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Somatosensory coding of visual self-identity

Mattia Galigani [a], Marcella Romeo [a,b], Nicoletta Scanferlato [a], Massimiliano Valeriani [c], Bettina Forster [d], Francesca Garbarini [a,e,*]

[a] Manibus Lab, Department of Psychology, University of Turin, Turin, Italy
[b] MoMiLab, IMT School for Advanced Studies Lucca, Lucca, Italy
[c] Developmental Neurology Unit, Bambino Gesù Children's Hospital, IRCCS, Rome, Italy
[d] Centre for Clinical, Social and Cognitive Neuroscience, Department of Psychology, City St. George's, University of London, London, UK
[e] Neuroscience Institute of Turin, University of Turin, Turin, Italy

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ABSTRACT

How does the brain process our bodily identity? This question has long fascinated scientists because of its potential implications for the study of self-awareness. Here, to test the idea that the somatosensory system is directly involved in coding bodily self-identity even when conveyed through vision, we probed the somatosensory system with tactile stimuli while participants observed hand images, either belonging to them (self-hand) or to another person (other-hand). In three psychophysical experiments (discovery, replicating and control samples), we found faster reaction times to tactile stimuli when paired with the self- than the other-hand image. To explore the neural basis of this effect, we conducted two electrophysiological experiments (discovery and replicating samples), and we observed that visual activity did not vary as a function of bodily identity, whereas the activity of the primary (at around 40 ms) and secondary (from 100 ms) somatosensory cortices did vary, as revealed by significantly higher somatosensory responses to tactile probes when presenting the self- than the other-hand image. We propose that this somatosensory coding of visual self-identity may be the result of associative learning mechanisms, through which individuals learn that the association between visual and somatosensory input only pertains to the own body, thus representing a possible prerequisite for establishing self-awareness.

1. Introduction

The existence of dedicated brain areas and networks involved in processing body and body-parts is well-established (Devue and Brédart, 2011; Kanwisher and Yovel, 2006; Suddendorf and Butler, 2013). But how does our brain code body identity and, more specifically, bodily self-identity? Intuitively, we would be inclined to respond that the neural coding of bodily self-images may be exclusively or mainly due to purely visual processes, with the same visual areas involved in body perception also mediating identity recognition (Myers and Sowden, 2008; Vocks et al., 2010). However, we constantly receive unique somatosensory information from our body, and the resulting sensations contribute to draw the boundary between self and non-self contents (Apps and Tsakiris, 2014; Bretas et al., 2021). So, while vision may be considered the dominant sense through which we identify other people's body parts, the visual processing of own body-parts may involve an additional recruitment of somatosensory cortices beyond visual areas. In our study, to investigate the contribution of the somatosensory system in coding visual self-identity, we focused on the hand given the complex and rich interplay of multisensory input arising from it during everyday life interactions (Bonzano et al., 2023; Ferri et al., 2012a; Fossataro et al., 2020; Gentile et al., 2011; Limanowski and Blankenburg, 2016). Thus, we combined psychophysical (Experiment 1, 2, and 3) and electrophysiological (EEG; Experiment 4 and 5) approaches to investigate somatosensory responses to tactile probe while participants observed images of either the participant's hand (self-hand) or someone else's hand (other-hand).

In the first psychophysical experiment (Experiment 1: psychophysical discovery sample), we presented images of the self- and the other-hand that, in half of the trials, were coupled with tactile probes. Participants had to respond to tactile stimuli while observing visual stimuli, and differences in reaction times (RTs) to tactile stimuli (that were identical between conditions) should directly reflect the differential modulation of tactile responses induced by the visual content (self-hand

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* Corresponding author at: Psychology Department, University of Turin, Via Verdi 10, 10124 Turin, Italy.
E-mail address: francesca.garbarini@unito.it (F. Garbarini).

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or other-hand images). The second psychophysical experiment (Experiment 2: psychophysical replicating sample) was designed to replicate the results of the Experiment 1, by also changing the timing of visual and tactile stimuli delivery in visuo-tactile trials, which was simultaneous in Experiment 1 and delayed in Experiment 2, with tactile stimulation occurring 50 ms later. This manipulation accounted for the different timings of cortical arrival between visual and tactile information, as evidence from studies in both humans and monkeys suggests that tactile stimuli reach the cortex approximately 50 ms faster than visual stimuli (Musacchia and Schroeder, 2009; Trojaborg and Petersen, 1979). By presenting the tactile stimuli with this delay, we ensured that both sensory modalities reached the brain at the same time, thereby enabling the observation of a direct modulation of the visual content over early somatosensory processing. In the third psychophysical experiment (Experiment 3: psychophysical control sample), we controlled for the role of familiarity biases in driving our results, by comparing the self-hand image to the image of a familiar hand (i.e., partner's hand) instead of a stranger's hand.

To explore the neural basis of the possible behavioral effects found in the psychophysical studies, we designed two electrophysiological experiments (Experiment 4: electrophysiological discovery sample and Experiment 5: electrophysiological replicating sample). As in the previous psychophysical protocols, we presented images of the self-hand and other-hand that, in half of the trials, were coupled with tactile probes, which were delivered simultaneously (Experiment 4) or 50 ms delayed (Experiment 5). In this context, investigating electrophysiological responses to tactile probes allows to observe the contribution of visual stimuli in modulating somatosensory processing (Arslanova et al., 2023, 2019; Fanghella et al., 2022; Forster and Abad-Hernando, 2024; Galvez-Pol et al., 2020; Sel et al., 2020). Importantly, this approach, originally developed and validated to detect visuo-somatosensory interactions when observing body-related stimuli, was here applied with the aim of testing whether it could also reveal somatosensory engagement in coding bodily self-identity even when conveyed through vision. In other words, with the same rationale of behavioral experiments, differences in somatosensory evoked potentials (where tactile stimulation is identical between conditions) should directly reflect the differential modulation of somatosensory activity induced by identity-related visual contents (self-hand or other-hand images).

We predict that, if somatosensory system plays a role in coding visual self-identity, we should observe a modulation of somatosensory processing as a function of body identity, with faster RTs (Experiment 1, 2, and 3) and higher somatosensory activity (Experiment 4 and 5) when probing the somatosensory system during the presentation of the self-hand as compared to the other-hand (or familiar-hand) image.

2. Materials and method

2.1. Experiment 1, 2, and 3: psychophysical discovery, replicating and control sample

2.1.1. Participants

In the psychophysical experiments we recruited 52 right-handed participants (18 in Experiment 1 – discovery sample: mean age = 25.82, SD± =± ±3.45 years, 10 females; 17 in Experiment 2– replicating sample: mean age = 25.52, SD = ±1.43 years, 9 females, 17 in Experiment 3– control sample: mean age = 29.65, SD = ±3.57 years, 9 females). In Experiment 3, all participants were homosexual to avoid confounds related to the sex of the hand used as the other stimulus (i.e., partner's hand). Due to technical problems during the reaction times recording, data from one participant in Experiment 1 was missing, thus the behavioral analysis was performed on 17 participants and 17 participants were recruited in Experiment 2 and 3. No participants took part in more than one experiment. All subjects had normal (self-reported) or corrected to normal vision and were right-handed according to the Edinburgh Handedness Inventory. All participants signed the informed consent, and the studies conformed to the standards required by the Declaration of Helsinki and was approved by the Ethics Committee of the University of Torino (prot. N. 122,572). The size of the samples was decided in accordance with previous studies employing behavioral measures to investigate how bodily visual stimuli affects tactile performance (e.g., Kennett et al., 2001; Leo et al., 2020)

2.1.2. Experimental design

Experimental protocol. Psychophysical experiments were designed to investigate a modulation induced by hand images with different identities over tactile performance. To this aim, we presented single images of right hands (age- and sex-matched) belonging either to the participants (self-hand image) or to someone else (other-hand image) that, in half of the trials, were coupled with tactile stimulation on both index fingers (Experiment 1: delivered at the onset of the visual stimulus, as in Experiment 1; Experiment 2 and 3: delivered 50 ms after the onset of the visual stimulus) (Fig.1A). In Experiment 1 and 2, as other stimulus we used an image of an unfamiliar hand, while in Experiment 3, where we controlled for familiarity biases, we used the image of the partner's hand. Note that, as inclusion criteria, participants had to be homosexual (to avoid confounds related to the sex of the person to whom the hand used as the other stimulus belongs), had to be in a romantic relationship with the partner for at least three years and had to live in the same city.

Participants were asked to respond as fast as possible to the tactile stimulation by pressing a pedal with the right foot. Note that we opted to use the foot, rather than hand, to respond because we wanted to isolate possible pure modulations of implicit self-hand recognition over tactile processing, without introducing confounding effects related to visuo-motor congruency (i.e., responding with the right hand that was also presented on the screen). Participants performed 160 trials (80 visual-only and 80 visual-tactile – 40 per condition) and reaction times were recorded. Before the experiments, to familiarize with the task and to balance the low-level familiarity across visual stimuli, we implemented a training session lasting 8-minutes (for a similar procedure see Galigani et al., 2021b), where participants performed the task with the hand images used in the main experiments (Self- and Other/Familiar-hand image).

Visual and tactile stimulation. Visual stimuli consisted of grey-scale pictures (20 * 15 cm) of the dorsum of right hands belonging either to the participants or to other people (matched for age and sex). We took the picture of hands before the experiments, all in the same room and with controlled illumination conditions. We post-processed the images by removing and replacing the background with a black uniform one. Then, we converted original color pictures into grey-scale images to standardize different skin colors. The resulting visual stimuli were displayed using E-Prime2 Software (Psychology Software Tools, Pittsburgh, PA) for 300 ms at the center of a 21-inch Sony CRT computer screen.

In half of the trials, in addition to the image of hands, participants received a brief task-irrelevant tactile stimulation concurrently to the index fingers of both hands to elicit somatosensory evoked activity. Tactile stimulations were brief (200± μs) transcutaneous electrical stimuli consisting in constant current square-wave pulses (DS7A, Digitimer) delivered to the index finger of both hands. The stimulation intensity was adjusted according to the individual sensory threshold (estimated using the methods of limits (Gescheider, 1997)). Starting from very low-magnitude stimulations (1.5–2 mA), the experimenter gradually increased intensity by steps of 0.02 mA until the subject reported a bilateral tactile stimulation. Then, the experimenter lowered the intensity by 0.02 mA until the participant did not report the bilateral stimulation. Hence, the experimenter enhanced the current intensity again, and so on until the electric stimulation intensity which caused participants to report exactly 5 stimuli out of 10 on both hands was determined. The number of trials needed to estimate the threshold

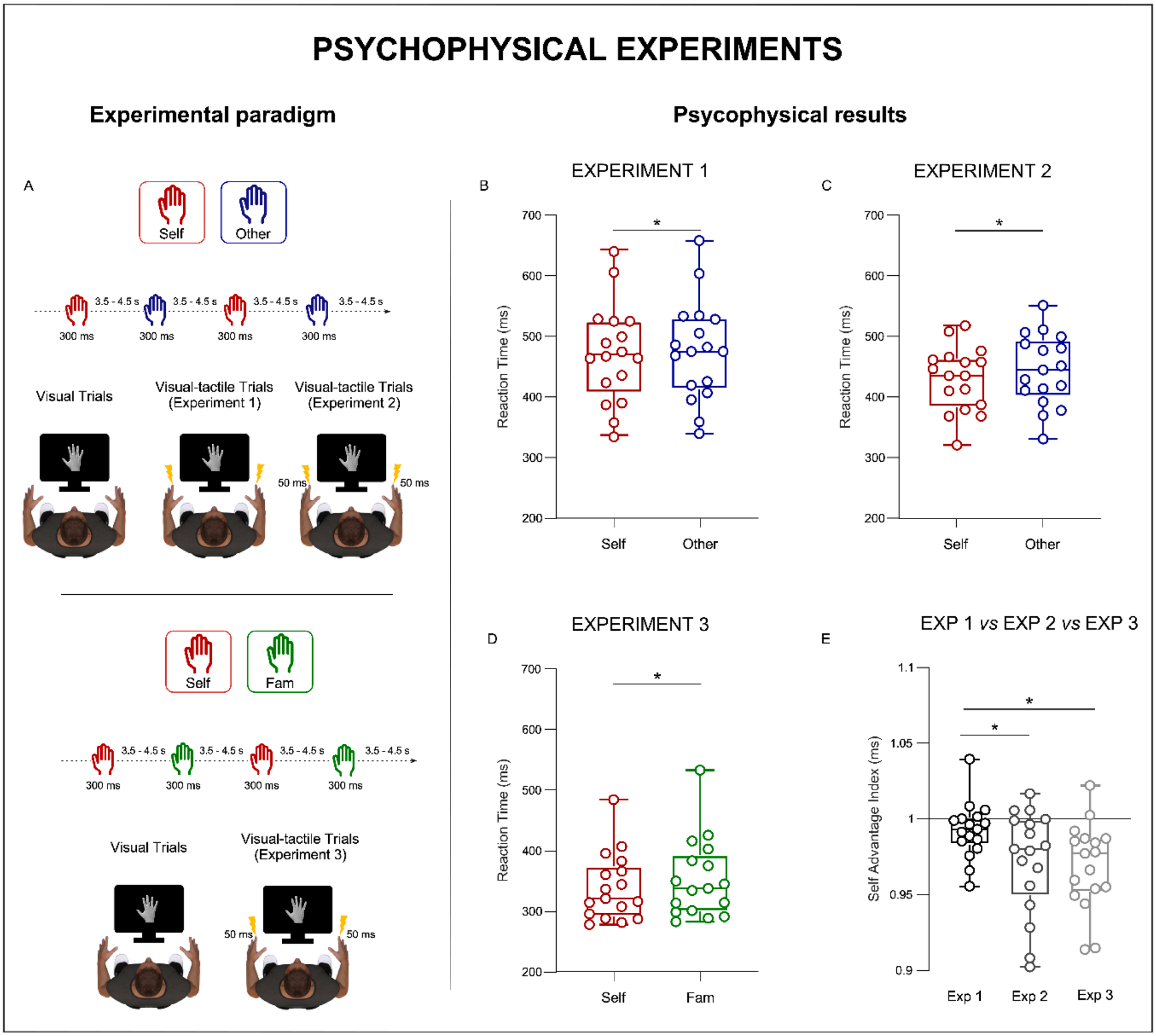

Fig. 1. A) Experimental paradigm. Images of the self-hand and the other/familiar-hand were presented, and in the half of the trials were coupled with a tactile stimulation simultaneously delivered to both index fingers (simultaneous in Experiment 1 and 50 ms delayed in Experiment 2 and 3). The task of the participants was to press as fast as possible a foot pedal in response to the tactile stimulation.

varied depending on the subject. During the threshold estimation, participants wore headphones delivering a white noise to prevent hearing any click associated with pressing the stimulator bottom. The mean (± SD) bilateral threshold stimulus intensity was 3.53 ± 0.98 mA in Experiment 1, 3.39 ± 1.12 mA in Experiment 2, and 3.98 ± 1.15 mA in Experiment 3. During the experiments, the stimulation intensity was set slightly above the threshold (stimulation intensity = threshold intensity*2), so that participants always perceived the tactile stimulation, which was never painful (see e.g., Fossataro et al., 2023; Ronga et al., 2021; Rossi Sebastiano et al., 2022).

2.1.3. *Data analysis*

In Experiment 1, 2, and 3, participants' reaction times to tactile stimulations were collected for each condition and averaged. Outlier responses (<3 % of all trials) were excluded based on an arbitrary rule if they exceeded two standards deviations from the mean. Then, the mean of the remaining trials with correct detections was computed. In the three experiments, we performed a paired-sample *t*-test between the reaction times of the two conditions (Self and Other in Experiment 1 and 2, Self and Familiar in Experiment 3). Furthermore, to investigate whether the timing of visual and tactile stimuli delivery in visuo-tactile trials, which was simultaneous in Experiment 1 and delayed in Experiment 2, and the level of familiarity of stimuli affected responses to tactile stimuli, we computed a self-advantage index in the three experiments (RTs in Self condition *divided by* RTs in Other condition) and we compared them with a one-way ANOVA with Experiment (Exp1, Exp2, Exp3) as between subjects factor, and the significant effect was explored with Fisher LSD test. This ratio-based index was chosen to normalize individual differences in overall response speed and to allow for proportional comparisons of the self-advantage effect across different participant samples (see e.g., Hosel and Tremblay, 2021; Labruna et al., 2011).

2.2. Experiment 4 and 5: electrophysiological discovery and replicating sample

2.2.1. Participants

In the EEG experiments we enrolled 36 healthy right-handed participants (18 in Experiment 4 - discovery sample: mean age = 26.12, SD = ±3.11 years, 10 females; and 18 in Experiment 5 - replicating sample: mean age = 24.37, SD = ±1.75 years, 9 females). All subjects had normal (self-reported) or corrected to normal vision and were right-handed according to the Edinburgh Handedness Inventory. No participants took part in more than one experiment. All participants signed the informed consent, and the studies conformed to the standards required by the Declaration of Helsinki and was approved by the Ethics Committee of the University of Torino (prot. n. 122,572). The size of the samples was decided in accordance with previous studies employing the same experimental protocol (Arslanova et al., 2023, 2019; Fanghella et al., 2022; Galigani et al., 2021b; Sel et al., 2020).

2.2.2. Experimental design

Experimental protocol. Experiments 4 and 5 were designed to investigate a modulation induced by hand images with different identities over electrophysiological tactile responses.

To this aim, EEG was recorded while participants were presented with grey-scale pictures of the right-hand dorsum belonging either to the participants (self-hand image) or to someone else (other-hand image). To unveil the modulation of somatosensory activity induced by the visual content, we applied the method proposed by Galvez-Pol et al., 2020 and extensively replicated by several studies (Arslanova et al., 2023, 2019; Fanghella et al., 2022; Forster and Abad-Hernando, 2024; Galvez-Pol et al., 2018; Sel et al., 2020). By applying this method, participants viewed visual stimuli either alone (visual-only trials) or, in half of the trials, combined with a brief task-irrelevant tactile stimulation (visual-tactile trials). Next, by subtracting brain activity of visual-only trials from visual-tactile trials, thus removing the propagation of visual evoked potentials on the scalp, we can observe how visual contents modulate somatosensory processing, over and above carry-over effects

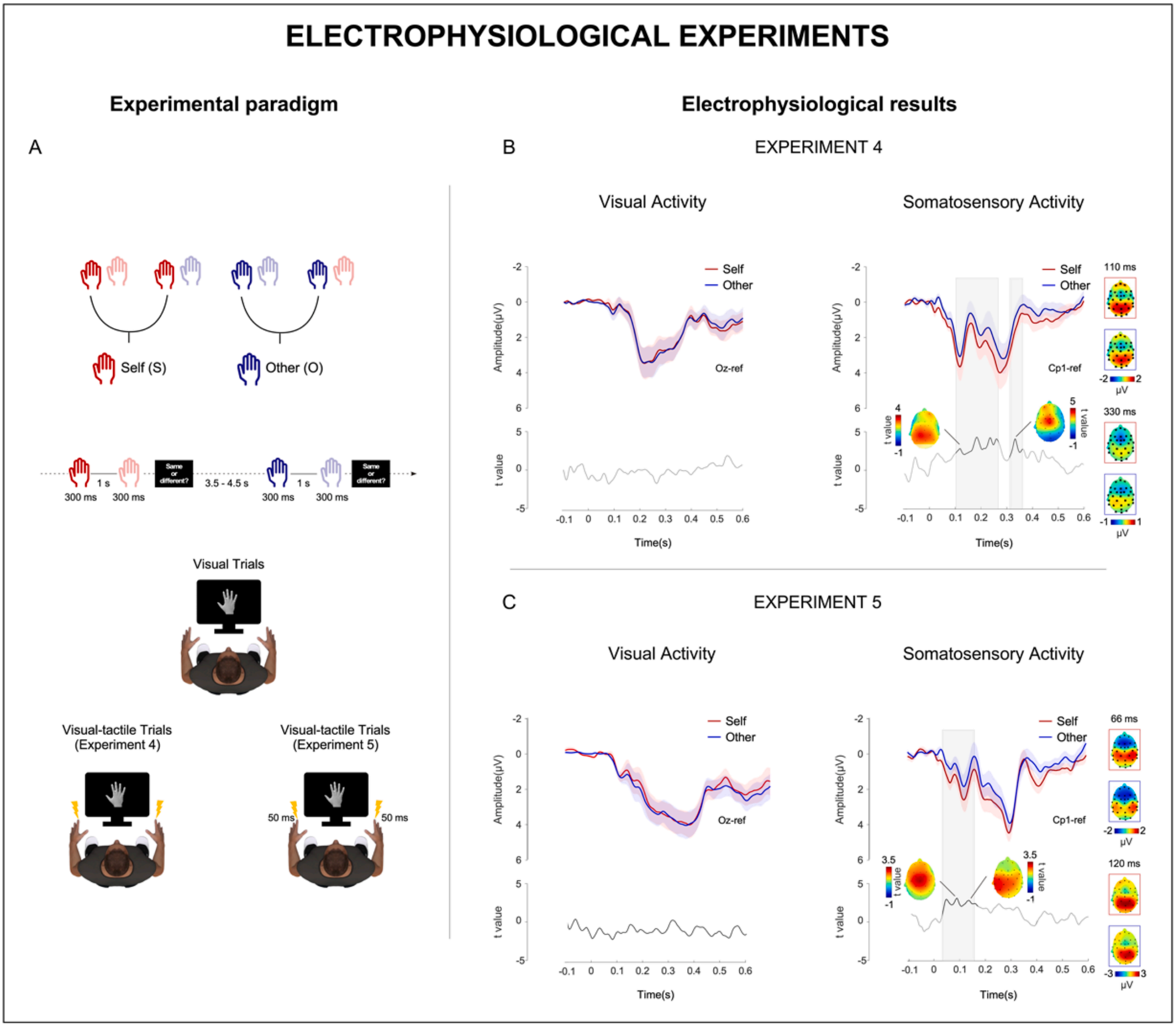

Fig. 2. A) Experimental paradigm. Visual stimuli (lasting 300 ms) were presented in pairs of subsequentially displayed (1 s interstimulus interval) hand images representing either the self-hand or the other-hand. The offset of the second stimulus was followed by an inter-trial interval that was randomly jittered between 3.5 and 4.5 s. In half of the trials tactile stimulation to both index fingers was concomitantly administered (Experiment 4) or 50 ms delayed (Experiment 5).

(Arslanova et al., 2023, 2019; Fanghella et al., 2022; Forster and Abad-Hernando, 2024; Galvez-Pol et al., 2018; Galvez-Pol et al., 2018; Sel et al., 2020).

In Experiment 4, as in Experiment 1, visual and tactile stimuli were simultaneously delivered in visuo-tactile trials (Fig.2A). Experiment 5, as Experiment 2, was designed to align the cortical processing of visual and tactile stimuli in visual-tactile trials (Fig.2A). Thus, we replicated the very same experimental design of Experiment 4 but introducing a 50 ms delay between the visual and tactile stimuli, with tactile stimulation occurring later.

Visual (self-hand and other-hand pictures) and tactile (electrical) stimuli were identical to those administered in Experiments 1, 2, and 3. Crucially, tactile stimuli were delivered to both hands to assess whether the visual modulation of tactile responses would have been lateralized (i.e., contralateral to the seen hand) or more general and bilateral, which would reflect a broader effect on somatosensory processing. The stimulation intensity was adjusted according to the individual sensory threshold (estimated using the methods of limits (Gescheider, 1997). The mean (± SD) bilateral threshold stimulus intensity was 3.18 ± 0.82 mA in Experiment 4, 3.58 ± 0.91 mA in Experiment 5. During the experiments, the stimulation intensity was set slightly above the threshold (stimulation intensity = threshold intensity*2), so that participants always perceived the tactile stimulation, which was never painful (see e.g., Fossataro et al., 2023; Ronga et al., 2021; Rossi Sebastiano et al., 2022).

Orthogonal match-to-sample protocol. To ensure that participants maintained constant attention to the visual stimuli (i.e., hand images) through the EEG recording, participants were engaged in an orthogonal match-to-sample protocol that we recently employed in a previous study (Galigani et al., 2021b). According to this protocol, visual stimuli consisted in pairs of sequentially displayed hand images. In each pair, visual stimuli, lasting 300 ms, could be either identical or different and were delivered at a constant 1-*sec* inter-stimulus interval. The inter-trial interval between each pair was randomly jittered between 3.5 and 4.5 s, in a way that participants could not anticipate stimulus occurrence. We presented four different pairs: Self-Self (with both stimuli depicting the self-hand); Other-Other (with both stimuli depicting the other-hand); Self-Other (with the first stimulus representing the self-hand and the second stimulus the other-hand); Other-Self (with the first stimulus representing the other-hand and the second stimulus the self-hand). The match-to sample task consisted of deciding whether the second stimulus was identical or different as compared to the first one, and vocal reaction times to the second stimulus were recorded (saying ‘s’ for same and ‘d’ for different). Orthogonal behavioral responses to the second stimulus, which represent a replication of a previous study (Galigani et al., 2021b), are presented in Supplementary materials. What is relevant for the purpose of this study is the analysis of the EEG responses to the first stimulus of the pair, which can be either the self-hand or the other-hand image. This analysis allows to directly discriminate the neural activity in response to self-hand and other-hand images (see EEG data analysis details below), without the occurrence of additional mechanisms, such as the mismatch detection elicited by the second stimulus. In our previous study (Galigani et al., 2021b), we demonstrated that mismatch detection responses are elicited only when the hand identity change involves the self-hand (in a scenario including the self-hand as that of the present work) and not when involves only strangers’ hands (in a scenario not including the self-hand).

Overall, participants performed a total of 640 trials: this equals 320 trials (160 visual-only and 160 visual-tactile) for each condition (Self and Other).

2.2.3. Electroencephalographic recording

EEG were recorded using 32 Ag- AgCl electrodes mounted on the scalp according to the International 10–20 system and referenced to the nose. Electrode impedances were kept below 5 kΩ. To track ocular movements and eye blinks, the electrooculogram was recorded placing two surface electrodes, one placed over the right lower eyelid and the other placed lateral to the outer canthus of the right eye. Continuous EEG was recorded using a *HandyEEG-SystemPLUS Evolution* amplifier (Micromed) and a 1024 Hz sampling rate.

EEG data were pre-processed using Letswave v.6 (www.nocions.org/letswave/). The EEG signal was band-pass filtered (0.05–30 Hz) using a fast Butterworth filter (4th order) and then segmented into epochs lasting from 100 ms before to 1000 ms after the tactile stimulus, and then baseline corrected to the first 100 ms before the stimulus. Artifacts due to eye blinks and eye movements were subtracted using a validated method based on an Independent Component Analysis (ICA- Jung et al., 2000). Blinks were found to be the most frequent cause of rejection. Finally, grand averages were computed separately for each condition and for visual-only and visual-tactile trials.

2.2.4. Data analysis

Since the EEG analysis, as explained above (see section *Orthogonal match-to-sample task*), focused on the first stimulus of the pair, we firstly merged the conditions with the same first stimulus (Self-Self with Self-Other, and Other-Other with Other-Self) and we obtained two conditions: Self and Other. Each condition was composed by 320 trials (160 visual-only and 160 visual-tactile trials). Then, we analyzed both visual and somatosensory activity. Visual activity was elicited by visual-only trials, while somatosensory evoked potentials were obtained by subtracting activity elicited by visual trials from activity elicited by visual-tactile trials.

To compare the evoked responses in the different conditions, we performed two point-by-point *t*-tests (one for visual and one for somatosensory activity) corrected with 1000 permutations between Self and Other conditions. We opted for a time-resolved, point-by-point analysis to quantify potential effects across all time points and electrodes, without restricting the analysis to predefined latencies or components. This choice was guided by our hypothesis that somatosensory modulation related to self-hand processing could impact distinct stages of processing: either early responses reflecting primary somatosensory activity and/or later components associated with secondary or multisensory areas. Therefore, we employed a method that is sensitive to the full spatiotemporal dynamics of the EEG signal, allowing us to detect both early and late effects that may otherwise be overlooked. This method represents a statistical approach common in EEG studies (Bruno et al., 2020; Galigani et al., 2021a; Harris et al., 2018; Novembre et al., 2018; Ronga et al., 2021; Sarasso et al., 2022) directed to highlight significantly different event-related potentials time windows among different experimental conditions, that might be unnoticed if analyses were restricted to predefined regions or time windows. By examining the entire spatiotemporal EEG signal, we can objectively identify where and when experimental conditions diverge, rather than relying on subjective selections that risk introducing false positives or missing subtle effects. Indeed, point-by-point analysis allow to point out significant amplitude differences and possible latency shifts at the same time, since both are captured by divergent responses distributions across time. Since this statistical approach is based on one comparison per time point, this raises the problem of multiple comparisons. To face this issue, a cluster-based non-parametric test statistic was performed (1000 random permutations; alpha level=0.05; percentile of mean cluster sum set as threshold=95) (Maris and Oostenveld, 2007). Permutation testing is based on temporal adjacency and yields the identification of significantly different time point clusters between conditions for each channel. More specifically, we employed permutation testing as implemented in Letswave6 toolbox (Nocions, Louvain, Belgium) for Matlab (Mathworks, Natick, MA), based *On maris* and Oostenveld (2007). The toolbox compares the EEG signal of different conditions by means of a t-value. Then, all samples whose t-value is greater than threshold are clustered in connected sets on the basis of temporal adjacency (i.e., time-windows) and, after computing the sum of the t-values within each time-window, cluster level statistics are calculated by selecting the largest of the time-windows statistics, i.e., this method selects the portion of the curves in which the difference between conditions is significant for the greatest number of adjacent points. Then, the statistical test is performed by calculating a p-value under the permutation distribution and comparing it with the critical alpha level. The permutation distribution is obtained by randomly permuting the subject-specific average waveforms in the different conditions within every subject for 1000 times and, after the test statistic is calculated for each random partition, a histogram of the random partitions' test statistics is created. From the test statistic that was actually observed, and the histogram obtained from random partitions' test statistics, the proportion of random partitions that results in a larger test statistic than the observed one is calculated. This proportion is the p-value under the permutation distribution. If the p-value is smaller than the critical alpha level, then the datasets in the experimental conditions are considered as significantly different.

3. Results

3.1. Experiment 1, 2, and 3: psychophysical discovery, replicating, and control sample

In Experiment 1, we found that participants were significantly faster to react to tactile stimulation when they concomitantly saw the self-hand as compared to the other-hand image ($t_{16} = -2.193$; $p = 0.035$; median ± SD, Self: 469.11 ± 80.86, Other: 476.95 ± 82.13), thus revealing that the implicit coding of the self-hand identity facilitated tactile performance (Fig.1B). In Experiment 2, we replicated the modulation of reaction times driven by the identity of the visually presented hand image, with a significantly facilitated performance when responding to tactile stimulation (presented 50 ms after the visual stimulus) when they saw the self-hand as compared to the other-hand image ($t_{16} = -3.297$; $p = 0.003$; median±SD, Self: 434.51 ± 51.19, Other: 443.94 ± 58.56) (Fig.1C). In Experiment 3, the results (Fig.1D) confirmed the self-specific modulation of reaction times, with a significantly facilitated responses to tactile stimuli coupled with the self- than familiar-hand image ($t_{16} = -3.960$; $p = 0.001$; median±SD, Self: 320.51 ± 55.16, Other: 337.36 ± 65.14).

Importantly, the one-way ANOVA performed to compare the self-advantage indexes (values below zero indicate faster RTs in the self than other condition) in the three experiments revealed a significant effect of Experiment ($F_{2,48}=3.450$; $p = 0.040$). Post-hoc test showed that the self-related enhancement of tactile processing was greater in Experiment 2 and 3, when the cortical arrival of visual and tactile stimuli was aligned due to the 50 ms delay, with the respect to Experiment 1, when the stimuli delivery was simultaneous (Exp 1 vs Exp2: $p = 0.044$; mean±SD, Exp 1: 0.990 ± 0.191, Exp 2: 0.969 ± 0.036; Exp 1 vs 3: $p = 0.018$; mean±SD, 0.990 ± 0.191, Exp 3: 0.966 ± 0.030) (Fig.1E). Furthermore, the presence of this RTs facilitation was not affected by the familiarity of the hand used as other stimuli (Exp 2 vs 3: $p = 0.712$; mean ±SD, Exp 2: 0.969 ± 0.036, Exp 3: 0.966 ± 0.030) (Fig.1E).

B-C-d-E) Behavioral results. The panels depict Reaction Times (ms) in the different conditions, and, in the boxplots, the whiskers represent the minimum and the maximum value, dots depict individual values, the limits of the box represent the first and the third quartile, and the median is depicted by the line that divides the box into two parts. The asterisk represents significant differences. Panel B represents the results of Experiment 1, Panel C the results of Experiment 2, while Panel D the results of the Experiment 3 designed to control familiarity effects. Panel E depicts the comparison between Experiments 1, 2, and 3.

3.2. Experiment 4 and 5: electrophysiological discovery and replicating sample

In visual evoked potentials (VEPs) analysis of Experiment 4 (Fig.2B– left panel), we did not observe any significant difference between visual responses to self- and other-hand images (t_{17} always <1.701). By contrast, when we analyze somatosensory activity, generated by subtracting visual-only from visual-tactile trials (Fig.2B– right panel), we found that somatosensory cortex activity was greater when the self-hand (as compared to the other-hand) image was displayed, despite tactile stimulation was always the same across conditions. In particular, the enhancement of somatosensory processing driven by the self-hand image was present around the somatosensory cortices of both hemispheres but was maximal at Cp1 from 106 ms to 280 ms ($t_{17}=4.392$; $p = 0.0006$), and from 314 ms to 373 ms ($t_{17}=4.174$; $p = 0.0008$) after the stimulus onset.

As in Experiment 4, in Experiment 5 the presentation of the self-hand did not elicit significantly different visual activity as compared to the other-hand (t_{17} always <2.532) (Fig.2C– left panel), but elicited higher somatosensory activity (maximal at Cp1, 32–74 ms, $t_{17} = 3.631$; $p = 0.003$; maximal at Cz, 87–156 ms, $t_{17} = 3.561$; $p = 0.004$; maximal at C3, 205–242 ms, $t_{17} = 3.162$; $p = 0.007$) (Fig.2C– right panel). Importantly, the latency of this effect encompasses not only the late latencies already found in Experiment 4, but also early latencies including the P45 component.

B-C) Electrophysiological results. The panels represent visual activity (left panels) and visually-driven somatosensory activity (generated by subtracting visual-only from visual-tactile trials - right panels) in response to self- and other-hand images. Waveforms are plotted for electrodes located over visual (Oz) and somatosensory (CP1) cortex, referenced to the nose (i.e., CP1-ref and Oz-ref). The minus sign ("-") denotes this standard referencing convention (electrode minus reference). By convention, negative deflections appear toward the top of the plot and positive toward the bottom. Note that after the subtraction, the somatosensory potentials exhibit the classical components (N20, P50, N80, P100 and N140). We performed a point-by-point analysis that allowed to quantify possible effects at all time points and electrodes. Time windows with significantly different ERPs are highlighted by grey bars. T values appear below waveforms; scalp distribution of effects is shown on topographical t maps. CSD maps for peak latencies within the significant range are also displayed. Shaded areas represent ERP sem.

4. Discussion

In the present study, we investigated the contribution of the somatosensory system in coding visual self-identity, based on the idea that the visual processing of the own body may involve the recruitment of somatosensory cortices beyond visual areas. Indeed, the only body whose visual image is constantly associated with a somatosensory representation is the own body. In five experiments, we recorded either psychophysical (Experiment 1: discovery sample; Experiment 2: replicating sample; Experiment 3: control sample) or electrophysiological (Experiment 4: discovery sample; Experiment 5: replicating sample) responses of the somatosensory system while presenting hand images of both participant's hand (self-hand) and someone else's hand (other-hand). In all experiments, we observed significant modulations of somatosensory processing as a function of bodily identity, with faster RTs (Experiment 1, 2, and 3) and higher SEPs amplitude (Experiment 4 and 5) when probing the somatosensory system during the presentation of the self-hand as compared to the other-hand image. Taken together, these findings support the view that the somatosensory system plays a crucial role in coding visual self-identity, at least when it is conveyed by body effectors.

As for the psychophysical findings, in both discovery (Experiment 1) and replicating sample (Experiment 2), we found that participants were significantly faster to react to tactile stimulation when they saw the self-than the other-hand image, thus revealing that the visual presentation of the self-hand image facilitated tactile performance. Interestingly, as revealed by the control sample (Experiment 3), this self-specific somatosensory effect cannot be attributed merely to the greater familiarity of the self-hand image. Indeed, evidence from Experiment 3, where we compared RTs to tactile stimuli coupled with the self- and the familiar-hand (i.e. the partner's hand) image, showed facilitated behavioral responses to the former as compared to the latter stimulus, thus strongly indicating that the familiarity of visual features does not explain the results observed in Experiments 1 and 2. These behavioral results are fully in line with previous evidence showing that the observation of the body enhances spatial tactile acuity on the seen body-part (Beck et al., 2015; Kennett et al., 2001; Taylor-Clarke et al., 2002), also adding the self-specific effect as an important new finding.

In Experiment 4 and 5, we investigated the neural basis of this somatosensory coding of visual self-identity reflected in the modulation of tactile performance. To capture the full temporal dynamics of somatosensory processing, we employed a time-resolved, point-by-point EEG analysis corrected for multiple comparisons, which allowed us to test our hypothesis across different latencies and components. By leveraging an EEG method designed and extensively validated to unveil the role of somatosensory system during a visual task (Arslanova et al., 2023, 2019; Fanghella et al., 2022; Forster and Abad-Hernando, 2024; Galvez-Pol et al., 2020, 2018a; Sel et al., 2020), we confirmed that the somatosensory system constitutes a crucial hub in the neural coding of the visual self-identity. Indeed, we found that visual activity did not vary as a function of bodily identity (when seeing self- and other-hand images), whereas somatosensory activity did vary. To explain the (negative) finding from the visual system, one possible explanation, also capitalizing on previous evidence (Chan et al., 2004; Downing and Peelen, 2011; Hodzic et al., 2009), could be related to the fact that visual areas may primarily encode shape details about visually perceived bodies but are less involved in identity-related function (but see for instance Myers and Sowden, 2008; Okamoto et al., 2021; Urgesi et al., 2006 for opposite evidence). Alternatively, the visual parameters of the experimental stimuli used in our study (degraded visibility using grey-scale pictures) may have modulated identity-related visual activity (Martini et al., 2015; Matsumuro et al., 2022; Okumura et al., 2020; Pamplona et al., 2024), by reducing the role of visual areas and favoring sensorimotor ones. As for the (positive) finding from the somatosensory system, the results of Experiment 4 reveal a significant enhancement of somatosensory responses to the tactile probe driven by the observation of the self-hand as compared to the other-hand image. Although we cannot quantify this enhancement with respect to a tactile-only condition, since we did not include this condition in our experimental design, the differences observed in the amplitude of tactile responses allow us to describe the differential modulation of somatosensory activity induced by the visual content of bodily identity. Interestingly, we observed stronger modulations over left-hemisphere electrodes (contralateral to the seen right hand). However, when we formally tested this effect by introducing hemisphere as a factor in the analysis, no statistically significant interaction emerged, thus suggesting a bilateral recruitment of somatosensory cortices in self-hand processing. Furthermore, the latency of the observed self-specific effects is modulated by the timing of visual and tactile stimuli delivery in visual-tactile trials, which was simultaneous in Experiment 4 and delayed in Experiment 5. In Experiment 4 we observed significant modulations in the somatosensory domain at around 100 ms, and this middle-late latency may be more consistent with the involvement of the secondary somatosensory cortex and multisensory regions rather than the primary somatosensory area (Allison et al., 1991; Bernasconi et al., 2018; Valeriani et al., 2001). Yet, since evidence from both monkeys and humans indicates that tactile stimuli reach the cortex approximately 50 ms faster than visual ones (Musacchia and Schroeder, 2009; Trojaborg and Petersen, 1979), the latency of the effect may be related to the different velocity of conduction of visual and tactile stimuli. Indeed, presenting tactile probes at the onset of hand images may have led to a situation where, by the time visual information reached the somatosensory area, the processing of the tactile stimulus had already propagated to secondary somatosensory cortices and multisensory areas. Accordingly, in Experiment 5 where tactile stimulus was delivered 50 ms visual stimulus onset, somatosensory cortex activity showed an earlier modulation, encompassing the P45 component, revealing a direct involvement of the primary somatosensory area. We again observed significant differences at middle-late latency suggesting a multi-stage coding of bodily self-identity, which likely involves primary somatosensory cortex at an early stage, but also secondary somatosensory cortex and multisensory areas at a later stage. This stronger enhancement of visually induced somatosensory processing driven by the synchronized cortical arrival of visual and tactile inputs mirrors the results of our psychophysical experiments. Consistently, presenting tactile stimuli 50 ms after visual ones (Experiments 2 and 3) also led to greater behavioral facilitation compared to the simultaneous presentation (Experiment 1).

Taken together, these novel findings challenge the long-held view that portrays the somatosensory system as a purely sensory structure of low-level feature detectors. Instead, our results suggest that somatosensory system dynamics instantiate high-level sensorimotor models of an organism (Bolognini et al., 2014; Brecht, 2017; El Rassi et al., 2024; Miller et al., 2018), such as body identity. But which is the mechanism that allows somatosensory areas to code visual self-identity? We propose that such function of the somatosensory system is the result of associative learning mechanisms, so that through daily multisensory experience individuals form associations between visual and tactile signals originating from the own body (Bahrick, 2013; De Klerk et al., 2021; Keysers and Gazzola, 2014). This visual-tactile contingency is unique and exclusive for our body, thus representing a possible prerequisite for establishing self-awareness (Bretas et al., 2021). Through this associative learning, neurons of the somatosensory cortex fire in response to a visual stimulus (in our case the self-hand image) that has been previously associated with a tactile stimulus (Zhou and Fuster, 2000). In particular, the early somatosensory effect found in Experiment 2 at around 40 ms may be explained by cross-modal mechanisms that can be supported by the activity of multisensory neurons in primary somatosensory cortex, mediated by direct, abundant visual-somatosensory connections or by thalamo-cortical feed-forward interactions (Beck et al., 2015; Bieler et al., 2017; Ghazanfar and Schroeder, 2006; Pisoni et al., 2018). Previous results in different domains support the role of visual-tactile associations in the context of bodily self-identity. The extended literature on the Rubber Hand Illusion (e.g., Botvinick and Cohen, 1998) shows that induced manipulation of visual-tactile inputs causes changes of the body representation, whereby the rubber hand is experienced as part of the own body, and the real hand is visually perceived as more similar to the dummy hand (Longo et al., 2009). In a complementary way, enhancing visual-tactile contingency promotes self-recognition ability. Indeed, rhesus monkeys, that are not able to pass the mirror test, learned to recognize themselves in a mirror after a training of visual-somatosensory associations (Chang et al., 2015). Furthermore, in the neuropsychological context, it has been shown that fiber-tracts disconnection between fronto-parietal regions, involved in the sensorimotor representation of the body, and occipito-temporal regions, involved in the visual representation of the body, are strongly associated to a severe impairment of the ability to visually recognize the own hand (Candini et al., 2022; Errante et al., 2022).

Overall, the present findings show that, regardless of the presentation modality (visual, in our case), the brain processes the bodily self-identity based on its intrinsic somatosensory content, since the association between visual and somatosensory input only pertains to the own body. Together with a theoretical advancement in understanding neural mechanisms of self-awareness, these findings may open the way for future investigations of neurological (Errante et al., 2022; Moro et al., 2023; Rossi Sebastiano et al., 2022) and psychiatric (Ambrosecchia et al., 2023; De Meulemeester et al., 2021; Ferri et al., 2012b; Keizer et al., 2014) self-image disturbances.

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CRediT authorship contribution statement

Mattia Galigani: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marcella Romeo:** Writing – review & editing, Investigation. **Nicoletta Scanferlato:** Writing – review & editing, Investigation. **Massimiliano Valeriani:** Writing – review & editing, Methodology, Conceptualization. **Bettina Forster:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Francesca Garbarini:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

None.

Data and code availability statement

De-identified data will be deposited at Zenodo. It will be publicly available as of the date of publication.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2025.121405.

Data availability

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References

Allison, T., McCarthy, G., Wood, C.C., Jones, S.J., 1991. Potentials evoked In Human and monkey cerebral cortex by stimulation of the median nerve. Brain 114, 2465–2503. https://doi.org/10.1093/brain/114.6.2465.

Ambrosecchia, M., Ardizzi, M., Russo, E.C., Ditaranto, F., Speciale, M., Vinai, P., Todisco, P., Maestro, S., Gallese, V., 2023. Bodily self-recognition and body size overestimation in restrictive anorexia nervosa: implicit and explicit mechanisms. Front. Psychol. 14, 1197319. https://doi.org/10.3389/FPSYG.2023.1197319.

Apps, M.A.J., Tsakiris, M., 2014. The free-energy self: a predictive coding account of self-recognition. Neurosci. Biobehav. Rev. https://doi.org/10.1016/j.neubiorev.2013.01.029.

Arslanova, I., Galvez-Pol, A., Calvo-Merino, B., Forster, B., 2019. Searching for bodies: ERP evidence for independent somatosensory processing during visual search for body-related information. Neuroimage 195, 140–149. https://doi.org/10.1016/j.neuroimage.2019.03.037.

Arslanova, I., Meletaki, V., Calvo-Merino, B., Forster, B., 2023. Perception of facial expressions involves emotion specific somatosensory cortex activations which are shaped by alexithymia. Cortex. https://doi.org/10.1016/J.CORTEX.2023.06.010.

Bahrick, L.E., 2013. Body perception: intersensory origins of self and other perception in newborns. Curr. Biol. 23, R1039–R1041. https://doi.org/10.1016/j.cub.2013.10.060.

Beck, B., Bertini, C., Haggard, P., Làdavas, E., 2015. Dissociable routes for personal and interpersonal visual enhancement of touch. Cortex 73, 289–297. https://doi.org/10.1016/j.cortex.2015.09.008.

Bernasconi, F., Noel, J.P., Park, H.D., Faivre, N., Seeck, M., Spinelli, L., Schaller, K., Blanke, O., Serino, A., 2018. Audio-tactile and peripersonal space processing around the trunk in human parietal and temporal cortex: an intracranial EEG study. Cereb. Cortex 28, 3385–3397. https://doi.org/10.1093/cercor/bhy156.

Bieler, M., Sieben, K., Schildt, S., Röder, B., Hanganu-Opatz, I.L., 2017. Visual-tactile processing in primary somatosensory cortex emerges before cross-modal experience. Synapse 71. https://doi.org/10.1002/SYN.21958.

Bolognini, N., Rossetti, A., Fusaro, M., Vallar, G., Miniussi, C., 2014. Sharing social touch in the primary somatosensory cortex. Curr. Biol. 24, 1513–1517. https://doi.org/10.1016/j.cub.2014.05.025.

Bonzano, L., Biggio, M., Brigadoi, S., Pedullà, L., Pagliai, M., Iester, C., Brichetto, G., Cutini, S., Bove, M., 2023. Don't plan, just do it: cognitive and sensorimotor contributions to manual dexterity. Neuroimage 280. https://doi.org/10.1016/J.NEUROIMAGE.2023.120348.

Botvinick, M., Cohen, J., 1998. Rubber hands "feel" touch that eyes see. Nature 391, 756. https://doi.org/10.1038/35784.

Brecht, M., 2017. The body model theory of somatosensory cortex. Neuron. https://doi.org/10.1016/j.neuron.2017.05.018.

Bretas, R., Taoka, M., Hihara, S., Cleeremans, A., Iriki, A., 2021. Neural evidence of mirror self-recognition in the secondary somatosensory cortex of macaque: observations from a single-cell recording experiment and implications for consciousness. Brain Sci. 11, 1–12. https://doi.org/10.3390/brainsci11020157.

Bruno, V., Ronga, I., Fossataro, C., Galigani, M., Sacco, K., Garbarini, F., 2020. Long-term limb immobilization modulates inhibition-related electrophysiological brain activity. Neuroimage 218. https://doi.org/10.1016/j.neuroimage.2020.116911.

Candini, M., Fossataro, C., Pia, L., Vezzadini, G., Gindri, P., Galigani, M., Berti, A., Frassinetti, F., Garbarini, F., 2022. Bodily self-recognition in patients with pathological embodiment. J. Neurosci. Res. 100, 1987–2003. https://doi.org/10.1002/jnr.25109.

Chan, A.W.Y., Peelen, M.V., Downing, P.E., 2004. The effect of viewpoint on body representation in the extrastriate body area. Neuroreport 15, 2407–2410. https://doi.org/10.1097/00001756-200410250-00021.

Chang, L., Fang, Q., Zhang, S., Poo, M.M., Gong, N., 2015. Mirror-induced self-directed behaviors in rhesus monkeys after visual-somatosensory training. Curr. Biol. 25, 212–217. https://doi.org/10.1016/J.CUB.2014.11.016.

De Klerk, C.C.J.M., Filippetti, M.L., Rigato, S., 2021. The development of body representations: an associative learning account. Proc. Biol. Sci. 288. https://doi.org/10.1098/RSPB.2021.0070.

De Meulemeester, C., Lowyck, B., Panagiotopoulou, E., Fotopoulou, A., Luyten, P., 2021. Self–other distinction and borderline personality disorder features: evidence for egocentric and altercentric bias in a self–other facial morphing task. Pers. Disord 12, 377. https://doi.org/10.1037/PER0000415.

Devue, C., Brédart, S., 2011. The neural correlates of visual self-recognition. Conscious. Cogn. 20, 40–51. https://doi.org/10.1016/j.concog.2010.09.007.

Downing, P.E., Peelen, M.V., 2011. The role of occipitotemporal body-selective regions in person perception. Cogn. Neurosci. 2, 186–203. https://doi.org/10.1080/17588928.2011.582945.

El Rassi, Y., Handjaras, G., Perciballi, C., Leo, A., Papale, P., Corbetta, M., Ricciardi, E., Betti, V., 2024. A visual representation of the hand in the resting somatomotor regions of the human brain. Sci. Rep. 14, 18298. https://doi.org/10.1038/S41598-024-69248-Z.

Errante, A., Rossi Sebastiano, A., Ziccarelli, S., Bruno, V., Rozzi, S., Pia, L., Fogassi, L., Garbarini, F., 2022. Structural connectivity associated with the sense of body ownership: a diffusion tensor imaging and disconnection study in patients with bodily awareness disorder. Brain Commun. 4, fcac032. https://doi.org/10.1093/braincomms/fcac032.

Fanghella, M., Gaigg, S.B., Candidi, M., Forster, B., Calvo-Merino, B., 2022. Somatosensory evoked potentials reveal reduced embodiment of emotions in autism. J. Neurosci. 42, 2298–2312. https://doi.org/10.1523/JNEUROSCI.0706-21.2022.

Ferri, F., Frassinetti, F., Ardizzi, M., Costantini, M., Gallese, V., 2012a. A sensorimotor network for the bodily self.

Ferri, F., Frassinetti, F., Mastrangelo, F., Salone, A., Ferro, F.M., Gallese, V., 2012b. Bodily self and schizophrenia: the loss of implicit self-body knowledge. Conscious. Cogn. 21, 1365–1374. https://doi.org/10.1016/J.CONCOG.2012.05.001.

Forster, B., Abad-Hernando, S., 2024. In your skin? Somatosensory cortex is purposely recruited to situate but not simulate vicarious touch. Neuroimage 289, 120561. https://doi.org/10.1016/J.NEUROIMAGE.2024.120561.

Fossataro, C., Galigani, M., Rossi Sebastiano, A., Bruno, V., Ronga, I., Garbarini, F., 2023. Spatial proximity to others induces plastic changes in the neural representation of the peripersonal space. iScience 26. https://doi.org/10.1016/j.isci.2022.105879.

Fossataro, C., Tieri, G., Grollero, D., Bruno, V., Garbarini, F., 2020. Hand blink reflex in virtual reality: the role of vision and proprioception in modulating defensive responses. Eur. J. Neurosci. 51, 937–951. https://doi.org/10.1111/EJN.14601.

Galigani, M., Ronga, I., Bruno, V., Castellani, N., Rossi Sebastiano, A., Fossataro, C., Garbarini, F., 2021a. Face-like configurations modulate electrophysiological mismatch responses. Eur. J. Neurosci. 53, 1869–1884. https://doi.org/10.1111/ejn.15088.

Galigani, M., Ronga, I., Fossataro, C., Bruno, V., Castellani, N., Rossi Sebastiano, A., Forster, B., Garbarini, F., 2021b. Like the back of my hand: visual ERPs reveal a specific change detection mechanism for the bodily self. Cortex 134, 239–252. https://doi.org/10.1016/j.cortex.2020.10.014.

Galvez-Pol, A., Calvo-Merino, B., Capilla, A., Forster, B., 2018a. Persistent recruitment of somatosensory cortex during active maintenance of hand images in working memory. Neuroimage 174, 153–163. https://doi.org/10.1016/J.NEUROIMAGE.2018.03.024.

Galvez-Pol, A., Calvo-Merino, B., Forster, B., 2020. Revealing the body in the brain: an ERP method to examine sensorimotor activity during visual perception of body-related information. Cortex. https://doi.org/10.1016/j.cortex.2020.01.017.

Galvez-Pol, A., Forster, B., Calvo-Merino, B., 2018b. Modulation of motor cortex activity in a visual working memory task of hand images. Neuropsychologia 117, 75–83. https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2018.05.005.

Gentile, G., Petkova, V.I., Ehrsson, H.H., 2011. Integration of visual and tactile signals from the hand in the human brain: an FMRI study. J. Neurophysiol. 105, 910–922. https://doi.org/10.1152/JN.00840.2010.

Gescheider, G.A., 1997. Psychophysics: The fundamentals, [WWW Document]. Lawrence Erlbaum Associates Publishers. https://psycnet.apa.org/record/1997-08651-000. accessed 7.11.23.

Ghazanfar, A., Schroeder, C., 2006. Is neocortex essentially multisensory? Trends. Cogn. Sci. 10, 278–285. https://doi.org/10.1016/j.tics.2006.04.008.

Harris, A.M., Dux, P.E., Mattingley, J.B., 2018. Detecting unattended stimuli depends on the phase of prestimulus neural oscillations. J. Neurosci. 38, 3092–3101. https://doi.org/10.1523/JNEUROSCI.3006-17.2018.

Hodzic, A., Muckli, L., Singer, W., Stirn, A., 2009. Cortical responses to self and others. Hum. Brain Mapp. 30, 951–962. https://doi.org/10.1002/hbm.20558.

Hosel, K., Tremblay, F., 2021. Facilitation of motor evoked potentials in response to a modified 30 hz intermittent theta-burst stimulation protocol in healthy adults. https://doi.org/10.3390/brainsci11121640.

Jung, T.P., Makeig, S., Humphries, C., Lee, T.W., McKeown, M.J., Iragui, V., Sejnowski, T.J., 2000. Removing electroencephalographic artifacts by blind source separation. Psychophysiology 37, 163–178.

Kanwisher, N., Yovel, G., 2006. The fusiform face area: a cortical region specialized for the perception of faces. Philos. Trans. R. Soc. B: Biol. Sci. https://doi.org/10.1098/rstb.2006.1934.

Keizer, A., Smeets, M.A.M., Postma, A., van Elburg, A., Dijkerman, H.C., 2014. Does the experience of ownership over a rubber hand change body size perception in anorexia nervosa patients? Neuropsychologia 62, 26–37. https://doi.org/10.1016/J.NEUROPSYCHOLOGIA.2014.07.003.

Kennett, S., Taylor-Clarke, M., Haggard, P., 2001. Noninformative vision improves the spatial resolution of touch in humans. Curr. Biol. 11, 1188–1191. https://doi.org/10.1016/S0960-9822(01)00327-X.

Keysers, C., Gazzola, V., 2014. Hebbian learning and predictive mirror neurons for actions, sensations and emotions. Philos. Trans. R. Soc. B: Biol. Sci. 369. https://doi.org/10.1098/rstb.2013.0175.

Labruna, L., Fern Andez-Del-Olmo, M., Ivry, R.B., 2011. Comparison of different baseline conditions in evaluating factors that influence motor cortex excitability. https://doi.org/10.1016/j.brs.2010.09.010.

Leo, F., Nataletti, S., Brayda, Luca, 2020. Non-informative vision improves spatial tactile discrimination on the shoulder but does not influence detection sensitivity. Exp. Brain Res. 238, 2865–2875. https://doi.org/10.1007/s00221-020-05944-2.

Limanowski, J., Blankenburg, F., 2016. Integration of visual and proprioceptive limb position information in human posterior parietal, premotor, and extrastriate cortex. J. Neurosci. 36, 2582–2589. https://doi.org/10.1523/JNEUROSCI.3987-15.2016.

Longo, M.R., Schüür, F., Kammers, M.P.M., Tsakiris, M., Haggard, P., 2009. Self awareness and the body image. Acta Psychol. (Amst) 132, 166–172. https://doi.org/10.1016/J.ACTPSY.2009.02.003.

Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. J. Neurosci. Methods 164, 177–190. https://doi.org/10.1016/J.JNEUMETH.2007.03.024.

Martini, M., Kilteni, K., Maselli, A., Sanchez-Vives, M.V., 2015. The body fades away: investigating the effects of transparency of an embodied virtual body on pain threshold and body ownership. Sci. Rep. 1 (5), 1–8. https://doi.org/10.1038/srep13948, 2015 5.

Matsumuro, M., Ma, N., Miura, Y., Shibata, F., Kimura, A., 2022. Top-down effect of body representation on pain perception. PLoS. One 17, e0268618. https://doi.org/10.1371/JOURNAL.PONE.0268618.

Miller, L.E., Montroni, L., Koun, E., Salemme, R., Hayward, V., Farnè, A., 2018. Sensing with tools extends somatosensory processing beyond the body. Nature 7722 (561), 239–242. https://doi.org/10.1038/s41586-018-0460-0, 2018 561.

Moro, V., Pacella, V., Scandola, M., Besharati, S., Rossato, E., Jenkinson, P.M., Fotopoulou, A., 2023. A fronto-insular-parietal network for the sense of body ownership. Cereb. Cortex. 33, 512–522. https://doi.org/10.1093/CERCOR/BHAC081.

Musacchia, G., Schroeder, C.E., 2009. Neuronal mechanisms, response dynamics and perceptual functions of multisensory interactions in auditory cortex. Hear. Res. 258, 72–79. https://doi.org/10.1016/j.heares.2009.06.018.

Myers, A., Sowden, P.T., 2008. Your hand or mine? The extrastriate body area. Neuroimage 42, 1669–1677. https://doi.org/10.1016/j.neuroimage.2008.05.045.

Novembre, G., Pawar, V.M., Bufacchi, R.J., Kilintari, M., Srinivasan, M., Rothwell, J.C., Haggard, P., Iannetti, G.D., 2018. Saliency detection as a reactive process: unexpected sensory events evoke corticomuscular coupling. J. Neurosci. 38, 2385–2397. https://doi.org/10.1523/JNEUROSCI.2474-17.2017.

Okamoto, Y., Kitada, R., Kochiyama, T., Miyahara, M., Naruse, H., Sadato, N., Okazawa, H., Kosaka, H., 2021. Importance of the early visual cortex and the lateral occipito-temporal cortex for the self-hand specific perspective process. Neuroimage: Rep. 1, 100046. https://doi.org/10.1016/J.YNIRP.2021.100046.

Okumura, K., Ora, H., Miyake, Y., 2020. Investigating the hand ownership illusion with two views merged in. Front. Robot. AI. 7, 493927. https://doi.org/10.3389/FROBT.2020.00049/BIBTEX.

Pamplona, G.S.P., Giussani, A., Salzmann, L., Staempfli, P., Schneller, S., Gassert, R., Ionta, S., 2024. Neuro-cognitive effects of degraded visibility on illusory body ownership. Neuroimage 300, 120870. https://doi.org/10.1016/J.NEUROIMAGE.2024.120870.

Pisoni, A., Romero Lauro, L.J., Vergallito, A., Maddaluno, O., Bolognini, N., 2018. Cortical dynamics underpinning the self-other distinction of touch: a TMS-EEG study. Neuroimage 178, 475–484. https://doi.org/10.1016/J.NEUROIMAGE.2018.05.078.

Ronga, I., Galigani, M., Bruno, V., Castellani, N., Rossi Sebastiano, A., Valentini, E., Fossataro, C., Neppi-Modona, M., Garbarini, F., 2021. Seeming confines: electrophysiological evidence of peripersonal space remapping following tool-use in humans. Cortex 144, 133–150. https://doi.org/10.1016/j.cortex.2021.08.004.

Rossi Sebastiano, A., Poles, K., Miller, L.E., Fossataro, C., Milano, E., Gindri, P., Garbarini, F., 2022. Reach planning with someone else's hand. Cortex 153, 207–219. https://doi.org/10.1016/J.CORTEX.2022.05.005.

Rossi Sebastiano, A., Ronga, I., Fossataro, C., Galigani, M., Poles, K., Garbarini, F., 2022. Multisensory-driven facilitation within the peripersonal space is modulated by the expectations about stimulus location on the body. Sci. Rep. 12. https://doi.org/10.1038/s41598-022-21469-w.

Sarasso, P., Neppi-Modona, M., Rosaia, N., Perna, P., Barbieri, P., Fante, E.Del, Ricci, R., Sacco, K., Ronga, I., 2022. Nice and easy: mismatch negativity responses reveal a significant correlation between aesthetic appreciation and perceptual learning. J. Exp. Psychol. Gen. 151, 1433–1445. https://doi.org/10.1037/XGE0001149.

Sel, A., Calvo-Merino, B., Tsakiris, M., Forster, B., 2020. The somatotopy of observed emotions. Cortex 129, 11–22. https://doi.org/10.1016/j.cortex.2020.04.002.

Suddendorf, T., Butler, D.L., 2013. The nature of visual self-recognition. Trends. Cogn. Sci. 17, 121–127. https://doi.org/10.1016/j.tics.2013.01.004.

Taylor-Clarke, M., Kennett, S., Haggard, P., 2002. Vision modulates somatosensory cortical processing. Curr. Biol. 12, 233–236. https://doi.org/10.1016/S0960-9822(01)00681-9.

Trojaborg, W., Petersen, E., 1979. Visual and somatosensory evoked cortical potentials in multiple sclerosis. J. Neurol. Neurosurg. Psychiatry 42, 323–330. https://doi.org/10.1136/jnnp.42.4.323.

Urgesi, C., Candidi, M., Ionta, S., Aglioti, S.M., 2006. Representation of body identity and body actions in extrastriate body area and ventral premotor cortex. Nat. Neurosci 1 (10), 30–31. https://doi.org/10.1038/nn1815, 2007 10.

Valeriani, M., Insola, A., Restuccia, D., Le Pera, D., Mazzone, P., Altibrandi, M.G., Tonali, P., 2001. Source generators of the early somatosensory evoked potentials to tibial nerve stimulation: an intracerebral and scalp recording study. Clin. Neurophysiol. 112, 1999–2006. https://doi.org/10.1016/S1388-2457(01)00670-8.

Vocks, S., Busch, M., Grönemeyer, D., Schulte, D., Herpertz, S., Suchan, B., 2010. Differential neuronal responses to the self and others in the extrastriate body area and the fusiform body area. Cogn. Affect. Behav. Neurosci. https://doi.org/10.3758/CABN.10.3.422.

Zhou, Y.-D., Fuster, J.M., 2000. Visuo-tactile cross-modal associations in cortical somatosensory cells. Proc. Natl. Acad. Sci. 97, 9777–9782. https://doi.org/10.1073/pnas.97.17.9777.