperature effect found in the present study may reflect more a loss in the sense of agency than in ownership [118]. Nevertheless, an interpretation based on the possible loss of agency cannot account completely for the differential effects that we obtained with right displacing, compared to left displacing, prisms, given that participants were aware of their pointing error performance in both cases.

Another explanation that can be considered in order to address the differential pattern of thermoregulatory results that we found in the present study, could be based on a different amount of discrepancy between the predicted sensory information and the actual sensory feedback in the processing of the location of the right pointing hand with respect to the body midline, exerted by the two prism adaptation conditions. During sensorimotor adaptation with the right hand (Experiment #1) to a rightward displacement of the visual scene, the body midline is coded and perceived rightward, coherently with the visual displacement. In order to point correctly to the actual central target (assuming an average central position of the target), the right hand is felt as crossing the perceived body midline. Thus, when pointing correctly to the target, the hand felt position is coded into the perceived left side of space, but is actually (and discordantly) located in the right side of the space. Instead, in Experiment #2, during sensorimotor adaptation performed with the right hand to a leftward displacement of the visual scene, the body midline is coded and perceived more leftward, coherently with the visual displacement. Therefore, in this case, in order to point correctly to the actual central target, the right hand must be felt as not crossing the perceived body midline, and the hand's felt position and its actual location are coherently encoded in the same side of space (the right side). It might be the case that, in Experiment #1, participants could have experienced more discrepancy between the actual and the felt position of their limb in the two sides of space (with reference to the body midline), than in Experiment #2, and this, in turn, could have affected differently thermoregulation. Also, in line with this hypothesis, we might expect an opposite pattern of thermoregulatory effects exerted by different displacing prisms, when the pointing movements are executed with the left hand.

The importance of an egocentric, body-centered coordinate system in maintaining a coherent perception of peri-personal space has been shown in right brain-damaged patients with left spatial neglect [119]. Also in in healthy participants, direction-specific sensorimotor manipulations, such as galvanic [120], vestibular [121,122], optokinetic [123] and posterior neck muscle vibration [124] stimulations may alter egocentric coordinates. Ecologically-valid modulations, that involve interactions with the environment without artificial alterations of normal sensorimotor spatial relationships, may also bring about changes of egocentric reference frames [125,126]. Moreover, there is evidence that CRPS patients' hand temperature can be modulated by changing the perceived location of the limb with respect to the body midline, both by directly placing the affected hand in the unaffected side of space [8], and by means of prism glasses [31].

At last, one might question whether the modulation of skin temperature exerted by adaptation to rightward displacing prisms (Experiment #1) is due to an effect of the visual-proprioceptive incongruence induced by prisms [127]. Critically, however, despite of the similarity and symmetry of the direct effects of sensorimotor adaptation and the aftereffects in the proprioceptive straight-ahead task with right-displacing and left-displacing prisms [101,102,128], the skin temperature changes found in our two experiments were asymmetrical and directional. In fact, temperature decreased only after adaptation to right displacing prisms, whereas no differences between the neutral condition and left displacing prisms were found. These results can be taken to suggest that the change in thermoregulatory control found in Experiment #1 cannot be solely caused by a visual-proprioceptive conflict.

Finally, our results do not provide evidence of a hand-to-hand difference in the PA effect on temperature regulation. That is, adaptation to a rightward deviation of the visual field results in skin temperature reduction for both hands, and adaptation to a leftward deviation in skin temperature increase for both hands (cfr. [59], where a temperature drop in both hands followed rTMS interference over the activity of the PPCs). Prism exposure brings about a uniform shift of the visual field, manipulating the body-space interface in egocentric coordinates [129]; thus, sensorimotor aftereffects reflect changes in the whole of the egocentric space, as indexed by the proprioceptive straight-ahead shift. Also in line with this view, after a PA session, the proprioceptive drift centered on the hand is in the same direction for both hands [103], namely: after PA with the left hand to left deviating prisms, the felt position of both hands is shifted leftward. Thus, the process of spatial realignment within egocentric space, which occurs during sensorimotor adaptation to both rightward and leftward prism-induced displacement of the visual scene, may bring about a body-space remapping centered on the body midline. Accordingly, bodily space, including hands' position, is shifted coherently with the prism-induced displacement of the visual scene, but the relative position of the hands remains the same, with resulting bilateral symmetric effects, as far as the two hands are concerned. In our study, the lack of hands' specific effects indicates that the mechanisms involved in the prism-induced modulation of thermoregulation are likely to be related to the activity of higher-order, rather than more sensory-specific, brain networks.

5. Conclusion

In conclusion, the sensorimotor manipulation occurring during PA, and its consequent aftereffects, can be effective in modulating thermoregulatory control in healthy participants, with bilateral effects on both hands, and asymmetric effects, related to the direction of the prism-induced deviation of the visual scene. The suggestion is made that these effects may be due to the changes exerted by PA on spatial remapping within a body-centered cortical representation of the body.

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