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Spatial sensorimotor mismatch increases the excitability of the primary somatosensory cortex: Insight from an EEG-virtual reality study

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ABSTRACT

Under typical conditions, the somatosensory system maintains stable functionality. However, the somatosensory cortex can rapidly reorganize in response to sensory input changes, as demonstrated by studies on sensory deprivation and experience-dependent plasticity. Nevertheless, somatosensory plasticity related to unusual sensorimotor activation, such as spatial incongruence between motor commands and somatosensory feedback patterns during body–environment interactions, remains less investigated. This study aims to extend the evidence for functional reorganization of the somatosensory cortex by investigating the interdependency between motor and somatosensory activity during environmental interactions. We employed an innovative virtual reality (VR) paradigm to investigate the effects of spatial mismatch in sensorimotor loops, dissociating motor and somatosensory components in thespatial domain during sensorimotor interactions. Participants (n = 21) performed two experimental sessions composed of 10 minutes each, involving an interaction task in VR, whereby they interacted with a virtual object with their right hand and received either congruent (on the right hand) or incongruent (on their left ankle) sensory tactile feedback. To assess changes in somatosensory processing, we measured EEG-somatosensory evoked potentials elicited by right median nerve stimulation before and after the task. Our results evidenced increased excitability in the early component of somatosensory evoked potentials (P45) following the incongruent condition, with an opposite trend (decrease of excitability) on the congruent condition. These findings may suggest functional changes in the primary somatosensory cortex (SI), likely driven by the temporal coupling of neural activity from unrelated body parts during the task.

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However, attentional mechanisms may also contribute to this effect. While preliminary, these results open new avenues for investigating sensorimotor adaptation driven by repeated associative activity between motor and somatosensory cortices during active interactions.

1. Introduction

The somatosensory cortex is responsible for processing tactile inputs from peripheral receptive fields distributed across the skin. These inputs, detected by somatosensory receptors, are transmitted as electrical signals through the spinal cord to the primary somatosensory cortex (S1) (Kaas, 1993). A key characteristic of S1 is its somatotopic organization, represented by Penfield's Homunculus, which establishes a direct mapping between peripheral receptors and corresponding cortical regions. Stimulation of a body part activates a specific region in the primary somatosensory cortex, in accordance with this somatotopic organization (Sanchez Panchuelo et al., 2018; Sanchez-Panchuelo et al., 2010). Similarly, electrical stimulation of these cortical areas elicits tactile sensations in the corresponding body part (Sun et al., 2021). Despite its structured organization, the somatosensory neuronal circuitry remains highly dynamic, adapting and evolving in response to external stimuli (Tamè & Longo, 2023). One key factor influencing somatosensory functionality is the use or disuse of sensory pathways, which can alter both perception and neural activity (Björkman et al., 2004; Godde et al., 2003). That is, changes in synaptic processing can drive cortical reorganization and shape somatosensory function (Harding-Forrester & Feldman, 2018).

Research in animals and humans show that short-term sensory deafferentation alters cortical somatosensory processing. In animal models, such as studies involving whisker deprivation in rodents or experimentally induced spinal cord injury in monkeys, deafferentation leads to synaptic remodeling and shifts in cortical maps (Bender et al., 2006; Feldman & Brecht, 2005; Kaas, 1993; Merzenich et al., 1983; Merzenich & Jenkins, 1993; Qi et al., 2019). In humans, short-term local deafferentation, as induced by anesthesia or body part immobilization, modifies primary somatosensory cortex activity, for instance by modulating the early component of cortical somatosensory evoked potentials (SEPs) (Allison, 1982; Tinazzi et al., 1997, 2003; Murphy et al., 2003). That is, research on sensory deprivation—an extreme form of sensory input manipulation—continues to highlight the remarkable plasticity and adaptability of the human somatosensory system, although the precise mechanisms driving cortical reorganization remain not yet fully understood, and the concept itself remains subject to debate (Makin & Krakauer, 2023; Wesselink et al., 2022). Conversely, experience-dependent plasticity is typically driven by repeated neural activation through Hebbian-like mechanisms such as short-term potentiation (STP), long-term potentiation (LTP), and long-term depression (LTD) (Lisman, 2017). Repetitive somatosensory stimulation (rSS)—delivered passively at varying frequencies—modulates S1 activity and promotes cortical reorganization (Godde et al., 1997; Muret et al., 2016; Parianen Lesemann et al., 2015). Synchronous coactivation of hand digits enhances neuronal synchrony, promoting improved tactile processing and behavioral discrimination (Godde et al., 2003; Höffken et al., 2007; Kowalewski et al., 2012; Pilz et al., 2004). Importantly, asynchronous stimulation fails to produce similar effects, underscoring the importance of temporal binding in driving adaptive plasticity in S1 (Pilz et al., 2004).

Overall, a substantial body of evidence indicates that somatosensory processing can be shaped by either depriving or reinforcing somatosensory pathways over time. However, protocols that focus exclusively on passive sensory manipulations—such as somatosensory deprivation or repetitive stimulation-tend to overlook the critical role of motor activity (or the integration between the two systems) in shaping somatosensory cortex function (Tamè & Longo, 2023). In real-world scenarios, sensorimotor function emerges from the intricate interplay between the somatosensory and motor systems, with their interdependence evident across multiple levels of neural processing (Edwards et al., 2019; Wolpert et al., 1995). Anatomically and functionally, the motor and somatosensory cortices are interconnected to ensure optimal communication between perception and action, displaying bidirectional neurophysiological properties and adaptable neural representations (Mao et al., 2011; Matyas et al., 2010). Furthermore, these systems operate in a continuous loop, where sensory input refines motor output, and motor actions can influence subsequent sensory perception (Umeda, et al., 2019). A forward-looking approach to studying the properties of the human somatosensory system, therefore, should require an integrative approach that considers both sensory input and motor output as mutually reinforcing components of cortical functionality, examining how the sensorimotor system responds and adapts to new neural pathways while actively engaging the body in interactions with the environment.

Among others, a key feature of the sensorimotor system is the spatial alignment of motor and somatosensory processes, supported by anatomical organization in which efferent and afferent pathways serve the same body regions. The peripheral anatomical arrangement of motor efferent and somatosensory afferent nerves facilitates the co-activation of motor and somatosensory cortical representations during sensorimotor interactions (Makin & Bensmaia, 2017). This alignment ensures precise coordination during actions such as reaching, where sensory feedback must match motor commands. In contrast, integrating artificial somatosensation, as in prosthetics, requires training to remap this spatial relationship. Spatial congruency is thus a fundamental principle in sensorimotor function, as shown by phenomena like short- and

long-latency afferent inhibition (SAI and LAI), where motor responses—measured through transcranial magnetic stimulation (TMS)-induced evoked potentials - are either facilitated or inhibited depending on the timing of afferent input from the corresponding body region (Tamè et al., 2015; Tokimura et al., 2000). Despite its importance, surprisingly little is known about how the sensorimotor system adapts to prolonged spatial mismatches between motor commands and somatosensory feedback. Specifically, the effects of activating motor and somatosensory regions associated with non-spatially related body parts—and how this influences somatosensory processing at the central level—remain largely unexplored. We recently developed a VR-based sensorimotor task that creates a spatial mismatch between motor commands and somatosensory feedback (Girondini, Montanaro, Lega, et al., 2024). Participants moved a virtual object with their right hand while receiving vibrotactile feedback either on the right hand (congruent) or the left ankle (incongruent). After 10 min of mismatch, motor cortical excitability in the right hand's FDI muscle was reduced, suggesting functional adaptation to the co-activation of the left motor cortex and right somatosensory cortex.

Building on these premises, the current study employs the same paradigm—introducing a spatial mismatch between visuomotor commands and somatosensory feedback—to examine changes in somatosensory processing via electroencephalography (EEG) recordings of SEPs. Leveraging the high temporal resolution of EEG, we analyzed SEP components across early (~20–50 msec), mid (~100–140 msec), and late (>150 msec) time windows to investigate how sensorimotor conflict modulates cortical responses. Previous research indicates that early SEPs primarily reflect activity in the primary somatosensory cortex (S1), while later components are associated with higher-order somatosensory processing and attentional mechanisms (Allison, 1982; Eimer & Forster, 2003; Tinazzi et al., 1997, 2003). In our study, SEPs were recorded before and after a VR-based task in two separate conditions: a congruent condition (vibration feedback on the right hand) and an incongruent condition (vibration feedback on the left ankle), with as region of interest being the right hand and median nerve stimulation to evoke SEPs.

2. Methods

2.1. Participants

The sample size for this study was determined using G*Power 3.1 (Faul et al., 2007), based on our previous research on spatial sensorimotor mismatch (Girondini et al., 2024a). Using $\alpha = .05$, power $(1\text{-}\beta) = .80$, and effect size $= 0.3$, the estimated sample size for this study was at least 18 participants. To account for potential dropouts and poor EEG data, we recruited 24 participants (14 female) aged 20–46 years ($M = 24.9$, $SD = 7.01$) through self-enrollment via the University of Lausanne's Sona system. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971), revealing that all participants except one were right-handed. After recording, three participants were excluded from the analysis due to technical issues with data streaming ($n = 2$) and excessive artifacts ($n = 1$), resulting in a final sample of 21 participants ($M = 25.9$, $SD = 5.80$). The study was conducted according to the ethical principles of the Declaration of Helsinki and was approved by the Vaud Canton (Switzerland) ethical committee.

2.2. Experimental design

The experimental design involved participants performing two virtual reality (VR) visuomotor-tactile tasks (congruent and incongruent) on separate days, with a minimum three-day interval between sessions. The order of conditions was randomized and counterbalanced across participants. Both VR tasks were identical in duration and structure, differing only in the spatial location of the tactile feedback. Participants controlled a virtual stick with their right hand to move a virtual cube toward a target. Each contact between the stick and cube triggered both movement and tactile feedback (a vibration well above the sensory threshold) at one of two body locations (Auvray et al., 2011; Gallace et al., 2006). In the **incongruent** condition, contact elicited tactile feedback on the contralateral (left) ankle, creating a spatial sensorimotor conflict. In the **congruent** condition, feedback was delivered to the right hand, which controlled the virtual stick (Fig. 1). To assess changes in somatosensory processing at the cortical level, resting-state SEPs were recorded before and after both experimental conditions.

2.3. Somatosensory evoked potentials (SEPs)

To record SEPs, electrocutaneous stimuli lasting 2 msec were administered to the right median nerve at the right wrist using 10 mm ag/agCl electrodes connected to a Digitimer DS7AH constant-current high-voltage stimulator manufactured by Digitimer in Welwyn Garden City, United Kingdom. The median nerve was chosen for stimulation because it is widely recognized to evoke strong and extensively studied SEPs and it is considered gold-standard in somatosensory-evoked potential studies. The stimulation intensity was set to the participants' motor threshold, defined as the minimum intensity capable of evoking a twitch in the right-hand thumb without inducing pain sensations (Hu et al., 2011; Rossi Sebastiano et al., 2024). The stimulation was controlled by an Arduino microprocessor, which delivered a 5 volt pulse to the Digitimer to trigger the stimulation and simultaneously sent an analog trigger to the EEG system. During the recording session, 200 pulses were delivered to the right hand, with a jittered inter-stimulus interval (ISI) between 1500 and 2500 msec.

2.4. VR sensorimotor task

The VR equipment used for the experiment included a Meta Quest 2 Head-Mounted Display (HMD), with a resolution of 1920×1832 pixels. The HMD was connected via Oculus Link to an Asus ROG Strix notebook, featuring 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 virtual reality environment was developed using the Unity 3D graphics engine. One coin-shaped vibrotactile actuator (3 volt) was used to deliver tactile sensation and attached with tape to the target body part (right hand or left ankle) before the

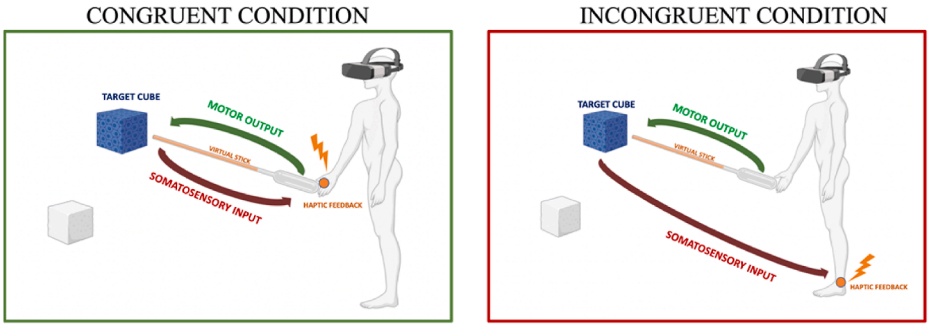

Fig. 1 – Experimental conditions: On the left side the sensorimotor task for the incongruent condition, on the right side the congruent condition.

beginning of the task. The vibrotactile actuator was powered by an Arduino Uno board (5 volt) connected to the VR notebook and synchronized with the virtual environment using the Uduino library.

The VR sensorimotor task was developed in Unity and previously validated in previous studies (Girondini et al., 2024a, 2024b; Girondini, Montanaro, Lega, et al., 2024). An empty room served as the virtual space. When participants wore the HMD and took the right controller, a virtual stick appeared as the tool to interact with the virtual environment, controlled by their right hand. Once participants were familiarized with the virtual environment and the virtual stick, the experiment began with the first trial upon 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). Each participant received the same instruction in both sessions: touch and move the target cube using the virtual stick to match its position with that of the semi-transparent cube. Whenever the virtual stick collided with the target cube, participants received precisely time-locked somatosensory feedback aligned with the interaction (to the right hand or the left ankle, depending on the experimental condition). Once the target cube reached the semi-transparent cube, the trial ended, and a new target cube appeared in the center of the room. The task lasted 10 min and terminated automatically upon reaching the time limit. No specific instructions were provided regarding performance, and participants were informed that metrics, such as number of trials completed, were not relevant to task execution.

2.5. *Procedure*

Participants arrived at the laboratory and signed the informed consent form. Before starting the experiment, each participant completed the handedness questionnaire. The following experimental procedure was carried out in the same way for both sessions, which were performed on different days. First, we determined the participant's somatosensory threshold by identifying the minimum stimulation intensity that elicited a visible thumb twitch. Then, the EEG cap was mounted to the participant's head, and the baseline recording started. During the recording, the participant sat in a comfortable position, with the eyes open and their hand in a resting position on the leg. The instruction was to remain relaxed and to look in front of the room without looking at the hand during the stimulation. Each recording consisted of 200 stimulations delivered to the median nerve of the right hand. When the baseline measurement was concluded, the participant wore the HMD and held the VR hand controller. In the incongruent condition, while the participant remained blindfolded due to the presence of the HMD dark display, the experimenter attached the vibrotactile actuator to the left ankle using tape. In the congruent condition, the actuator was already pre-attached to the controller. The sensorimotor training lasted for a total duration of 10 min (controlled by VR software). Meanwhile, the experimenter remained in the same room to check the correct functioning of the VR setup and the vibrotactile actuators. Once the task was completed, the experimenter carefully removed the HMD from the participant's head to preserve the stability of the EEG cap, and the post-measurement recording began. Following the second SEPs recording, the electrodes were detached, and the experiment was concluded (Fig. 2). After the second session, each participant received a debriefing regarding the purpose of the study.

2.6. *Questionnaires*

Participants' experience of the sensorimotor task was evaluated using a Likert scale ranging from −3 (completely disagree) to 3 (completely agree) across several dimensions: *embodiment* (e.g., "I felt like I could control the virtual stick as if it were attached to my body"), *sense of agency* (e.g., "I had the feeling that the movements of the virtual stick were affecting my own movements"), *temporal consistency* (e.g., "I felt a temporal contiguity between my actions and the feedback I received from the virtual interaction"), *spatial consistency* (e.g., "I felt a spatial contiguity between my actions and the feedback I received from the virtual interaction"), *altered body perception* (e.g., "I had an altered perception of my body during the task in the virtual environment"), and *unpleasantness* (e.g., "The bodily sensations I felt during the virtual interaction were unpleasant").

2.7. *Electroencephalography measurements (EEG)*

EEG data was collected via a 64-channel EEG eego mylab amplifier (AntNeuro, Hengelo, Netherlands), according to the

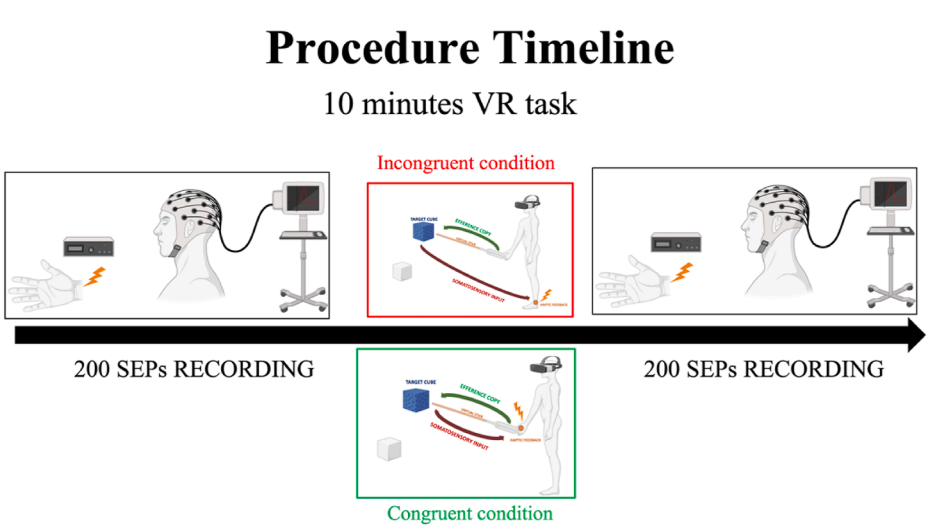

Fig. 2 – Experimental timeline.

10–20 reference system. The signal was recorded with a sampling rate of 1024 Hz (with CPz as the online reference), and impedances were kept below 20 KOhm. Once stored, signal preprocessing was performed using EEGLAB (Delorme & Makeig, 2004) and the MATLAB toolbox Fieldtrip (Oostenveld et al., 2011) with a standardized pipeline: data was bandpass filtered between .5 and 40 Hz and downsampled to 512 Hz. Eye blinks and electrical stimulation were removed using independent component analysis (ICA) performed on the continuous EEG recording. Stimulus-locked epochs were calculated from −100 msec to 300 msec from the electric shock and epochs were visually inspected for artifacts. Finally, the data were average-referenced, and somatosensory event-related potentials were baseline-corrected using the signal over 100 msec prior to each stimulus.

2.8. *Data analysis*

2.8.1. *Questionnaire analysis*

Scores on each questionnaire dimension captured by the questionnaire were analyzed using a Wilcoxon signed-rank test to compare congruent and incongruent conditions.

2.8.2. *Analysis of sensorimotor task metrics*

VR task performance was evaluated by counting the number of trials completed and the mean number of interactions required to complete each trial during the task. A paired-sample *t*-test was conducted to compare VR performance between congruent and incongruent conditions.

2.8.3. *EEG analysis*

SEPs were analyzed using a cluster-based permutation test (CBPT) across frontal, central, and parietal electrodes on both the ipsilateral and contralateral sides relative to the stimulation. CBPT, a robust statistical method widely used in EEG analysis, identifies significant spatiotemporal clusters of activity without requiring a prior hypothesis (Luck & Gaspelin, 2017; Oostenveld et al., 2011). We applied CBPT (500 permutations, random seed = 42) to examine the main effects of Time (pre versus post) and Condition (congruent versus incongruent), as well as the Time × Condition interaction. The interaction effect was tested by calculating the difference between pre- and post-intervention measurements for each condition and then comparing these differences across conditions using a point-by-point dependent samples *t*-test. If CBPT revealed significant clusters, a follow-up parametric *t*-test was performed on the average amplitude within channels identified by cluster tests. Additionally, the analysis was supplemented by describing the average topography across the entire scalp to clarify the distribution of electrical signals during significant intervals. For post-hoc comparisons, marginal statistics (e.g., pre-congruent versus post-congruent, and pre-incongruent versus post-incongruent) were calculated with Bonferroni correction for multiple comparisons, using a *p*-value threshold of .025.

2.8.4. *Correlation analysis between EEG data and sensorimotor task metrics*

Spearman correlation analyses was performed to examine the relationship between P45 amplitude differences and the performance metrics recorded during the VR task, specifically the number of cubes completed and the average number of touches per cube.

3. Results

3.1. *Questionnaires*

A Wilcoxon signed-rank test revealed no significant difference in ratings between the congruent and incongruent conditions for *embodiment* ($W = 31$, $df = 20$, $p = .542$), *sense of agency* ($W = 25$, $df = 20$, $p = .666$), *temporal consistency* ($W = 31.5$, $df = 20$, $p = .301$), *unpleasantness* ($W = 5.5$, $df = 20$, $p = .341$), and *altered body perception* ($W = 40.0$, $df = 20$, $p = .968$). The ratings for *spatial consistency* differed significantly between the congruent and incongruent conditions ($W = 15.0$, $df = 20$, $p = .019$). Participants perceived the incongruent condition as having lower spatial consistency ($M = -.952$, $SE = .39$) compared to the congruent condition ($M = .28$, $SE = .37$) (Fig. 3).

3.2. VR sensorimotor performance

There was no significant effect of Condition on the number of trials completed during the VR task ($t = -.34$, df = 20, $p = .734$). On average, participants completed 175 trials (SE = 6.52) in the congruent condition and 177.3 trials (SE = 9.34) in the incongruent condition. Similarly, no significant difference was found in the average number of cube touches between the conditions ($t = 1.84$, df = 20, $p = .080$). Participants averaged 3.66 touches (SE = .18) in the congruent condition and 3.38 touches (SE = .18) in the incongruent condition (Fig. 4). These results suggest that there were no significant differences in task performance based on the spatial manipulation during the task.

3.3. Cluster-based permutation test (CBPT) revealed modulation in the early component of the contralateral somatosensory cortex

The cluster-based permutation test found no significant main effect of Condition, with two non-significant clusters: Cluster 1 (CP6, P4, CP4, CP6; 256 msec; $p = .481$) and Cluster 2 (FC2, C4, FC4, C2; 273–281 msec; $p = .325$). Similarly, the main effect of Time was not significant, with three non-significant clusters: Cluster 1 (F3, F5, FC3, FC5, C3, C5; 175–187 msec; $p = .096$), Cluster 2 (C6, CP4, CP6, P6, T8, TP8; 246–250 msec; $p = .270$), and Cluster 3 (F4, F6, FC4, FC6; 285–293 msec; $p = .243$).

Crucially, the Time × Condition interaction was significant, with one significant cluster localized over the frontocentral

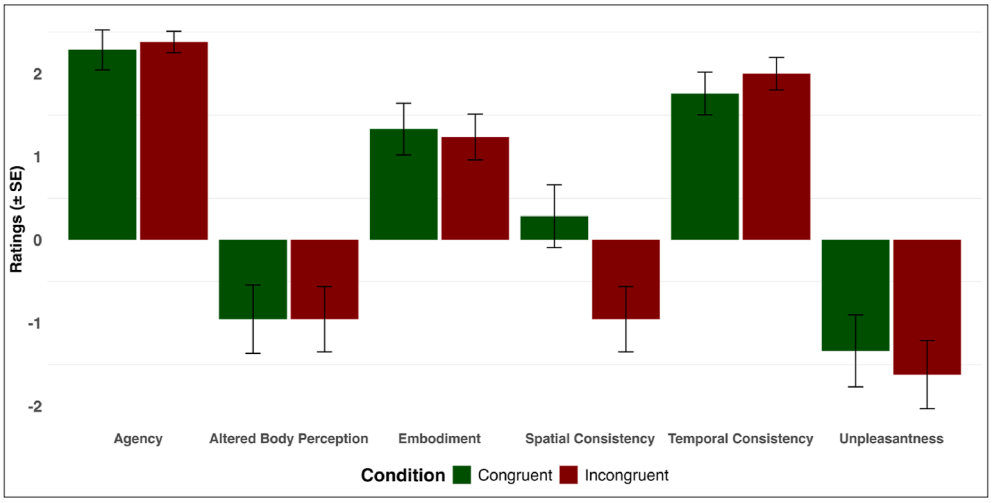

Fig. 3 – Self-report questionnaire ratings.

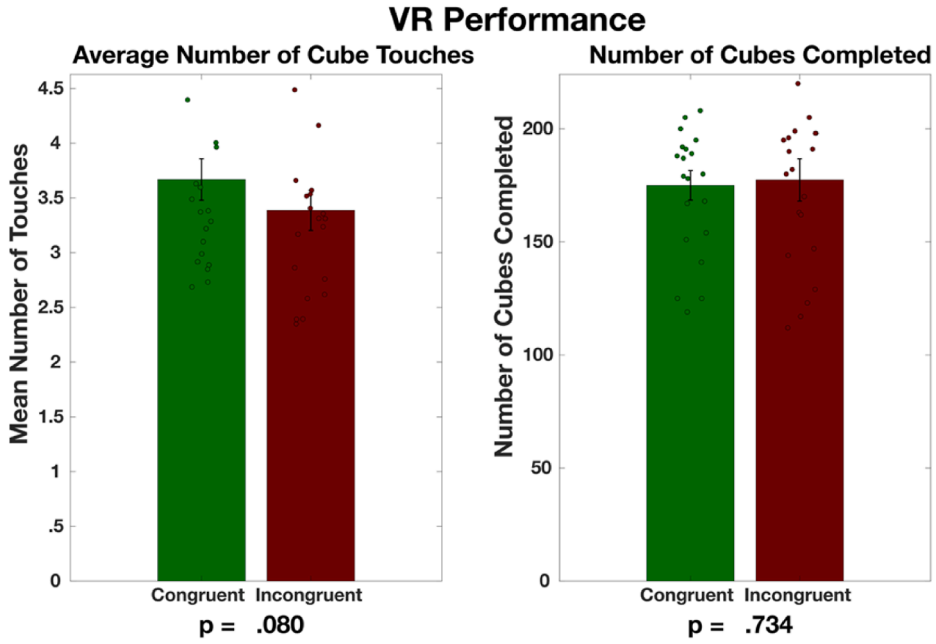

Fig. 4 – VR Performance. On the left side, the average number of touches performed for each trial. On the right side, the average number of cubes completed during the task.

and parietal cortices contralateral to the stimulation site (FC5, C3, C5, CP3, CP5, P5, P7, TP7; 35–59 msec; $p = .024$). This cluster revealed the presence of an interaction effect during the early stages of somatosensory processing (Fig. 5A). To further understand and describe the nature of this effect, we conducted a follow-up analysis of the somatosensory-evoked potentials by averaging responses across the identified electrodes.

3.4. *The P45 amplitude changes differently after the congruent and incongruent condition*

Fig. 5B illustrates waveforms representing the averaged signal from the nine electrodes (FC5, C3, C5, CP3, CP5, P5, P7, TP7) from the significant cluster, separated by condition: congruent (green, left) and incongruent (red, right). Fig. 5C

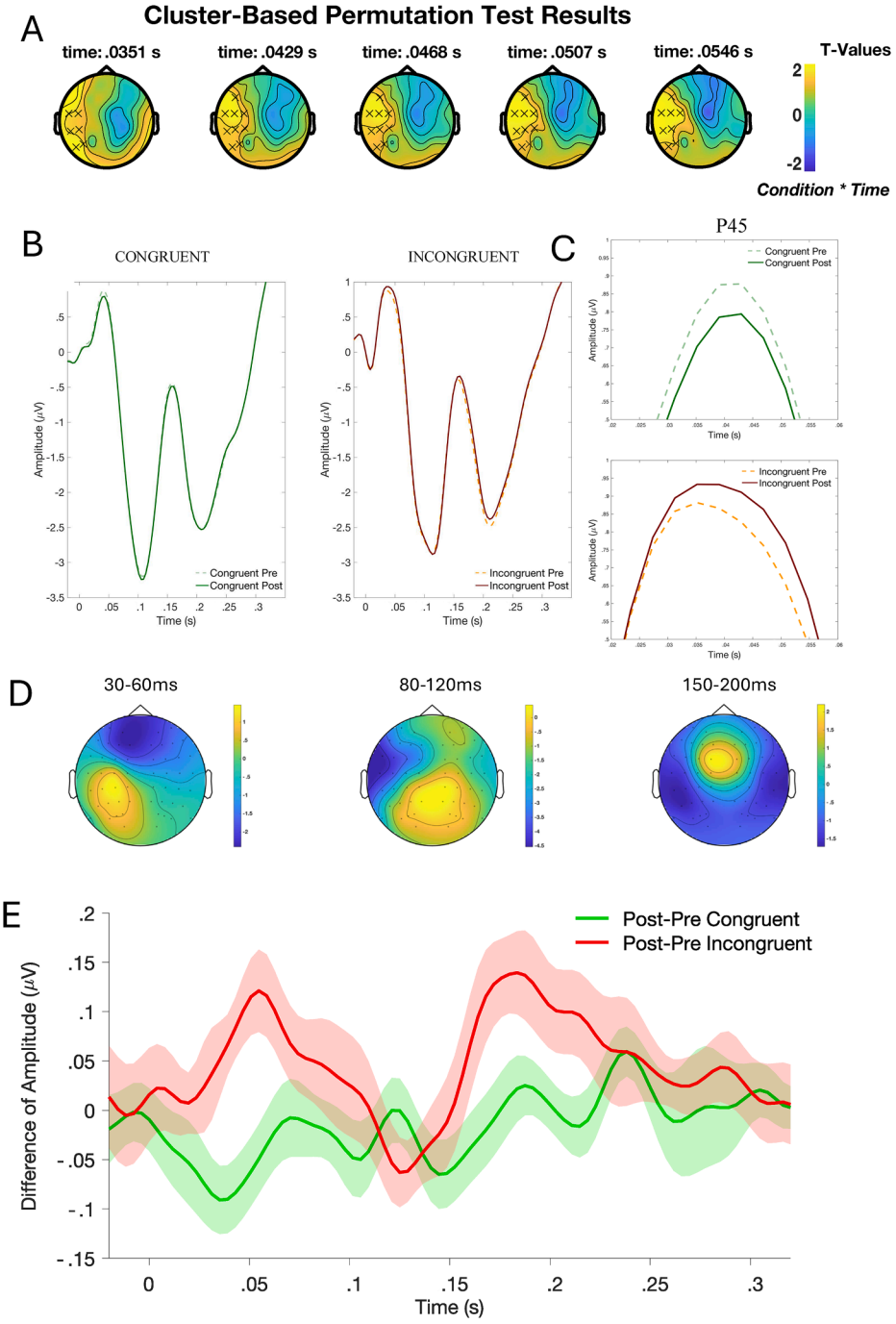

Fig. 5 – Panel A: Results of the cluster-based permutation test, highlighting channels from significant clusters. Panel B: Waveform results from the averaged signal of channels significant in the cluster-based analysis. Panel C: Zoom-in on the P45 component for congruent and incongruent conditions. Panel D: Topography at selected time windows of early, middle, and late SEP components.

provides a magnified view of the signal within the time window identified as significant in the analysis, which represents the P45 component. For the P45 component (average amplitude of the channels in the cluster, 35–59 msec), the main effect of the *Condition* ($t = -.374$, df = 20, $p = .711$) and *Time* ($t = -.528$, df = 20, $p = .602$) were not significant. interaction effect *Time x Condition* was significant ($t = -3.45$, df = 20, $p = .002$). The interaction effect is explained by the opposite direction of P45 amplitude relative to the baseline: the amplitude increased after the incongruent condition ($M = .070$ μV, SE = .030) and decreased after the congruent condition ($M = -.075$ μV, SE = .032) (Fig. 6A).

3.5. *Spatial sensorimotor mismatch increased the excitability of the primary somatosensory cortex*

To further explore the interaction effect, we performed two post hoc paired-sample *t*-tests (*p*-value set to .05/2 = .025) comparing the pre-vs. post- average potentials for the congruent and incongruent conditions (contralateral sensorimotor channels, time windows 35–59 msec). In the congruent condition, the pre-post contrast did not survive multiple comparisons correction, although a non-significant trend indicated a decrease in amplitude compared to the baseline ($t = 2.28$, $p = .045$, Mean Pre Congruent = .73 μV, SE = .21; Mean Post Congruent = .66 μV, SE = .26). On the contrary, the pre- vs. post- comparison in the incongruent condition was significant, showing an increase in amplitude compared to the baseline ($t = -2.90$, $p = .008$, Mean Pre Incongruent = .74 μV, SE = .20; Mean Post Incongruent = .83 μV, SE = .21) (Fig. 6B and C).

3.6. *Correlation analysis between the difference in P45 amplitude and sensorimotor training performance*

We performed a Spearman correlation analysis to examine the relationship between the difference in P45 amplitude and performance metrics recorded during the task, specifically the number of cubes completed and the average number of cube touches. The difference in P45 amplitude is a baseline-corrected measure, where negative values indicate a reduction in neural activity relative to baseline, and positive values reflect an increase.

No significant correlation was found between the number of cubes completed and the P45 amplitude difference in either the congruent condition ($R = .291$, $p = .201$) or the incongruent condition ($R = .0169$, $p = .942$). For the average number of cube touches, no correlation was observed in the congruent condition ($R = -.377$, $p = .092$) and incongruent condition ($R = .319$, $p = .157$), indicating that the number of touches was not associated with modulation of P45 activity (Fig. 7).

4. Discussion

This study investigated the consequences of short-term exposure (10 min) to a sensorimotor spatial mismatch between the body part executing a motor command and the one receiving somatosensory feedback from the interaction on somatosensory processing. We manipulated the location of somatosensory feedback received every time a virtual stick collapsed with a cube: for the incongruent condition, the right-hand interaction produced a vibration in the left ankle, while for the congruent condition, spatial congruency between movement and feedback was maintained (feedback received on the right hand). Somatosensory evoked potentials were recorded before and after the task to assess cortical responses. To our knowledge, this is the first EEG study exploring how spatial congruency modulates somatosensory processing in the context of an active, ecologically valid sensorimotor task, specifically examining its interplay with the motor system during an active and more ecologically valid sensorimotor task. As a primary result, we found an increase in amplitude of the early component (P45) after the

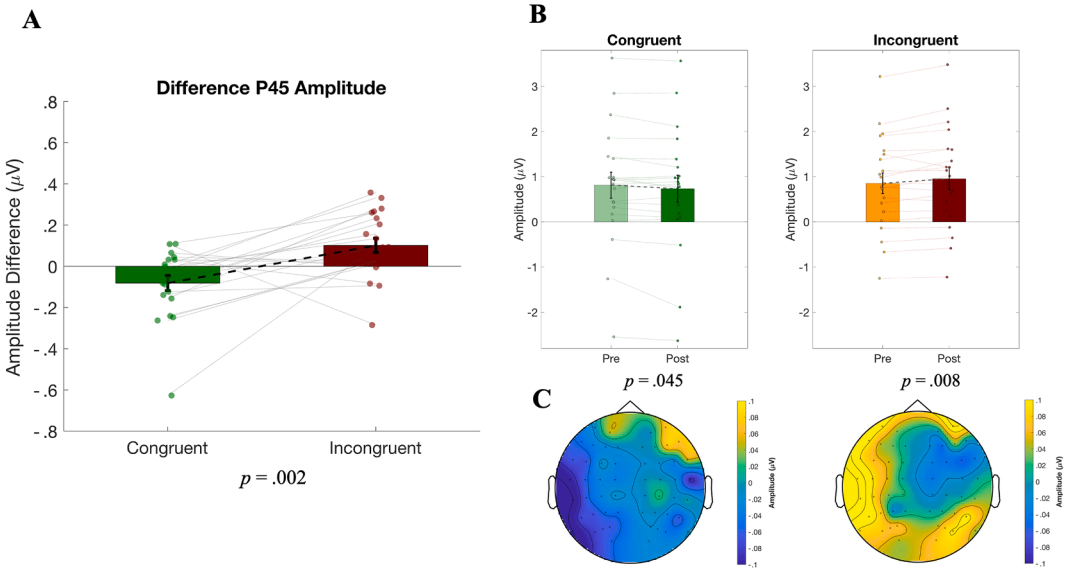

Fig. 6 – Panel A: Baseline-corrected amplitude of P45. Panel B: Difference in P45 amplitude across congruent and incongruent conditions. Panel C: Topoplots of the difference in the 30–60 msec time window (congruent condition on the left; incongruent condition on the right).

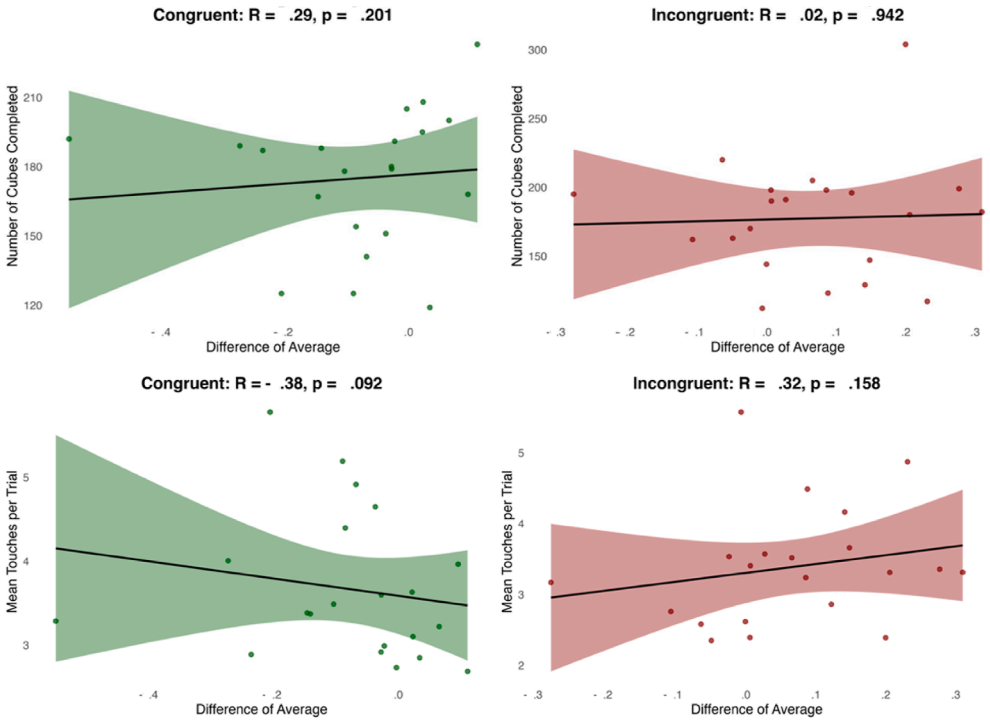

Fig. 7 – Correlation analysis between the difference in P45 amplitude and the number of cubes completed (upper panel), and the mean number of touches (lower panel) for both the congruent (green) and incongruent (red) conditions.

incongruent condition, with an opposite trend (decrease in amplitude) observed after the congruent condition.

The P45 component is an early somatosensory response hypothesized to reflect neural activity within the primary somatosensory cortex. Consistent with previous studies, scalp topography analyses suggest that this component originates from the central-posterior contralateral cortex (Schröder et al., 2021). Our findings suggest that manipulating spatial congruency in tactile feedback influences the early stages of somatosensory processing, with cortical responses either increasing or decreasing depending on whether spatial congruency was maintained or violated. The increased response in the early SEP component following the incongruent condition is particularly intriguing, as it may reflect functional adaptation in the somatosensory cortex to the novel association between motor commands and tactile feedback introduced by the task. Specifically, during the incongruent condition, participants were exposed to a novel spatial association between the motor command, executed with the right hand, and the tactile feedback continuously received at the left ankle, time-locked to virtual interactions during the task. This repeated spatial mismatch between movement and sensory input appears to have induced hyperexcitability in the primary somatosensory cortex following peripheral nerve stimulation of the hand. Conversely, we observed a reduced amplitude in the P45 component following the congruent condition, though this difference did not survive multiple comparison corrections. This diminished response may be related to habituation, likely driven by repeated tactile stimulation during the task (Bradley et al., 2016; Klingner et al., 2011). Throughout the congruent condition, participants consistently experienced tactile input corresponding to their right-hand movements. This continuous activation of cortical somatosensory neurons, receiving inputs from the right palm, may have led to progressive attenuation of neural responses, reducing sensitivity to peripheral stimulation after the task. We found no evidence of a relationship between task performance and changes in cortical excitability in either condition. Notably, high variability in participants' interactions—likely due to the lack of constraints or specific instructions—may have contributed to this result. Thus, the link between sensorimotor behavior and neurophysiological changes remains inconclusive, and a more controlled task design could help clarify this relationship in future studies.

As this study explores the largely unexamined role of spatial congruency in sensorimotor function using a novel experimental paradigm, the mechanisms we propose to explain our findings should be considered preliminary. During voluntary movements, visual, proprioceptive, and somatosensory signals are integrated with motor commands to guide the body's movements in space (Edwards et al., 2019; Machado et al., 2010; Miall & Wolpert, 1996). In our experimental condition, however, participants were exposed to a novel spatial association: motor commands executed with the right hand were consistently paired with tactile feedback delivered to the left ankle, time-locked to virtual interactions during the task. This repeated coupling of two spatially unrelated body parts may have disrupted conventional neural pathways involved in sensorimotor integration, potentially altering typical processing of motor output and somatosensory feedback within the sensorimotor loop. Notably, our manipulation differs substantially from traditional models of somatosensory experience-dependent plasticity—such as repetitive sensory stimulation (rSS)—which typically involve passive co-

activation of spatially adjacent body parts (Godde et al., 1997; Parianen Lesemann et al., 2015). By contrast, our paradigm introduces a form of spatially incongruent, active sensorimotor pairing, raising new questions about how the human sensorimotor system adapts to atypical crosstalk between motor and somatosensory cortices during active interactions with the environment.

One possible explanation for our effects is that they reflect neural adaptations resulting from repeated exposure to conflicting feedback. Typically, motor and somatosensory signals generated during interactions with a specific body part are processed and integrated with the corresponding somatotopic area of the same hemisphere, facilitated by dense cortico-cortical connections (Borich et al., 2015; Mao et al., 2011; Mastria et al., 2023). In the incongruent condition, however, the spatial misalignment—characterized by somatosensory feedback originating from a body part not directly involved in the motor command - challenges conventional neural processes related to the sensorimotor loop between motor and somatosensory cortex. Increased responses in early SEPs components have been reported in conditions where afferent input from a specific body part is suppressed or altered, for instance, during short-term anaesthesia or immobilization (Okamoto et al., 2022; Tinazzi et al., 1997). However, it is important to highlight that the incongruent condition in our paradigm did not involve somatosensory deprivation. Participants maintained continuous contact with the VR controller and engaged in active movements throughout the task, ensuring at least a minimal level of afferent feedback, primarily via proprioception. Taken together, these considerations suggest that the modulation observed in S1 following the incongruent condition might reflect a neurophysiological marker of a transiently altered somatosensory state—driven not by sensory deprivation, but by the brain's adaptive response to temporal binding of two independent body areas within the sensorimotor loop.

An alternative explanation for our results relies on attentional mechanisms, and in particular on the role of selective attention in somatosensory processing. Previous research on attentional mechanisms suggests that late SEP responses (>140 msec) are enhanced as markers of spatial attention, though some evidence also points to attentional influences on earlier components (~50 msec) (Eimer & Forster, 2003; García-Larrea et al., 1991; Johansen-Berg et al., 2000; Schubert et al., 2008). In general, spatial attention has been shown to enhance SEP amplitude toward the attended side (Eimer & Forster, 2003; Schubert et al., 2008). Within the context of our study, the increased amplitude observed in the incongruent condition suggests that attentional demands during the post-measurement phase were directed toward the body part affected by the mismatch. However, attentional shifts might be stronger toward the body part receiving the feedback rather than the unstimulated hand. Altough we instructed participants to ignore hand stimulation and fixate on a blank screen, covert attentonal shifts remains challenging to rule out during the resting-state stimulation period. While we cannot entirely exclude the contribution of attention in modulating early SEP components, it is important to note that attentional modulation is typically an online process (i.e., spatial attention directed to a body part during stimulation (Eimer & Forster, 2003; Schubert et al., 2008)), whereas the modulation observed in our study appeared as an after-effect during the resting state post-training recordings. It is also relevant to mention that we did not find significant differences either in the later SEP components, despite a noticeable increase in amplitude around 150–250 msec after stimulus onset in both conditions, with the effect being more pronounced in the incongruent condition. Potentially, spatial mismatch may enhance the salience of sensory inputs from a body part suffering from atypical sensorimotor activation patterns, potentially influencing high-order somatosensory processes. Future studies incorporating targeted manipulations of selective spatial attention, as well as varying the salience of the stimuli (i.e., nociceptive), will be useful to further clarify the relationship between spatial sensorimotor incongruency and high-order somatosensory processing (Iannetti et al., 2008; Ronga et al., 2013).

Finally, using the same paradigm, we recently reported a decrease in motor cortical excitability of the right hand (i.e., measured at FDI muscle) after being exposed to the incongruent condition of the task (Girondini et al., 2024). Here, we provide evidence that exposure to spatial sensorimotor mismatch during sensorimotor interaction induces functional changes extending beyond the motor domain to the somatosensory system. Additionally, it is important to note that subjective reports revealed that participants rated agency and embodiment similarly across conditions, indicating that the spatial mismatch—while maintaining temporal consistency—did not impact these aspects. Furthermore, participants evaluated the experience in terms of pleasantness similarly, without reporting any altered body perception. These results provide valuable insight on the lack of subjective side effects caused by the spatial mismatch manipulation.

5. Limitations of the study and future direction

The study has several limitations that must be acknowledged. A primary limitation is the absence of previous research that used a similar paradigm to manipulate the spatial component of sensorimotor interaction prevents us from directly comparing our findings with the extant literature on the same topic. As a result, this study remains exploratory, and the underlying mechanisms suggested must be considered largely hypothetical. Moreover, the current design cannot determine whether similar effects would occur without the use of VR or motor interaction, or whether they could result solely from the pairing of tactile stimulation with natural somatosensory feedback induced by movement.

In this initial investigation of spatial mismatch effects on somatosensory processing, we tested only one configuration—associating right-hand interaction with left-ankle feedback. This configuration was chosen to maximize incongruency between the body side and the effector. Using the ankle instead of the hand also helped minimize involuntary movements that could result from hand stimulation during the incongruent condition task. However, it remains unclear whether the observed effects are effector-dependent, hemisphere-dependent, or extend beyond temporal binding to

scenarios unrelated to motor interactions and somatosensory feedback. Future studies should explore various spatial mismatch configurations using multiple recording sites to assess broader changes in cortical excitability. Additionally, incorporating asynchronous stimulation conditions could help clarify the temporal dependence of these effects.

6. Conclusion

In summary, this study provides novel insights into how sensory processing in the somatosensory cortex is modulated through the artificial temporal binding of efferent and afferent signals. We demonstrated that short-term exposure (10 min) to a spatial mismatch between motor commands (to the right hand) and somatosensory inputs (to the left ankle) leads to increased excitability in the early SEPs component (P45). These findings, although preliminary, highlight the dynamic and adaptive properties of the somatosensory cortex, which likely depend on sensory-motor patterns activated over time. Further interpretations are possible, and additional studies are required to confirm our findings. Overall, the present study raises new questions about the interplay between the motor and somatosensory systems during active interaction, paving the way for future research. Such investigations are crucial for fully understanding the adaptability of the sensorimotor system, with important implications for tactile remapping in prosthetics and artificial somatosensory integration in human augmentation interfaces.

CRediT authorship contribution statement

Matteo Girondini: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Tommaso Bertoni:** Writing – review & editing, Methodology, Formal analysis. **Massimo Montanaro:** Software. **Andrea Serino:** Writing – review & editing, Project administration. **Alberto Gallace:** Writing – review & editing, Supervision, Project administration, Conceptualization.

Data availability statement

Experimental Data and code for analysis are available in the OSF repository: https://osf.io/7npbe/.

Declaration of competing interest

The author(s) declare no conflict of interest.

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