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Research Report

Shifting the body midline: The impact of visuomotor modulations in virtual reality on peripheral autonomic activity

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ABSTRACT

A coherent sense of body ownership and position depends on the integration of top-down and bottom-up sensory signals. Disrupting this coherence through experimental illusions can alter body representation and peripheral physiological states, such as body temperature. To further investigate this link, we developed a novel virtual reality (VR) paradigm that manipulates spatial body representation by virtually repositioning the left hand into the right side of the body during a visuomotor task. Participants ($n = 26$) engaged in a 15-min immersive VR task using their right hand to manipulate a virtual cube with a stick. In the congruent condition, the virtual hand matched their actual right hand. In the incongruent condition, the right hand was visually replaced by a left hand, shifting the perceived body midline. We recorded left-hand temperature before and during the task, skin conductance responses (SCRs) to electrocutaneous stimulation, proprioceptive drift (PD), and subjective measures (embodiment, agency, altered body perception, and unpleasantness). Results showed a significant decrease in left-hand temperature in the incongruent condition, compared to an increase in the congruent condition. SCR amplitude correlated with temperature: cooling was associated with reduced SCRs, while warming predicted stronger responses. PD revealed a rightward shift in perceived finger position across conditions, likely due to the task's unilateral nature. Subjective ratings were similar across conditions. Overall, our findings demonstrate that visuomotor manipulations disrupting coherent body reference frames can induce measurable physiological changes, even in the absence of altered subjective experience, highlighting a link between body representation and peripheral bodily signals.

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1. Introduction

In our everyday lives, we often take our bodies for granted, experiencing them from a first-person perspective and inherently ours, known as the sense of 'body ownership' (Tsakiris, 2010). However, extensive research in body representation and body ownership has shown that what we consider 'granted' is actually the result of an ongoing and probabilistic computational process that integrates multiple sensory inputs (Bertoni et al., 2023; Blanke et al., 2015; Chancel et al., 2022). Furthermore, depending on the available information and neural resources, the experience of one's own body and perceiving its actual position, also known as body self-awareness, can change dramatically. For instance, after brain damage in selected regions involved in higher-order multisensory processing (e.g., right hemisphere brain damage), patients may exhibit clinical symptoms such as pathological ownership, experiencing external limbs as their own (Fossataro et al., 2018; Garbarini et al., 2015), somatoparaphrenia, in which they feel disconnected from parts of their own bodies, or personal neglect, where patients fail to attend to the side of the body contralateral to the lesion (Di Vita et al., 2017; Gandola et al., 2012; Romano & Maravita, 2019; Vallar & Ronchi, 2009). Crucially, body ownership malleability is not limited to neurological cases, given that even healthy individuals can undergo altered body perception within minutes during multisensory illusions (De Vignemont, 2011; Ehrsson, 2019; Kilteni et al., 2015). Indeed, a coherent representation of one's own body is maintained through the integration of online sensory information with a top-down body model (Pavani et al., 2000; Tsakiris, 2010). However, when sensory inputs conflict, the brain works to resolve these discrepancies, leading to shifts in body experience, evident at multiple levels, such as subjective ownership experience, neural activity, and even peripheral bodily state.

A validated paradigm to study modulation of body ownership and body position comes from the rubber hand illusion (RHI), for which participants may experience ownership of a fake hand and mislocation of their own body (Botvinick & Cohen, 1998). Specifically, by synchronously stimulating the hidden real hand and the visible fake hand, participants tipically begin to perceive the fake hand as part of their own body within minutes (Ide, 2013; Shimada et al., 2009). Beyond self-reported experiences, the RHI effect has been observed by means of multiple objective measures, including proprioceptive drift (a shift in the perception of hand position) (Pavani et al., 2000; Rohde et al., 2011), cortical activity changes measured through EEG (somatosensory evoked potentials) (Golaszewski et al., 2021; Rossi Sebastiano et al., 2024; Zeller et al., 2015), fMRI (Bekrater-Bodmann et al., 2012; Ehrsson et al., 2005), TMS (Alaydin & Cengiz, 2021; della Gatta et al., 2016); but see Reader et al., 2023), and autonomic peripheral responses, such as fluctuations in body temperature (Moseley et al., 2008; Rohde et al., 2013) and electrodermal activity (skin conductance responses, Armel & Ramachandran, 2003). An intriguing aspect of the RHI is its impact on the real body part being replaced, as the illusion can induce a sense of "disownership" that may affect the peripheral functionality of the body (Ataka et al., 2022; De Vignemont, 2011; Riemer et al., 2019). Specifically, it has been hypothesized that the RHI modulates peripheral physiological parameters, such as a reduced skin conductance response (Tieri et al., 2015) or a decrease in skin temperature (Moseley et al., 2008), reflecting the body's response to the perceived replacement of the real hand with the rubber one during the illusion. However, while this hypothesis is theoretically compelling, empirical evidence linking disownership to changes in peripheral bodily activity remains inconclusive. Although early studies reported a significant drop in hand temperature during the illusion (Moseley et al., 2008), subsequent replication efforts have yielded inconsistent results (de Haan et al., 2017). One possible explanation for these discrepancies is methodological variation in how the RHI is induced, such as differences in stroking modality or timing (Riemer et al., 2019; Rohde et al., 2013; Van Stralen et al., 2014). Clarifying the relationship between altered body ownership experiences and peripheral autonomic responses within the RHI paradigm remains unclear, and further investigation is certainly required.

Notably, the RHI is not the only paradigm capable of inducing altered perceptions of a body part through multisensory illusions. An alternative illusion, the Mirror Box Illusion (MBI), involves positioning one hand behind a mirror while observing the reflection of the other hand (Medina et al., 2015). In this setup, one hand—typically the left—is hidden and visually replaced by the reflection of the right. In two recent studies, Crivelli and colleagues observed a temperature decrease in both hands during the MBI. However this effect occurred only when the illusion involved the left hand (Crivelli et al., 2021, 2023). Extending the concept from a single limb to the entire body—such as through a full-body illusion (FBI) in virtual reality, where participants view a virtual body being touched synchronously with their own—Salomon and colleagues detected a widespread decrease in temperature across the corresponding body parts (Salomon et al., 2013). These alternative paradigms provide additional evidence for a link between altered body ownership experiences, shaped by multisensory illusion, and changes in peripheral physiological states, thereby addressing some of the limitations inherent in the RHI.

A key framework often used for explaining changes in the peripheral body state during disownership or altered body ownership conditions is the concept of 'Body Matrix', which describes a dynamic, multisensory representation that integrates both the body and its surrounding space (Moseley, Gallace, & Spence, 2012a, b). The body matrix serves as a high-order framework that aligns the body with other mappings, such as the somatotopic organization of the somatosensory system and the retinotopic mapping of the visual system, in order to have a unique proto-representation of the body and the space. The parietal and temporal cortices—specifically, the superior and posterior parietal cortex, supramarginal, and temporal gyri—appear central to this process, integrating visual, proprioceptive, and tactile inputs based on spatial information (Bolognini & Maravita, 2007; Gallace et al., 2014; Moseley, Gallace, & Spence, 2012a, b). It has been demonstrated that interference with activity over the posterior parietal cortex (an area of the brain responsible for the

processing of body position and ownership) by inhibitory TMS also led to alterations in thermoregulatory control in humans (see Gallace et al., 2014). However, thermal modulations can also be generated by altering the alignment of visuo-proprioceptive spatial frames of reference by means of a prism adaptation procedure (also in this case, a manipulation often used to treat symptoms of neurological conditions involving visuospatial deficit, as in the case of visuospatial neglect; see Calzolari et al., 2016). According to the Body Matrix theory, the brain encodes sensory stimuli within a unified, body-centered reference frame divided into left and right space in respect to the body midline. Disruptions to this representation, via manipulations such as crossing hands over the body midline, can trigger sensory and homeostatic changes. For instance, crossing the arms slows the discrimination of stimuli on each side due to conflicts between somatotopic and space-based representations (Gallace et al., 2011; Sambo et al., 2013; Shore et al., 2002; see also Torta et al., 2013). Moreover, in complex regional pain syndrome (CRPS), where the affected hand exhibits (in addition to excruciating pain) an alteration of thermoregulatory control (i.e., cooling), repositioning the hand by crossing it over the body midline can reverse the temperature shift as it enters the spatial territory of the healthy (Calzolari et al., 2016; Moseley et al., 2009). Building on these findings, further investigation into the relationship between homeostatic regulation and the body matrix—using innovative paradigms that can disrupt coherent spatial body representations centered on the body midline—could offer valuable insights into how body representation influences peripheral homeostatic states.

An important consideration from previous studies is that the RHI, FBI, and MBI can be regarded as static paradigms. They typically involve either passive manipulation (as in the RHI and FBI) or minimal motor engagement (such as in the finger-tapping version of the MBI) to induce disownership for a body part. Furthermore, the RHI and MBI generally involve only a lateral shift in the spatial representation of a limb within the same side of the body, thereby preserving the visuomotor representation along the midline. What remains largely unexplored is whether homeostatic changes can also be induced through body illusions that involve spatial manipulation across the body midline for a single limb—an approach with significant implications for the body matrix theory, which suggests the brain maintains a bilateral representation of the body organized along the midline. In this context, virtual reality (VR) provides a valuable tool for manipulating spatial body representations in ways that challenge midline integration. For example, if the virtual left hand appears where the right hand should be—and the person uses their real right hand to control it—the brain has to treat the left hand as if itis on the right side of the body. When this remapped setup is repeated over time during ongoing sensorimotor engagement, it may lead to changes in the perceived or physiological state of the unattended real left hand, as it becomes excluded from the ongoing spatial representation of the body. Despite its theoretical significance, experimental research directly manipulating the bilateral representation along the midline remains scarce. Investigating these midline-crossing illusions may offer new insights into the properties of the spatial representation of the body and its influence on peripheral physiological regulation within the body matrix framework.

In the present study, we aimed to further investigate how peripheral autonomic activity is modulated by visuospatial manipulation of the body during active interactions, specifically by using an innovative virtual reality paradigm that spatially repositions the left hand into the right side of the body. Participants completed sensorimotor VR training, using their right hand to interact with virtual objects. Critically, during task execution, the visual representation of their hand appeared either as a right hand (congruent condition) or a left hand (incongruent condition), although they always used their real right hand to perform the task. Therefore, during the incongruent condition, the visual image of the left hand was shifted to the right hemispace of the body (i.e., space surrounding the body centered on the body midline). To reinforce the illusion, virtual interactions were paired with synchronous tactile feedback delivered to the right hand. Outcome measures included the temperature of the left hand both at baseline (prior to task onset) and during the task. Additionally, to further assess autonomic activity, we measured skin conductance responses (SCRs) to supra-threshold tactile stimulation applied to the dorsum of the left hand during the midpoint of the task. To evaluate potential changes in spatial representation, we included a proprioceptive finger localization task, administered before and after the VR session while participants were blindfolded. In addition, we collected subjective ratings following both the congruent and incongruent conditions. These ratings assessed aspects of the virtual experience, including embodiment of the virtual stick used to execute the task, sense of agency, pleasantness, and altered body perception.

2. Methods

2.1. *Participants*

Due to the lack of prior studies employing this specific paradigm, it was not possible to perform an a priori power analysis to determine the required sample size. Consequently, the sample size was informed by previous research utilizing virtual reality-based body illusions and temperature as primary measurements, which included, respectively, 20 (Llobera et al., 2013), 22 (Salomon et al., 2013), and 24 participants (Tieri et al., 2017). A total of 26 healthy participants (ages 18–38, M = 25.36, SD = 4.99) were recruited for the study. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971), revealing that all participants, except one (no preference), were right-handed.

2.2. *Experimental design*

Participants completed two distinct VR visuomotor-tactile tasks—one congruent and one incongruent—on separate days, with a minimum three-day interval between sessions. Each task lasted 15 min, and the order of conditions was counterbalanced across participants. During the task, participants used a VR controller-operated stick (held in their right

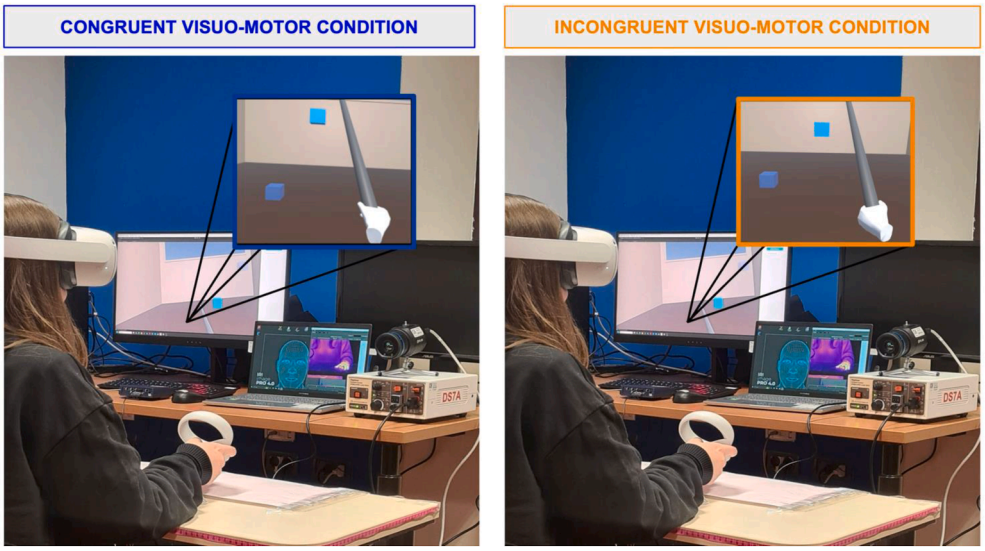

Fig. 1 – Participant performing the sensorimotor task equipped with skin conductance sensors and cutaneous stimulation electrodes placed on the dorsum of the hand. The left panel shows the congruent condition, while the right panel shows the incongruent condition. A zoomed-in view highlights the visual representation of the virtual right (congruent) and left (incongruent) hands, respectively.

hand) to move a virtual cube toward a target. Each contact between the stick and the cube triggered both movement and synchronous tactile vibration, reinforcing the sensorimotor experience. The sole difference between the congruent and incongruent conditions was the visual representation of the virtual hand. In the congruent condition, the virtual right hand was presented in its anatomically accurate position. In contrast, the incongruent condition presented a virtual left hand in the right hemispace, mirroring the position and movements of the participant's actual right hand. Importantly, the participant's (real) left hand—the body part potentially subject to the visuo-spatial manipulation—remained at rest on a table throughout the task. We analyzed the primary outcome measures—including proprioceptive drift, left-hand temperature, skin conductance responses, and subjective report experience—by comparing results between the congruent and incongruent conditions.

2.3. *VR environment and sensorimotor task*

The experiment used a Meta Quest 2 HMD with a resolution of 1920 × 1832 pixels per eye, connected via Oculus Link to an Asus ROG Strix notebook. The notebook featured an AMD Ryzen 9 5900HX CPU, 32 GB of RAM, a GeForce RTX 3080 GPU, and a 17.3" screen with a resolution of 1920 × 1080 pixels.

The sensorimotor task was based on an ad hoc adaptation of a paradigm previously employed in other studies (Girondini et al., 2024a, 2024b; Girondini, Montanaro, Lega, et al., 2024). The virtual environment was developed using the Unity engine, and the VR controller delivered haptic feedback through vibration buzzes. An empty room served as the virtual environment. After donning the HMD and picking up the right controller, participants initiated the task by pressing a designated button on the controller. Once the task began, a virtual hand attached to a virtual stick appeared. This stick, which mirrored the participant's real right-hand movements, was used to interact with the environment. Importantly, the virtual hand holding the stick was represented as either a right hand (congruent condition) or a left hand (incongruent condition). Once the participant was familiarized with the virtual environment and the virtual stick, the experiment began with the first trial after pressing the controller button. At the beginning of each trial, a blue virtual cube (the target cube) appeared in the center of the virtual environment, while a semi-transparent cube appeared randomly in one of four locations in the virtual room (bottom-left, bottom-right, upper-left, upper-right). In both sessions, each participant received the same instruction: touch-and-move the target cube using the virtual stick to match its position with that of the semi-transparent cube. Every time the virtual stick collided with the target cube, the participant received haptic feedback. Once the target cube reached the semi-transparent cube, the trial ended, and a new target cube appeared in the center of the virtual room (Fig. 1). The task had a fixed duration of 15 min.

2.4. *Left-hand temperature assessment*

Participants' hand temperature was recorded using a FLIR A700 24° Standard Science Kit thermal camera equipped with an uncooled microbolometer (spectral band: 7.5–14.0 μm). This non-contact thermographic device measures body temperature, heat distribution, blood flow, and muscle activity. The camera features a high resolution of 640 × 480 pixels, a maximum frame rate of 30 Hz, and thermal sensitivity (NETD) ranging from <30 mK to <50 mK (thermal sensitivity of .02 °C).

Left hand temperature was recorded at baseline (before the task) and continously during the VR task. Data were extracted using the Next2U IRI Image Pro 4.0 software, with the left-hand selected as the Region of Interest (ROI). The left-hand temperature was calculated as the temperature difference (Delta-T) between a baseline resting period (2 min before the task) and the temperature during the task (analyzed from 1 to 10 min after task initiation).

2.5. Skin conductance responses (SCRs)

During the task, electrodermal activity was continuously recorded at 256 Hz using the Procomp Infiniti 5 device (Thought Technology) with two AgCl electrodes attached to the participant's index and ring fingers of the left hand. To elicit skin conductance responses (SCR), electrocutaneous stimuli of .2 ms were delivered to the dorsum of the left hand at the right wrist via 10 mm Ag/AgCl electrodes connected to a Digitimer DS7AH constant current high-voltage stimulator (Digitimer, Welwyn Garden City, United Kingdom). After 5 min from the task beginning, the experimenter manually triggered the stimulator 15 times (intertrial interval of 20 s), with stimulation intensity set to twice the participant's individual tactile threshold. Offline preprocessing was performed using the MATLAB toolbox Ledalab, employing Continuous Decomposition Analysis (CDA) with a threshold of .01 μS within a time window of 1–5 s after stimulus onset. Two primary indices were used for the analysis: the number (nSCR) and the mean amplitude (meanSCR) of skin conductance responses that exceeded the threshold.

2.6. Hand localization task (proprioceptive drift)

Participants's ability to localize the position of their left-hand fingers was assessed before and after the VR training using a pointing task performed with the right hand while the participant was blindfolded. Initially, participants' hand length and width were measured to determine the central point of each hand. Subsequently, participants' hands were positioned at predetermined spots on the table to perform the proprioceptive drift task. During the task, participants were blindfolded and seated comfortably. They were instructed to use the index finger of their right hand to point to the locations of three points on their left hand: the thumb, middle finger, and little finger, indicating their positions on the table (Ingram et al., 2019). After each indication, participants were asked to keep their fingers still so the experimenter could record their position using a tape measure placed in front of the participant's hand. This procedure was then repeated with participants pointing to the positions of the three fingers on their right hand using the left index finger. Each finger was pointed six times, resulting in a total of 36 trials per hand. The task was performed before and after the VR training, during both experimental sessions.

2.7. Self-report measurements

Participants' evaluated the task using four Likert-scale questions with answers ranging from 1 (not at all) to 5 (completely agree). The questions assessed the *sense of embodiment* for the virtual stick (e.g., "I felt like I could control the virtual stick as if it were attached to my body"), the *sense of agency* over the virtual stick (e.g., "The movements of the virtual stick were caused by my movements"), the *perception of an altered body state* (e.g., "I had an altered perception of my body during the task in the virtual environment"), and the *unpleasantness of the experience* (e.g., "The bodily sensations I felt during the virtual interaction were unpleasant"). Responses were collected using a digitized version of the questionnaire implemented in Qualtrics software on a laptop.

2.8. Procedure

Participants arrived at the laboratory and signed the informed consent form. Before starting the experiment, participants completed the handedness questionnaire. The following experimental procedure was carried out in the same way for both sessions, which were performed on different days. Initially, the length and width of participants' hands were measured to determine their central point. Next, the left hand was positioned on predetermined spots on the table to conduct the proprioceptive drift task as a baseline. Then, the participant's somatosensory threshold was determined by identifying the minimum stimulation intensity that elicited tactile sensation. Next, a stimulation that was twice the tactile threshold was administered, ensuring it was not perceived as painful, as it would be repeated during the VR task. Baseline measurements of skin conductance and left-hand temperature were recorded while participants rested for 2 min. Following baseline recording, participants donned the Oculus Quest 2 headset to begin the VR task, which lasted approximately 15 min. Approximately 5 min into the session, 15 tactile stimulations were administered to the left hand at 20-s intervals over 3 min. The task then continued without further stimulation for the remaining duration. Throughout the VR task, skin conductance and temperature were continuously monitored. At the conclusion of the VR experience, participants repeated the proprioceptive drift task, after which self-report assessments of their VR experience were collected. Finally, participants were debriefed about their experiences during the experiment and the study's objectives (Fig. 2).

2.9. Statistical analysis

Statistical analyses were conducted using R and R-studio. Localization performance was evaluated by calculating the difference between the real and perceived positions for the three fingers (thumb, middle, and little) before and after the training in the two conditions. After checking for normality distribution (Shapiro–Wilk >.05), the proprioceptive data (drift) were analyzed using a 3 (fingers: thumb, middle, little) × 2 (time: pre *vs* post) × 2 (condition: congruent *vs* incongruent) repeated measures ANOVA. In case of a significant interaction effect, post-hoc analyses were performed using Tukey correction for multiple comparisons. A comparison was made between the two conditions (congruent *vs* incongruent) for physiological measurements. Skin conductance data (nSCR and meanSCR) and baseline-corrected temperature (Delta-T) violated the normality assumption (Shapiro–Wilk <.05), and non-parametric Wilcoxon signed-

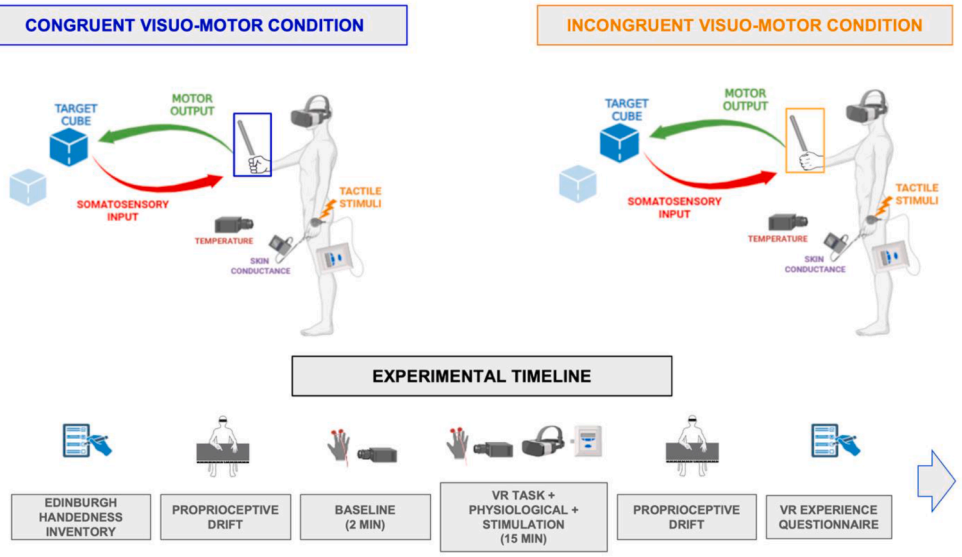

Fig. 2 – Graphical representation of the congruent and incongruent visuomotor conditions (top). Experimental timeline illustrating the sequence of events during each session (bottom).

rank tests were used to compare congruent *vs* incongruent conditions. Skin conductance measures were correlated (using Spearman's rho due to non-normali distribution) with the delta difference within a time window corresponding to the stimulation period to further explore the relationship between the physiological parameters. Finally, self-report data related to the VR experience were also analyzed using Wilcoxon signed-rank tests.

3. Results

3.1. *Left-hand temperature*

Four participants were excluded from the analysis due to a problem in data recording, resulting in a final sample of 22 participants included in the analysis. The grand average of left-hand temperature, separated into baseline (first 2 min) and task phases, is presented in Fig. 3. Delta temperature values represent the change from baseline, with positive values indicating an increase and negative values indicating a decrease in temperature during the task. A Wilcoxon signed-rank test on the delta temperature revealed a statistically significant difference between conditions ($V = 200$, $p = .016$), indicating that the temperature response differed significantly between the *Congruent* and *Incongruent* conditions. Specifically, the mean change in temperature for the *Congruent* condition increased by .149 °C (SE = .098), while for the *Incongruent* condition, it was −.109 °C (SE = .119), indicating a relative decrease in temperature (Fig. 3).

3.2. *Skin conductance response*

Two participants were excluded from the analysis due to a problem in data recording. Skin conductance responses were analyzed using two physiological indices: the total number of SCRs (nSCR) and the mean amplitude of SCRs (meanSCR). A Wilcoxon signed-rank test comparing the total number of SCRs between the Congruent and Incongruent conditions revealed no significant difference ($V = 143$, $p = .891$). Similarly, no significant difference was observed in mean SCR amplitude ($V = 107$, $p = .229$), suggesting that both the frequency and intensity of responses were comparable between conditions.

3.3. *Hand localization task*

A repeated-measures ANOVA was conducted to examine the effects of*Finger* (Index, Middle, Little), *Time* (Pre, Post), and *Condition* (Congruent, Incongruent) on the localization error, corrected for the real finger position. Positive values indicated an overestimation of the finger's location (perceived as farther from the actual position), while negative values indicated an underestimation (perceived as closer than the actual position). Greenhouse-Geisser corrections were applied where appropriate (violation of the assumption of sphericity). ANOVA results revealed a significant main effect of *Finger*, $F(1.08, 27.04) = 56.67$, $p < .001$, generalized $\eta^2 = .553$, indicating substantial differences in localization across fingers. Post hoc comparisons revealed significant differences between all finger pairs. Localization error was positive for the Little finger ($M = 2.06$ cm, SE = .253), indicating an overestimation relative to the actual position. The Middle finger showed a small negative error ($M = -.52$ cm, SE = .253), while the Thumb showed a negative error ($M = -2.13$ cm, SE = .253), reflecting an underestimation of its actual position. All pairwise differences remained significant after Bonferroni correction (*ps* < .001). There was also a significant main effect of *Time*, $F(1, 25) = 8.69$, $p = .007$, $\eta^2 = .035$. Localization errors increased over time: participants were more accurate before the task ($M = .10$ cm, SE = .148) compared to after the task ($M = -.49$ cm, SE = .148), $p = .0068$. The main effect of *Condition*

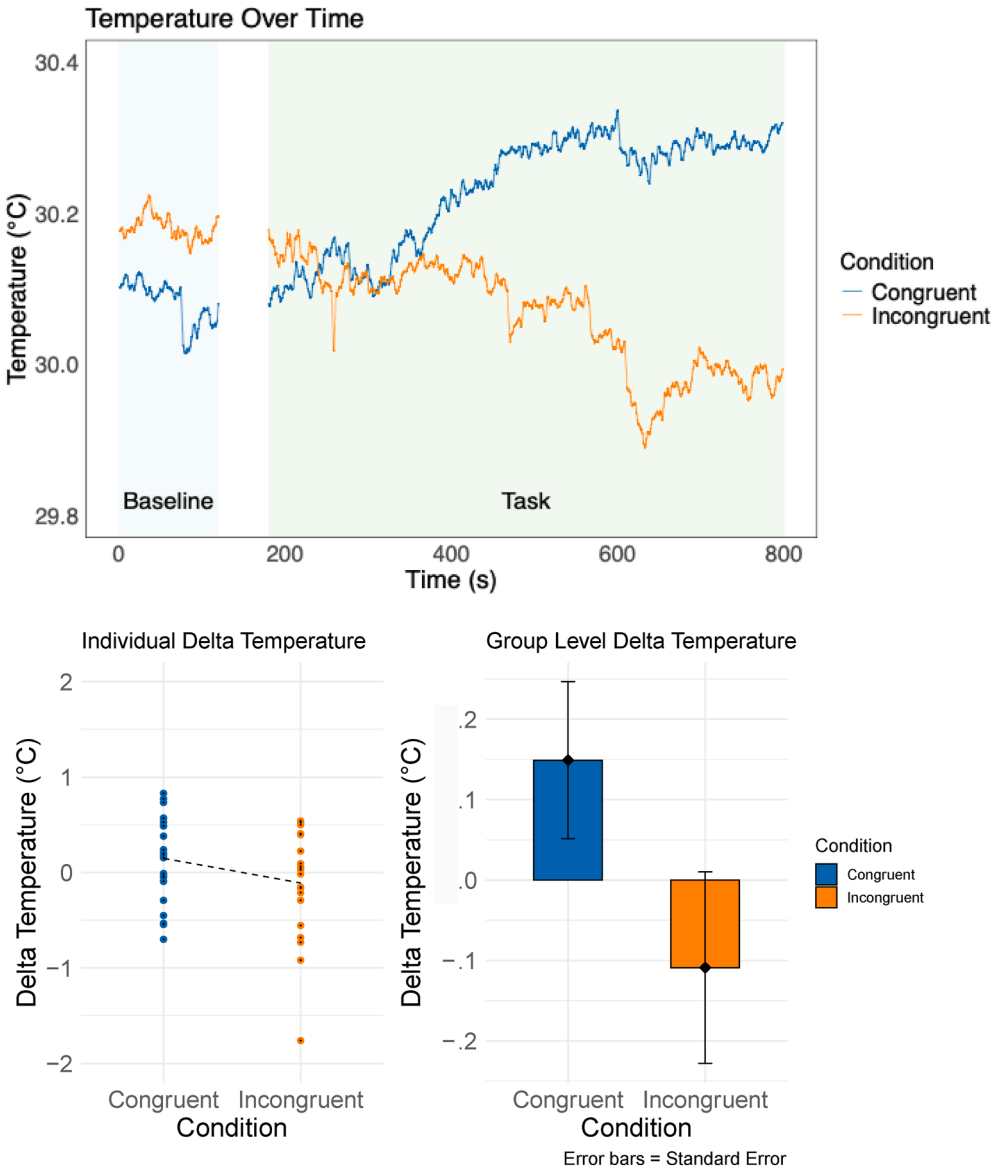

Fig. 3 – Upper panel: Skin temperature over time, shown at baseline and during the task. Lower panel: Left—individual Delta temperature (change form baseline) between congruent and incongruent conditions; Right—group-level average Delta temperature. Temperature and Delta Temperature are reported in degrees Celsius.

(Congruent *vs* Incongruent) was not significant, $F(1, 25) = 1.08$, $p = .309$, suggesting that visual congruency of the hand representation did not influence overall localization accuracy.

Interestingly, there was a significant *Finger* × *Time* interaction, $F(1.65, 41.30) = 3.65$, $p = .033$, generalized $\eta^2 = .003$, indicating that the change in localization accuracy over time varied by finger. Bonferroni-corrected pairwise comparisons between pre- and post-assessments were conducted separately for each finger. Results showed a significant decrease in accuracy over time for the Middle finger, with localization error becoming more negative (*Pre* = −.11 cm, *Post* = −.93 cm), $p = .0096$, indicating greater underestimation after training. In constrast, for the Thumb (*Pre* = −1.87 cm, *Post* = −2.38 cm, $p = .39$) and the Little finger (*Pre* = 2.28 cm, *Post* = 1.84 cm, $p = .72$), localization errors did not change over time. The two-way interactions Finger × Condition ($F(2, 50) = .83$, $p = .440$) and *Time* × *Condition* ($F(1, 25) = .001$, $p = .972$) were not significant. Likewise, the three-way interaction *Finger* × *Time* × *Condition* was not significant, $F(2, 50) = .02$, $p = .976$ (Fig. 4).

3.4. *Correlation between temperature and skin conductance response*

The correlation sample consistd of 20 participants, who had both temperature and skin conductance response data available for the analysis. A Spearman correlation was conducted to examine the association between changes in peripheral temperature (Delta-T) and skin conductance responses, indexed by the total number of SCRs (nSCR) and mean SCR amplitude. For nSCR, no significant correlation was found in

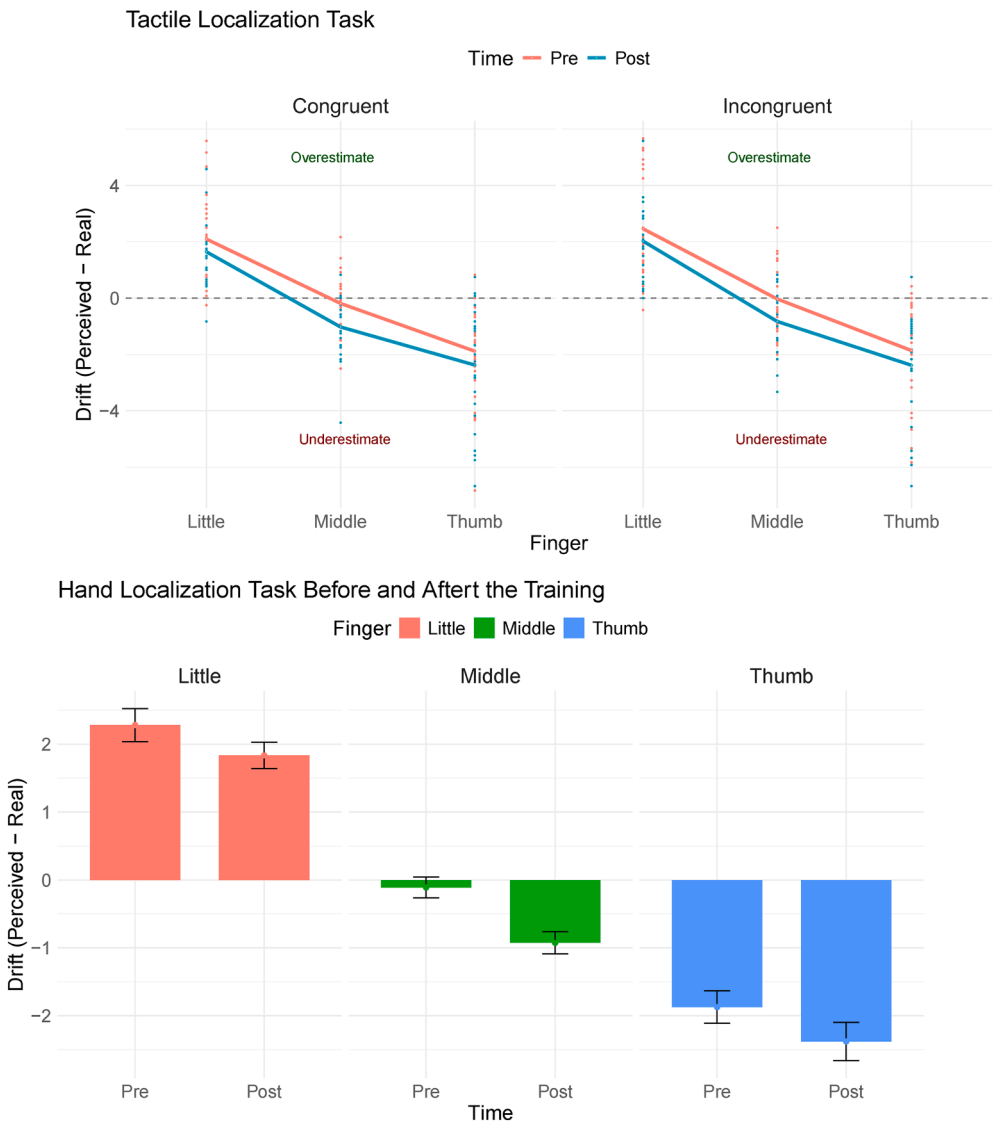

Fig. 4 – Hand localization task results. Upper panel: Perceived drift for the three fingers before and after the congruent (left) and incongruent (right) conditions. Lower panel: Little, Middle and Thumb finger drift before and after the task for the congruent and incongruent conditions. The Y-axis represents distance in centimeters (cm).

the Congruent condition ($\rho = .11$, $p = .631$). However, in the Incongruent condition, a significant positive correlation emerged ($\rho = .66$, $p = .002$), indicating that larger temperature changes were associated with an increased number of SCRs. Similarly, for mean SCR amplitude, no significant correlation was observed in the Congruent condition ($\rho = .15$, $p = .525$), whereas the Incongruent condition again showed a significant positive correlation ($\rho = .56$, $p = .011$). This suggests that larger temperature deviations were linked to stronger autonomic responses. Overall, these findings reveal a condition-specific relationship between peripheral temperature changes and autonomic arousal. Under the Incongruent condition, participants who exhibited a decrease in peripheral temperature also tended to show a reduced skin conductance response, both in terms of amplitude and frequency of the signal (Fig. 5).

3.5. *Self-report evaluation of VR experience*

None of the comparisons of the questions related to the VR experience significantly differed between the congruent and incongruent conditions. Participants gave similar ratings for the sense of embodiment for the virtual stick ($W = 59.5$, $p = .325$, $M_{incongruent} = 3.96$, $SE = .152$; $M_{congruent} = 3.77$, $SE = .195$), the sense of agency for the virtual stick ($W = 18$, $p = .608$, $M_{incongruent} = 4.42$, $SE = .177$; $M_{congruent} = 4.50$, $SE = .149$), the sense of altered body perception ($W = 42.5$, $p = .851$, $M_{incongruent} = 2.54$, $SE = .262$; $M_{congruent} = 2.58$, $SE = .256$), and the unpleasantness of the experience ($W = 46$, $p = .260$, $M_{incongruent} = 2.12$, $SE = .262$; $M_{congruent} = 1.77$, $SE = .187$) after the congruent and incongruent conditions (Fig. 6).

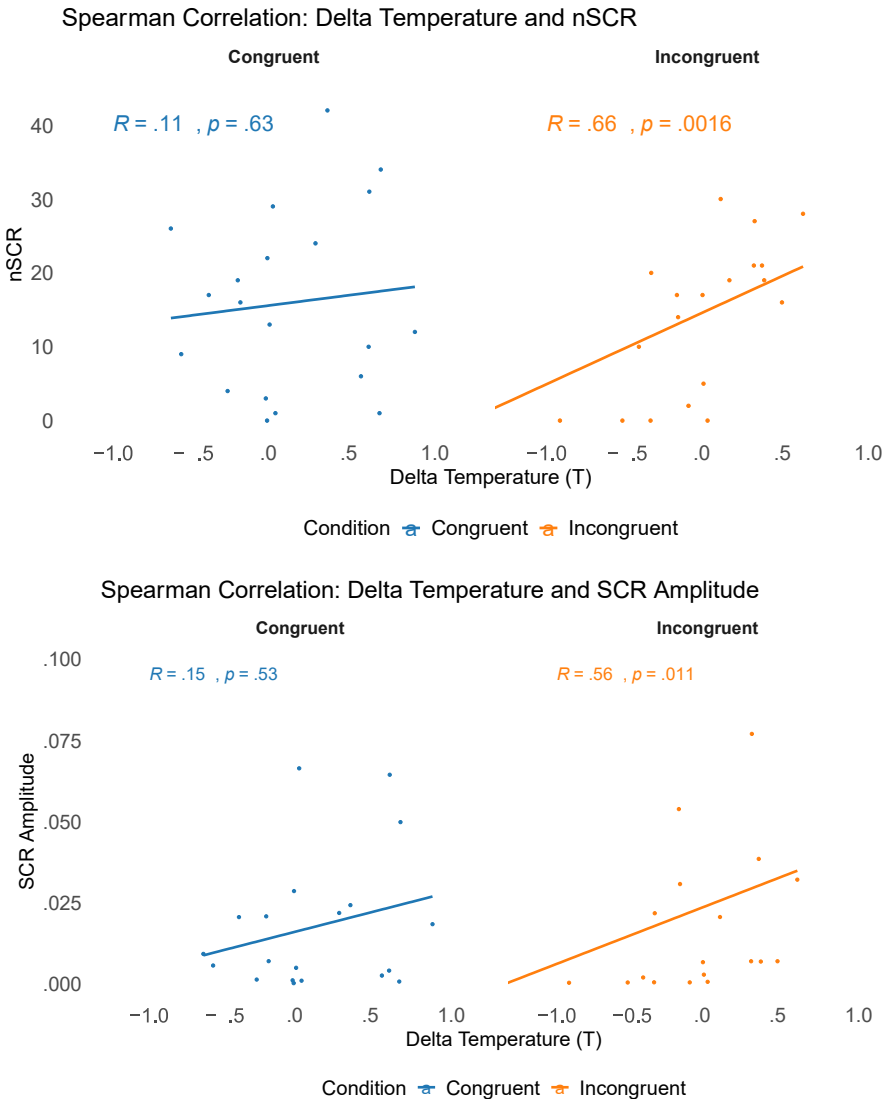

Fig. 5 – Upper panel: Correlation between the mean number of skin conductance responses (SCR) and temperature difference for the congruent (left) and incongruent (right) conditions. Lower panel: Correlation between the mean amplitude of SCR and temperature difference for the congruent (left) and incongruent (right) conditions.

4. Discussion

In the present study, we aimed to deepen our understanding of how peripheral autonomic responses are influenced by shifting the left hand across the midline to the right side of the body, using an immersive virtual reality (VR) environment. Building on prior research connecting physiological changes to body ownership illusions, we developed a novel VR paradigm that disrupts typical sensorimotor contingencies of hand position and visual feedback during virtual interactions. Participants engaged in a 15-min interaction task using their real right hand, while the VR system displayed either a congruent (right) or incongruent (left) virtual hand, visually shifted to the contralateral (right) side of the body. To evaluate how this visual shift of the left hand into the contralateral side of the body influenced autonomic regulation, we recorded left-hand temperature and skin conductance responses to supra-threshold tactile stimuli during task execution. To our knowledge, this is the first study to examine the relationship between skin conductance and skin temperature in response to a visuo-spatial body representation manipulation within the same participants. In addition to physiological measurements, we evaluated changes in proprioceptive localization of the left hand pre- and post-exposure to the illusion as well as subjective reports related to embodiment, agency, altered body perception, and unpleasantness.

Our results demonstrated that the visual replacement of the right hand with a virtual left hand model significantly influenced the skin temperature of the real, non-engaged left

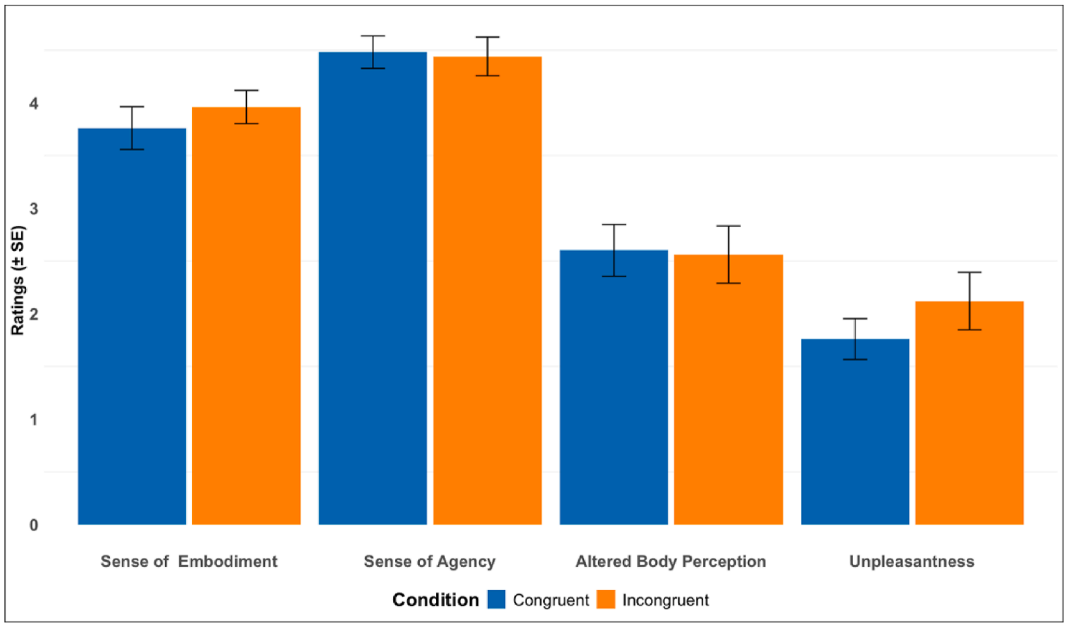

Fig. 6 – Mean ratings (± standard error) for self-report measures assessing the VR experience, including the sense of embodiment, sense of agency, altered body perception, and unpleasantness, are presented for both the congruent and incongruent conditions.

hand. Specifically, we observed distinct temperature trends during the task compared to baseline measurements. Following the congruent condition, where the virtual hand matched the real hand in identity and position, the temperature of the left hand tended to increase compared to the baseline. In contrast, during the incongruent condition—-where a virtual left hand was mirrored to replicate the movements of the right hand and visually repositioned to the right side of the body midline—the temperature of the real left hand decreased. The absence of temperature reduction during the congruent condition, where the left hand was not visually displayed but the visuospatial representation of the body was preserved, ruled out that thermoregulatory changes are caused solely by visual omission of the limb. We found no modulation in SCRs evoked by tactile stimulation of the left hand; neither the number nor the amplitude of SCRs differed between conditions. However, analyzing the relationship between temperature changes and SCRs revealed a positive correlation in the incongruent condition: larger decreases in left-hand temperature were linked to reduced SCR responsiveness, while higher temperatures corresponded to stronger SCRs. These findings may indicate a condition-specific interaction between thermoregulation and autonomic reactivity; however, the limited sample size included in the analysis warrants cautious interpretation of this result.

We also assessed participants' proprioceptive performance before and after the task without visual feedback of the left hand before and after the task to assess possible after-effect on hand position perception followed VR training. As in previous studies on finger perceptual maps, participants consistently misjudged hand width, overestimating the little finger's position and underestimating the thumb's (Longo, 2015; Longo & Haggard, 2010; Tamè et al., 2019). In addition, we observed a slight rightward shift in the localization of the left middle finger post-training, regardless of visual congruency. This likely reflects a proprioceptive recalibration of the left hand due to the greater engagement of the right side of the body during the task, since participants always used their right hand and received tactile stimulation on it in both conditions. The effect was specific to the middle finger, suggesting a moderate recalibration. Although preliminary, the dissociation between physiological re-adaptation occurring during the task and proprioceptive realignment observed afterward in the left hand suggests that these processes may rely on distinct mechanisms, driven by different sensorimotor inputs. At the subjective level, self-reported evaluations of the VR experience revealed no significant differences between the congruent and incongruent conditions in terms of embodiment, agency, perceived changes in body state, or overall pleasantness of the experience. While our study is limited by the absence of standardized measures for ownership or disownership of the unused left hand (which was difficult to assess due to its passive role), our findings suggest that visuospatial manipulation of the active effector (the hand controlling the stick) did not disrupt the sense of embodiment or agency for the stick used to execute the task. The preservation of embodiment and agency is likely attributable to the continuous visuomotor contingency between participants' actions and their sensory consequences, maintained throughout the entire duration of the task (~15 min), which may have led to a habituation effect of the illusion (Girondini et al., 2025). Thus, our results indicate that peripheral physiological changes can occur in the absence of altered subjective experience during the task.

The different trend of left-hand temperature during the congruent and incongruent conditions of the VR training further supports the link between strengthens the relationship between body illusion and autonomic responses, demonstrating that these thermoregulatory mechanisms also emerge as online readaptation during virtual interactions. Previous approaches to studying the relationship between body ownership manipulations and temperature involved the use of multisensory illusions, such as the RHI (de Haan et al., 2017; Kammers et al., 2011; Moseley et al., 2008), the MBI (Crivelli et al., 2021, 2023), or the FBI (Llobera et al., 2013; Salomon et al., 2013). Although the relationship between the RHI and peripheral temperature has recently been called into question (de Haan et al., 2017), alternative paradigms, such as the MBI and FBI, have demonstrated modulation of thermoregulatory responses during body ownership manipulations (Crivelli et al., 2021, 2023; Llobera et al., 2013; Salomon et al., 2013). These paradigms offer compelling evidence for a connection between a coherent sense of the body, which is rooted in multisensory integration underlying body ownership, and the regulation of peripheral temperature. Instead, a distinctive feature of our paradigm is that it generates a conflict extending beyond the isolated limb to the bilateral representation of the body organized around the midline. Notably, even in the absence of subjective changes in body ownership, visually shifting the representation of the left hand into the right body midline, thereby excluding the real left hand from its natural spatial context, elicited a thermoregulatory response. Interestingly, previous research has demonstrated that laterally displacing visual input through prism adaptation (without changing its real position) can also modulate peripheral body temperature as a form of shifts in spatial processing between the left and right sides of the body (Calzolari et al., 2016). Taken together, these findings suggest that our results may reflect a form of sensorimotor readaptation triggered by a reconfiguration of spatial body representation, and that task-induced remapping of body effectors likely contributed to the observed autonomic responses. Future research is needed to clarify whether such effects stem from a more subtle sense of disownership for the visually displaced limb or from spatial realignment mechanisms independent of body ownership itself.

It is worth noting that deficits in thermoregulation have also been observed in clinical populations where the sense of body ownership is compromised due to neurological conditions, such as in post-stroke patients with disturbed body awareness (Salvato et al., 2025) or individuals suffering from CRPS (Moseley et al., 2009, p. 2012). These thermoregulatory disturbances typically affect the hemiplegic or symptomatic side, suggesting that homeostatic processes are closely tied to the functional integrity of the limb. Interestingly, studies have shown that manipulating the spatial position of the limbs, for instance, by swapping the locations of the affected and unaffected arms, can shift patterns of temperature regulation between the two sides (Moseley et al., 2009). This implies that, beyond physical dysfunction, such disorders may involve altered high-level body-spatial representations that distinguish between the healthy and affected sides, potentially resulting in asymmetrical homeostatic regulation. By leveraging virtual reality, we were able to induce spatial manipulations of body parts without requiring physical crossing over the midline, and our findings provide additional empirical support for the relationship between space-based body representation and peripheral autonomic responses, demonstrating that thermoregulatory changes occur in real time during active interaction. Looking ahead, these insights open promising avenues for VR-based therapies that use controlled, sensorimotor-driven visuo-spatial body illusions to recalibrate disturbed body representations and restore autonomic balance in patients with neurological and pain disorders.

4.1. *Limits of the study and future direction*

This study presents several limitations that warrant discussion, beginning with the limited sample size, which necessitates cautious interpretation of the findings. First, visuomotor incongruence was applied only to the right hand, which was also the dominant hand for all participants. It remains unclear whether such incongruent conditions would have a differential impact on the dominant versus non-dominant hand, as previously tested in studies on the modulation of body ownership illusions and temperature through MBI (Crivelli et al., 2021, 2023). Moreover, due to the nature of the task, we were unable to monitor the temperature of the moving right hand, leaving it uncertain whether the observed temperature modulations are limited to the stationary, non-stimulated hand or extend to the actively engaged hand. Second, our findings cannot determine whether the observed temperature modulation results purely from sensorimotor readaptation—similar to what occurs during prism adaptation training—or whether it also involves a somewhat subtle experience of disownership for the displaced limb. Distinguishing between these mechanisms would require ad hoc assessments capable of capturing subjective experiences of ownership and disownership for both hands simultaneously during the task. Furthermore, our design does not permit isolation of the individual contributions of visual and tactile inputs. While the visual manipulation was central to the paradigm, it is plausible that the tactile feedback delivered via the VR controller reinforced the illusion, thereby enhancing the strength of the bodily conflict and its associated autonomic effects. Finally, future studies could benefit from incorporating neuromodulation techniques, such as inhibitory TMS or transcranial direct current stimulation (tDCS), either prior to or during the task. These methods would help disentangle the specific contributions of brain regions involved in the online readaptation of peripheral temperature. In particular, targeting the posterior parietal cortex, likely a central hub for integrating multisensory information, could provide valuable insights into the neural mechanisms underlying this process.

5. Conclusion

In summary, our findings offer new evidence that altered body positional representations in immersive virtual environments can modulate peripheral thermoregulatory responses. The observed differences in left-hand temperature between congruent and incongruent visuomotor conditions suggest that disruptions in spatial coherence of body representation can interfere with homeostatic regulation. These results extend prior research by demonstrating that thermoregulatory processes can dynamically adjust in real time during active, goal-directed virtual interactions. Additionally, the correlation between temperature changes and skin conductance responses in the incongruent condition reveals a condition-specific interaction between sympathetic activity and thermoregulation. Future research should aim to identify the neural mechanisms driving these effects by incorporating neurophysiological measures to better understand brain regions implicated in autonomic regulation.

CRediT authorship contribution statement

Matteo Girondini: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Valentina Saccone:** Data curation. **Massimo Montanaro:** Software. **Alberto Gallace:** Writing – review & editing, Writing – original draft, Project administration, Conceptualization.

Data availability statement

Experimental data and analysis performed are available for open access: https://osf.io/8qazs/

Declaration of competing interest

The author(s) declare no conflict of interest.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2025.08.008.

Scientific transparency statement

DATA: All raw and processed data supporting this research are publicly available: https://osf.io/8qazs/

CODE: All analysis code supporting this research is publicly available: https://osf.io/8qazs/

MATERIALS: No study materials supporting this research are publicly available.

DESIGN: This article reports, for all studies, how the author(s) determined all sample sizes, all data exclusions, all data inclusion and exclusion criteria, and whether inclusion and exclusion criteria were established prior to data analysis.

PRE-REGISTRATION: No part of the study procedures was pre-registered in a time-stamped, institutional registry prior to the research being conducted. No part of the analysis plans was pre-registered in a time-stamped, institutional registry prior to the research being conducted.

For full details, see the *Scientific Transparency Report* in the supplementary data to the online version of this article.

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