NeuroImage 317 (2025) 121322

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Facial expressions selectively modulate P300 somatosensory evoked-potential, but emotional scenes do not: Electrophysiological evidence for sensorimotor simulation

Sara Costa [a], Arianna Schiano Lomoriello [b], Thomas Quettier [c], Fausto Caruana [d], Pier Francesco Ferrari [a,e], Paola Sessa [b,f,*]

[a] Department of Medicine and Surgery, Neuroscience Unit, University of Parma, Parma, Italy
[b] Department of Developmental Psychology and Socialization, University of Padova, Via Venezia 8 35131, Padova, Italy
[c] Center for Studies and Research in Cognitive Neuroscience, Department of Psychology "Renzo Canestrari", Cesena Campus, Alma Mater Studiorum Università di Bologna, Cesena, Italy
[d] Institute of Neuroscience, National Research Council of Italy (CNR), Parma, Italy
[e] Institut des Sciences Cognitives Marc Jeannerod (CNRS)/Université Claude Bernard Lyon, Bron, France
[f] Padova Neuroscience Center (PNC), University of Padova, Padova, Italy

ARTICLE INFO

Keywords:
Sensorimotor simulation
Emotional images
Emotional facial expressions
Somatosensory evoked potentials
Tactile stimulation

ABSTRACT

The role of the sensorimotor cortices in processing facial expressions remains a topic of debate. While substantial evidence supports their involvement via simulation and mirroring mechanisms, an alternative view argues that sensorimotor activation reflects a general emotional tuning to affective content. To clarify these competing hypotheses, we examined sensorimotor responses to emotional (disgusting) scenes—which evoke affect without requiring simulation—and emotional (disgusted) facial expressions. In one-third of trials, gentle tactile stimulation was applied to the left levator labii superioris muscle at two time points to elicit somatosensory evoked potentials (SEPs). A subtraction approach was used to isolate pure somatosensory activity by removing visual-only responses (VEP) from combined visual-tactile responses (SEP+VEP), with a blank-screen condition as an additional baseline.

We observed a small but significant reduction in P300 SEP amplitude at right central, centro-frontal, and centro-parietal electrodes when tactile stimulation followed disgusted facial expressions compared to disgusting scenes. This effect was independent of subjective ratings of arousal and valence. Importantly, only SEPs following facial expressions differed significantly from those following tactile stimulation alone, suggesting a specific modulation by facial expression processing. Despite the relatively small amplitude of the observed effects, and the somewhat preliminary nature of the results, these findings provide novel evidence that facial expressions engage the sensorimotor system in a specific and privileged manner, consistent with the simulation hypothesis.

1. Introduction

Research increasingly emphasizes the somatosensory cortex's crucial role in processing emotional facial expressions, particularly in the right hemisphere. For instance, Pitcher et al. (2008) found that repetitive transcranial magnetic stimulation (rTMS) to the somatosensory cortex impaired facial expression recognition, while Pourtois et al. (2004) linked damage to this area with difficulties in recognizing fear and anger. Sel et al. (2014) further demonstrated that somatosensory-evoked potentials (SEPs) were significantly amplified when participants viewed emotional faces, especially within the P50 component, highlighting the somatosensory cortex's rapid response. Using the same paradigm, Fanghella et al. (2022) observed reduced somatosensory responses in individuals with autism, a condition known for challenges in recognizing facial expressions (Uljarevic and Hamilton, 2013). These findings have been interpreted in light of the theoretical framework of sensorimotor simulation, suggesting that the sensorimotor system plays a role in an embodied emotional recognition process, where sensory and motor systems contribute to the internal simulation of observed emotions (i.e., simulation hypothesis).

---

* Corresponding author at: Department of Developmental Psychology and Socialization, University of Padova, Via Venezia 8 35121, Padua, Italy.
E-mail address: paola.sessa@unipd.it (P. Sessa).

https://doi.org/10.1016/j.neuroimage.2025.121322
Received 25 March 2025; Received in revised form 28 May 2025; Accepted 10 June 2025

Notwithstanding the empirical support for sensorimotor simulation accounts, an equally compelling alternative interpretation warrants consideration. Damasio et al. (2000) emphasized that the somatosensory cortices map emotional changes through interoception, with links to the anterior insula and amygdala (Critchley et al., 2004; Gu et al., 2013). Straube and Miltner (2011) showed that aversive scenes (e.g., threatening or disturbing) elicited greater activation in the somatosensory cortex compared to neutral images, with attention to emotional aspects further amplifying this response. When combined with the notion that the somatosensory cortex is essential for general emotional awareness (Adolphs et al., 2002; Nummenmaa et al., 2014), these findings suggest that its role in processing emotional facial expressions may reflect a generalized function in responding to the content conveyed by any emotion-driven stimuli (i.e., generalized emotional processing hypothesis), rather than being exclusively tied to simulative mechanisms.

Taken together, the literature examining the involvement of sensorimotor cortices in facial expression processing to support the sensorimotor simulation mechanism highlights a crucial methodological issue, namely, the absence of control conditions using emotion-inducing non-facial stimuli (Kragel and LaBar, 2016; Pitcher et al., 2008; Sel et al., 2014; Arslanova et al., 2023). This critical methodological omission precludes definitive conclusions regarding whether sensorimotor cortical engagement represents a facial expression-specific mechanism or merely reflects a more generalized involvement in processing emotional content across diverse stimulus categories.

To address these objectives, in the present study, tactile stimulation was delivered at two post-stimulus intervals—105 ms and 245 ms—following the presentation of visual stimuli, which comprised disgusted facial expressions as well as low arousing disgust-inducing images (e.g., moldy food). To specifically isolate somatosensory activity, we employed a subtraction approach (Dell'Acqua et al., 2003; Fanghella et al., 2022; Sel et al., 2014). This method involved subtracting the neural responses elicited during visual-only trials (visual evoked potentials, i.e., VEP condition) from those elicited in trials featuring both visual and tactile stimuli (SEP+VEP condition). By implementing this approach, we isolated somatosensory responses while substantially reducing the potential confounding influence of overlapping visual processing effects.

The emotion of disgust was chosen for its consistent elicitation across both facial expressions and images, ensuring comparability between stimulus types. To reduce potential confounding effects associated with social rejection—commonly triggered by direct gaze in expressions of disgust (Mauersberger et al., 2022)—an averted or obstructed gaze was employed. An additional key distinguishing feature of this study was the inclusion of SEP elicited exclusively by tactile stimulation while participants viewed a blank screen. This served as a crucial baseline, enabling precise interpretation of the direction and magnitude of SEP modulation attributable to the concurrent processing of facial expressions and/or visual images.

Tactile stimulation, in different trials, was applied at two different time points following visual stimuli or a black screen. The earlier tactile stimulation condition (105 ms post-stimulus) was chosen based on previous studies (Sel et al., 2014; Fanghella et al., 2022), which demonstrated enhanced P50/P100 SEP components when participants were exposed to emotional facial expressions compared to neutral expressions. This early time window captures the initial sensory processing of emotional stimuli. On the other hand, the later tactile stimulation condition (245 ms post-stimulus) was introduced as an exploratory measure to investigate later processing stages, overlooked in previous research (Arslanova et al., 2023; Fanghella et al., 2022; Sel et al., 2014), offering insights into how our stimuli are processed over time and into their temporal dynamics. Furthermore, by incorporating both early and late stimulation conditions, this study aimed to minimize the risk of missing crucial interactions between visual stimulus categories and tactile stimulation over time. This approach aligns with the findings of Mavratzakis et al. (2016), who showed that peripheral emotional reactivity, like subtle facial changes, is delayed when processing emotional images compared to facial expressions.

Drawing on prior literature, two alternative hypotheses, equally plausible, will be tested based on the current body of knowledge:

Simulation Hypothesis (SH): SEPs elicited by tactile stimulation following facial expressions of disgust will differ significantly from those elicited by tactile stimulation following disgust-inducing images, with only the former SEP response showing a meaningful deviation from the baseline SEP recorded during the blank screen condition. This scenario aligns with the sensorimotor simulation framework, which proposes that the sensorimotor cortex is specifically attuned to simulate observed facial expressions, thereby enhancing their perception and interpretation.

Generalized Emotional Processing Hypothesis (GEPH): SEPs elicited by tactile stimulation following both facial expressions of disgust and disgust-inducing images may or may not significantly differ from each other, but both are expected to deviate from the baseline SEP. This scenario suggests that the sensorimotor cortex engages in a more generalized process of emotional processing or reactivity, responding similarly to various types of emotionally salient stimuli rather than demonstrating a unique specialization for facial expressions. Within this framework, one possibility is that arousal triggered by emotional visual stimuli of both categories serves as a more reliable predictor of SEP modulation.

These contrasting hypotheses provide a framework for interpreting SEP data in the context of emotional and sensorimotor processing, highlighting potential pathways through which the sensorimotor system contributes to the perception of emotionally relevant stimuli.

2. Method

2.1. Participants

Thirty-eight participants (mean age = 23.81; SD age = 1.70) were recruited for this study. Due to excessive signal noise resulting from head movements or ocular artifacts, 4 participants were excluded, resulting in a final sample of 34 right-handed participants (mean age = 23.79; SD age = 1.77), which included 24 females and 10 males.

The sample size and expected effect size were guided by previous studies by Sel et al. (2014) and Fanghella et al. (2022), both of which reported relatively large effects (Cohen's d ranging from approximately 0.6 to 0.8) despite small sample sizes. Drawing on these findings, we opted to nearly double our sample size in order to adopt a more conservative approach and ensure sufficient statistical power (80 %) to detect even medium-sized effects (Cohen's $d \approx 0.5$). Furthermore, to enhance statistical power and improve the reliability of our estimates, we included a large number of trials per experimental condition (200), in line with recent recommendations aimed at increasing measurement reliability in EEG research (Boudewyn et al., 2018).

Participants were recruited through personal networks and university bulletin boards. All participants were native Italian speakers. Exclusion criteria included a diagnosis of neurological or psychiatric disorders, the use of psychoactive medications, and left-handedness. The study was approved by the University of Padova Ethics Committee (protocol number: 348-a), and each participant received €10 compensation upon completion of the experiment. All participants provided written informed consent before taking part in the study, in accordance with the Declaration of Helsinki.

2.2. Materials and experimental design

2.2.1. Stimuli and paradigm

The experimental procedure entailed recording electroencephalographic (EEG) activity as participants viewed stimuli consisting of facial expressions of disgust and disgust-inducing images. In line with well-established methodologies (Fanghella et al., 2022; Sel et al., 2014), a tactile stimulation device was employed, which delivered controlled stimuli via a metal rod with a blunt conical tip applied to the participant's left cheek in the correspondence of the levator labis superioris. This setup enabled the recording of SEPs and allowed for the precise isolation of somatosensory-specific neural activity from electrodes positioned over the right hemi-scalp. The disgusted facial expressions were either sourced from Google Images or explicitly created for the study. Disgust-inducing images were selected from the IAPS and NAPS database (Lang et al., 1997; Marchewka et al., 2014) or Google Images. All images were chosen based on their consistent depiction of core disgust-related content, such as moldy food, bodily fluids, dirt, and decay, in order to ensure thematic coherence. The experiment comprised a total of 2150 trials, distributed across several conditions. Specifically, there were 200 trials each for the following four conditions: (1) facial expression stimuli followed by early tactile stimulation, (2) image stimuli followed by early tactile stimulation, (3) facial expression stimuli followed by late tactile stimulation, and (4) image stimuli followed by late tactile stimulation. Additionally, 400 trials featured facial expressions and 400 trials featured images without any tactile stimulation, forming the Visual-Only Conditions (VOC). To establish a baseline for somatosensory responses in the absence of visual input, blank screen trials were interspersed throughout the experiment approximately every four trials, presented in a randomized order. Half of these blank trials included early tactile stimulation, and the other half included late tactile stimulation. Furthermore, 15 catch trials per condition were included and randomly distributed across the session. These trials featured stimuli depicting different emotions to ensure sustained engagement.

The entire experimental session lasted approximately two hours, including EEG cap preparation and electrode setup.

Each trial followed a consistent temporal structure across all conditions. Trials began with the presentation of a blank screen displaying a central fixation cross for 800 ms. This was followed by the target stimulus presentation, which varied depending on the experimental condition, defined by a combination of three levels of visual stimulation (Blank Screen, i.e. no visual stimulation, Images, Faces) and three levels of tactile stimulation (no stimulation, tactile stimulation within an earlier temporal window and tactile stimulation within a later temporal window). In the *early visual-tactile* (e-VTC) condition, the visual stimulus was displayed for 800 ms, and the tactile stimulus was delivered 105 ms after the onset of the visual stimulus. In the *late visual-tactile* (l-VTC) condition, the visual stimulus was again presented for 800 ms, but the tactile stimulus was administered 245 ms after its onset. In the *tactile-only* (TOC) conditions, no visual stimulus was presented; instead, a tactile stimulus was applied while the screen remained blank. Finally, in the *visual-only* (VOC) condition, the visual stimulus was presented for 800 ms without any accompanying tactile stimulation (Fig. 1). After the main phase of each trial, a blank screen with a fixation cross reappeared for an additional 800 ms. To ensure sustained attention throughout the task, 10 % of the trials included a catch question, requiring participants to classify the valence of the visual stimulus (positive or negative) by pressing one of two keys ("n" for negative or "f" for positive) within a 3000 ms response window. The experimental outline is shown in supplementary materials (Fig. 1), which illustrates the trial sequence and the timing of the fixation cross and catch question.

2.3. Procedure

Two days preceding the experimental session, each participant completed a 20-minute questionnaire designed to validate the stimuli to

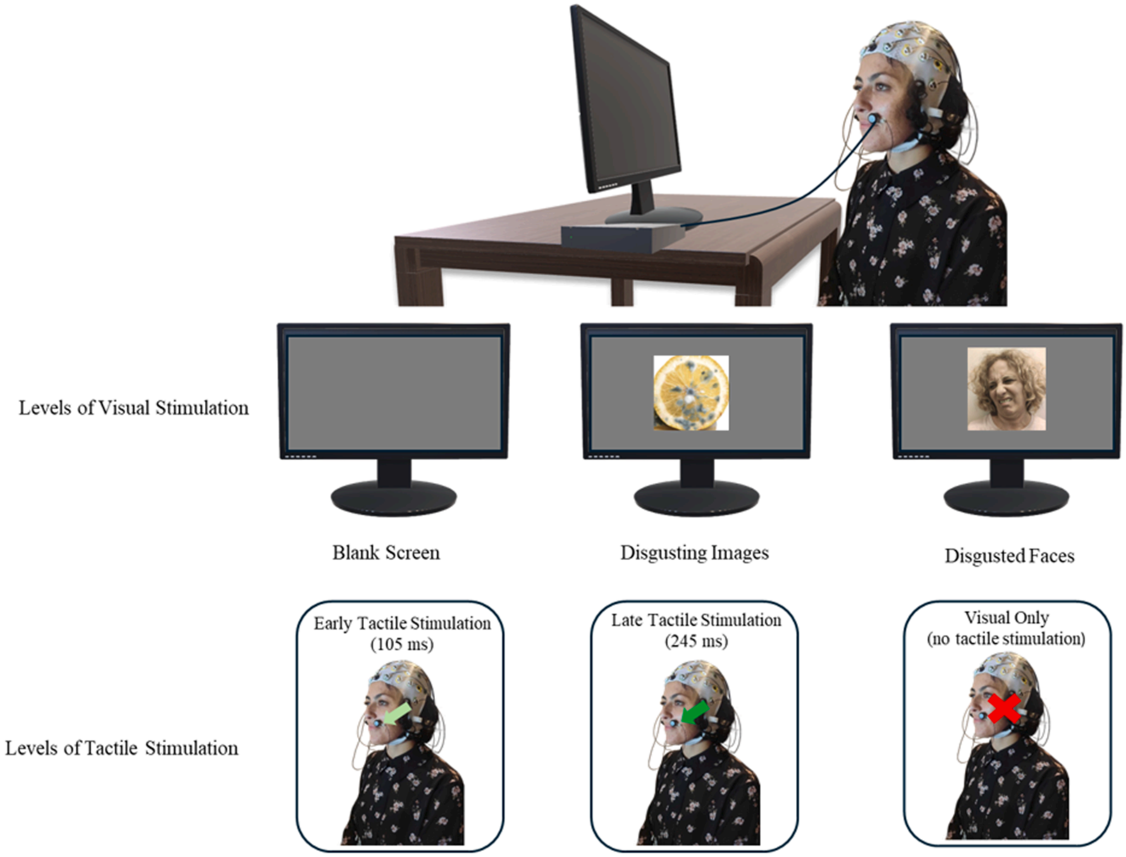

Fig. 1. Experimental setup. Experimental setup for studying the interaction between tactile stimulation and visual perception of disgusting stimuli. (Top) Participants wear an EEG cap and a tactile stimulation device applied to the levator labiis superioris. (Bottom) Three levels of tactile stimulations: Early Tactile Stimulation (105 ms), Late Tactile Stimulation (245 ms), and Visual Only (no tactile stimulation). Three levels of visual stimuli: Blank Screen, Disgusting Images, Disgusted Faces.

be used during EEG recording. The questionnaire required participants to evaluate each stimulus by providing ratings on two 9-point Likert scale items, followed by a final forced-choice question, offering four response options (happiness, neutral, disgust, other) aimed at identifying the emotion most strongly associated with each image. The pictures chosen were classified under the label of “disgust” while catch trials under the labels of “neutral” or “happy”. Facial expression stimuli received an average valence rating of 3.97 (SD = 0.90) and an arousal rating of 5.74 (SD = 0.53), whereas image stimuli were rated lower in valence (*M* = 2.79, SD = 0.82) and higher in arousal (*M* = 6.62, SD = 0.91). Regarding emotional categorization, the average percentage of responses indicating disgust for the target (disgust-related) images and faces across subjects was 68.25 % for facial expression stimuli and 77.21 % for image stimuli. The full dataset including arousal and valence ratings per subject and per stimulus, as well as the disgust response data, along with all related materials (e.g., stimuli and code) is available on OSF: https://osf.io/x8rpg.

Participants were seated in a quiet, isolated room designed to optimize EEG data acquisition. Each participant was fitted with an EEG cap with 64 active electrodes, and a tactile stimulator was positioned on the left cheek. A monitor and keyboard were placed directly in front of them to perform the task. Prior to the main experiment, participants completed a practice phase consisting of 10 trials to ensure familiarity with the procedure.

2.4. Data processing and statistical analysis

2.4.1. EEG preprocessing

EEG data were acquired through a 64-channel system configured according to the extended 10/20 layout, with signals referenced to the participant’s left earlobe and recorded using an elastic Acti-Cap. Data were initially sampled at 1000 Hz, with electrode impedances maintained below 10 kΩ. Continuous recordings were subsequently downsampled to 256 Hz and band-pass filtered between 0.1 Hz (high-pass) and 40 Hz (low-pass). Horizontal and vertical electro-oculograms (HEOG and VEOG) were recorded to monitor ocular artifacts. HEOG was captured bipolarly via electrodes placed laterally at the outer canthi of both eyes, while VEOG was recorded bipolarly from FP1 and an electrode positioned below the right eye. Data were segmented into epochs spanning −100 ms to 500 ms, time-locked to the onset of the tactile stimulation (across both VOC, e-VTC, L-VTC, and e-TOC, L-TOC). Baseline correction was applied to each epoch using the mean activity during the 100 ms pre-tactile stimulus interval. Independent Component Analysis (ICA) was performed to identify and remove ocular components. Following ICA correction, trials containing significant artifacts—defined as horizontal eye movements, eye blinks, or other noise exceeding ±30 μV, ±50 μV, and ±80 μV, respectively—were automatically excluded from further analysis. The average percentage of trials rejected due to artifacts was calculated per stimulus condition and found to be comparable across conditions: 20.8 % for facial expression (visual-only), 22.5 % for facial expression (followed by early stimulation), 20.6 % for facial expression (followed by late stimulation), 20.8 % for image (visual-only), 19.8 % for image (followed by early stimulation), 20.8 % for image (followed by late stimulation), and 19.1 % for tactile-only.

Average ERPs were computed across participants for each condition (VOC, e-VTC, L-VTC, e-TOC, L-TOC) and for each type of stimulus (facial expressions and images). In the VOC condition, the averaged ERPs reflected only visual-evoked potentials (VEPs), whereas the e-VTC and L-VTC conditions included both VEPs and somatosensory-evoked potentials (SEPs). To isolate somatosensory-specific activity, we applied a subtraction procedure in which the ERP waveforms from the visual-only condition (VOC) were subtracted from the corresponding waveforms of the visual-tactile conditions (e-VTC and L-VTC). Importantly, this subtraction was performed separately for each stimulus category: the ERP from VOC-face trials was subtracted from e-VTC-face and L-VTC-face trials, and the ERP from VOC-image trials was subtracted from e-VTC-image and L-VTC-image trials. This approach allowed us to control for category-specific low-level visual properties, ensuring that the resulting waveforms more accurately reflected somatosensory-specific processing. Importantly, although no actual tactile stimulation occurred in the VOC condition, these trials were nonetheless epoch-locked to the temporal onset points corresponding to when tactile stimulation would have been delivered, thereby ensuring temporal alignment for the subsequent subtraction and comparison procedure. In 50 % of trials, the epoch was time-locked such that 0 ms corresponded to 105 ms post-visual stimulus onset, while in the remaining 50 %, 0 ms corresponded to 245 ms post-visual stimulus onset. The resulting difference waveforms, reflecting somatosensory-evoked activity, were then analyzed and compared across the stimulus conditions (images and facial expressions).

2.4.2. Statistical analysis

Statistical analyses followed a data-driven approach, applying a *t*-test against zero to assess when the TOC SEPs significantly deviated from zero, allowing for the identification of temporal windows across the scalp where the SEP measure during the observation of the blank screen (TOC), differed significantly from zero. This step was crucial for determining when the stimulation was reliably detectable at the central electrode level, providing a solid foundation for selecting appropriate temporal windows for further analysis. Analyses were conducted using Brainstorm Software (Tadel et al., 2011). Temporal windows with significant deviations from zero were identified, with a minimum duration of 50 ms. A Bonferroni correction was applied for multiple comparisons, and the significance level was set at $\alpha = 0.05$. Electrodes of interest were located over central scalp regions (centro-parietal: CP1–6; central: C1–6; fronto-central: FC1–6), corresponding to the sensorimotor system. As shown in Fig. 2, a specific activation window in the sensorimotor system was identified between 280 and 360 ms after tactile stimulation, which became the focus of subsequent analyses.

In the TOC trials, electrophysiological data were acquired at two distinct intervals following the onset of the blank screen: an early interval at 105 ms and a late interval at 245 ms. However, our analysis exclusively targeted the late interval (245 ms; L-TOC), informed by two principal considerations. Firstly, as illustrated in Fig. 3, the SEP recorded during the early interval (e-TOC) may have been subject to contamination by visual potentials elicited by the offset of the fixation cross during the inter-trial interval. Secondly, as previously established, our analytical focus centered specifically on the time window spanning 280–360 ms, during which the waveforms corresponding to the two experimental conditions overlap.

We performed a linear mixed-effects model, including fixed effects for the interaction between experimental condition, hemisphere, and time window, as well as random intercepts and random slopes for experimental condition, hemisphere, and time window by subjects ID. This model enabled the examination of SEP amplitude variations under repeated measures across subjects, particularly assessing Early (105 ms) and Late (245 ms) post-stimulus tactile response windows. All analyses were performed using the software R (4.4.0) using the *lmer* function from the lme4 package (Bates, Mächler, Bolker, and Walker, 2015).

3. Results

3.1. Comparison between disgusted facial expressions SEP and disgusting images SEP

To evaluate the significance of the fixed effects and their interactions, we conducted a Type III Analysis of Variance using Satterthwaite’s approximation for degrees of freedom, implemented via the anova() function from the *car* package in R (Fox, 2019). The analysis revealed a significant three-way interaction among condition, hemisphere, and time window [$F(1, 197.95) = 7.23$, $p = 0.008$; marginal $R^2 =$ 0.02, and conditional $R^2 = 0.51$]. To further investigate the significant interaction, post-hoc comparisons were performed, with corrections for

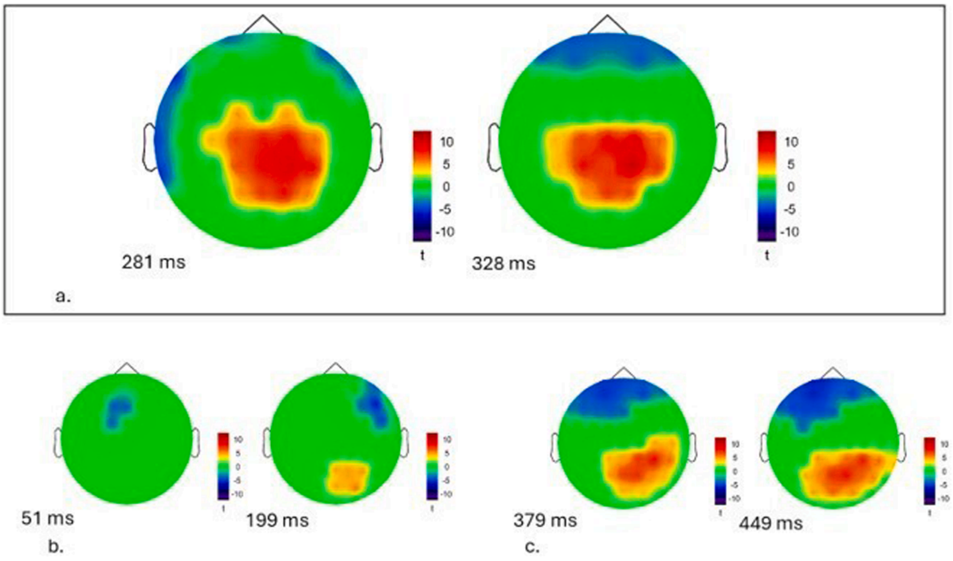

Fig. 2. Sensorimotor Activity Window. Heat map showing brain regions with significant activity during a specific time window, identified through a data-driven statistical approach. (a) The heat map illustrates brain activity during the 280–360 ms time window, displayed on two head models. Notably, the central region, corresponding anatomically to the sensorimotor cortex, shows heightened activity during this period. (b) The lower panel on the right depicts brain activity before the 280 ms time window, while (c) the lower panel on the left shows activity after 360 ms. In both these time windows, the central areas remain inactive.

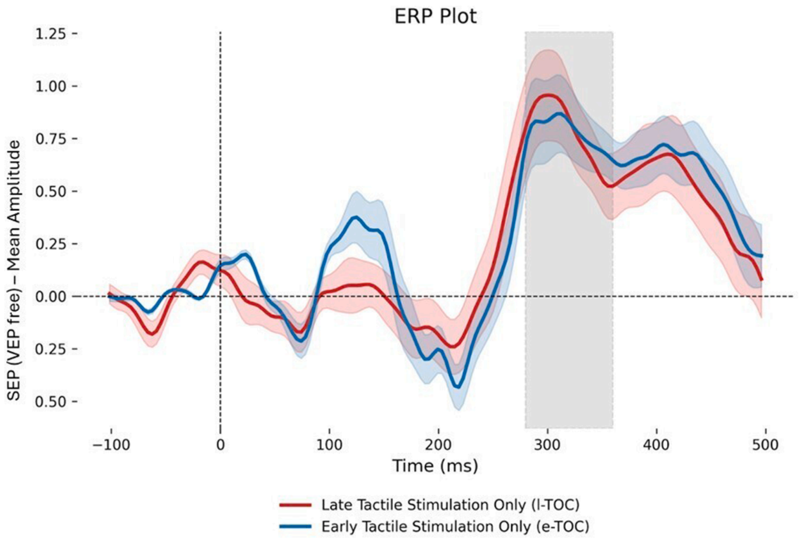

Fig. 3. ERP waveforms of e-TOC and l-TOC. Time windows of interest for the analysis, highlighting the overlap between the two SEPs in the 260–380 ms range. The figure illustrates the average SEPs recorded from sensorimotor electrodes over the right hemiscalps, with zero ms corresponding to the onset of tactile stimulation. Notably, early e-TOC activity may reflect visual potentials elicited by the disappearance of the fixation cross. The shaded time window represents the interval selected for statistical analyses, identified through a data-driven approach and consistent across both conditions.

multiple comparisons applied using the False Discovery Rate (FDR) method (Benjamini and Hochberg, 1995). The post-hoc analyses identified two statistically significant effects, as illustrated in Fig. 4. First, during the early time window (105 ms), a significant difference in SEP amplitude was observed between Facial Expressions and Images in the right hemisphere [t(157) = –2.45, $p = 0.015$] with a small but reliable effect size ($d = –0.19$, 95 % CI [–0.34, –0.04]*;* Fig. 5). Second, within Facial Expressions, a significant difference in SEP amplitude was found between the early time window (105 ms) and the late time window (245 ms), lateralized to the right hemisphere t(161) = –2.50, $p = 0.013$. The effect size was small $d = –0.20$, 95 % CI [–0.35, –0.04].

Collectively, these findings indicate that tactile stimulation of the face results in reduced right-hemisphere sensorimotor activity when immediately preceded by the observation of facial expressions, relative to emotionally salient images. This relative reduction is not observed when the temporal interval between the visual and tactile stimuli is increased. Notably, this effect appears to be localized within the right hemisphere.

3.2. Contrast between disgusted facial expression and disgusting images and blank screen SEP

To gain deeper insight into the previously described findings, we compared SEP amplitudes elicited by facial expression and image stimuli to those elicited by trials using tactile-only control (TOC) stimuli. Specifically, we examined whether observing facial expressions and image influenced SEP responses compared to tactile stimulation presented without preceding visual input. A linear mixed-effects model was

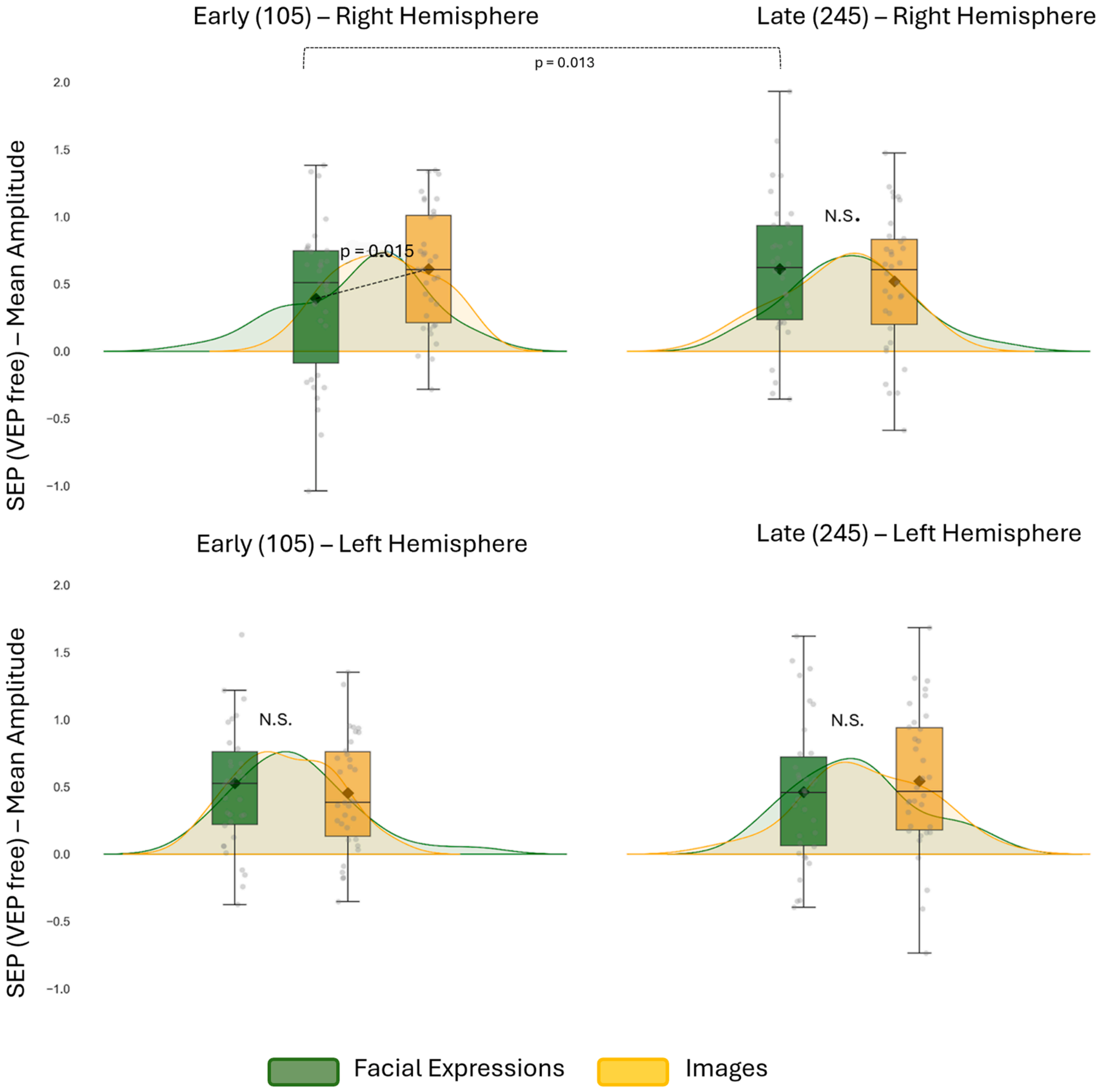

Fig. 4. Condition and Time-Specific SEP Amplitude Differences Across Hemisphere. Comparison of SEP (VEP-Free) mean amplitude responses across conditions and hemispheres. Density plots illustrate the distribution of mean amplitudes for the facial expression (green) and image (orange) conditions in the Early (105 ms) and Late (245 ms) time windows, for both left and right hemispheres. The black diamonds represent the mean values, and the boxplots within the violins indicate the interquartile range (IQR) and median of the data. A significant difference was observed between the conditions in the Early (105 ms) time window in the right hemisphere ($p = 0.015$), as indicated by the connecting line and statistical annotation. Within Facial Expressions, a significant difference in SEP amplitude was found between the early time window (105 ms) and the late time window (245 ms), lateralized to the right hemisphere ($p = 0.013$). No significant differences were observed in other conditions or time windows.

utilized for this comparison, with experimental conditions (Facial Expressions vs. Image vs. TOC) included as fixed effects. Participant ID was included as a random effect to account for individual differences in SEP responses. Since our analysis specifically focused on early tactile stimulation (i.e., at 105 ms) in the right hemisphere—the time window and hemisphere previously identified as showing significant differences—neither the time window nor the hemisphere were included as additional fixed effects in this model. Type III Analysis of Variance Table with Satterthwaite's method showed a significant main effect of condition [$F(2, 66) = 6.99$, $p = 0.002$, marginal $R^2 = 0.08$, conditional $R^2 = 0.43$], indicating that neural responses differed across the three conditions. Post-hoc pairwise comparisons with FDR-adjusted p-values revealed that neural activation was significantly lower in the facial expression condition compared to TOC [$t(66) = -3.72$, $p = 0.001$; $d = 0.46$, 95 % CI [0.20, 0.71]], and compared to the image condition [$t(66) = -2.15$, $p = 0.05$; $d = 0.27$, 95 % CI [0.02, 0.51]]. No significant difference emerged between image and TOC conditions [$t(66) = -1.57$, $p = 0.12$]. These results confirm that facial expressions uniquely modulate somatosensory processing. The results are shown in Fig. 6.

3.3. *Valence and arousal*

To determine whether the observed differences in SEP amplitudes between the two stimulus categories were influenced by variations in individual arousal and valence levels, we performed a Pearson correlation analysis. These analyses were conducted to examine whether individual differences in the subjective perception of emotional intensity (i.e., arousal and valence ratings) between faces and images could account for the observed modulation in SEP amplitudes across conditions. No significant correlations were found between the change in SEP amplitude (Δ_amplitude) between facial expressions and images in the early time window and the difference in arousal scores (Δ_arousal; $R = -0.13$, $p = 0.473$) and valence scores (Δ_valence; $R = -0.11$, $p = 0.53$). The absence of significant correlations suggests that SEP differences

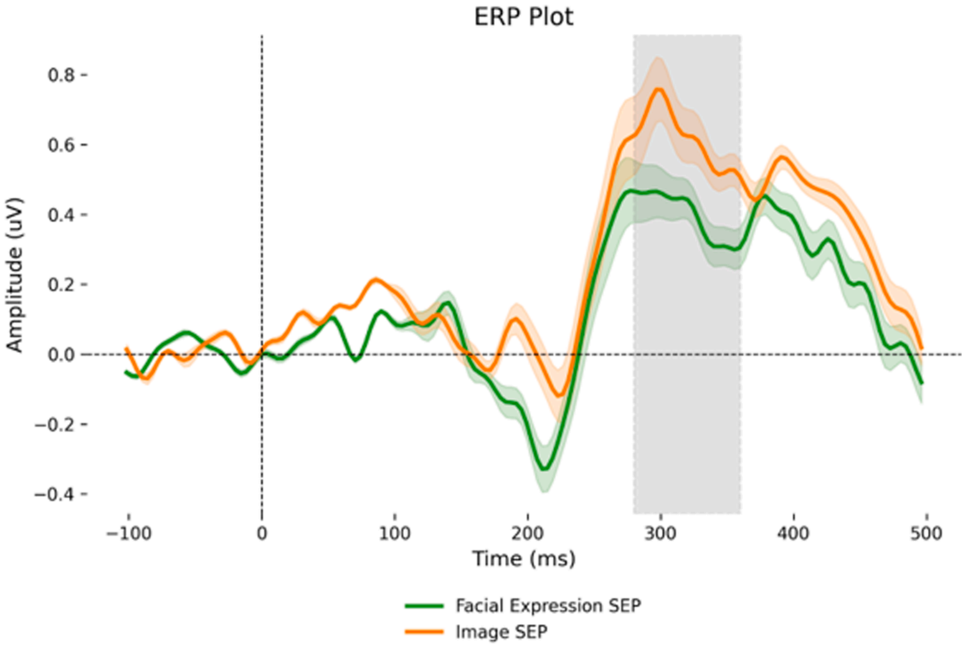

Fig. 5. Facial Expression vs Image ERP in the right hemisphere (105 ms Time Window). ERP waveforms comparing facial expression (green) and image (orange) conditions. The plot shows the amplitude (μV) of the SEP signal over time (ms) in the right electrodes, with shaded areas representing the standard error of the mean. The shaded time window represents the interval selected for statistical analyses. The zero point on the x-axis marks tactile stimulus onset, and the dashed lines indicate the baseline and time reference.

between facial expressions and images are not explained by general affective intensity, but are more likely attributable to differences in stimulus category or processing mechanisms (see Supplementary Materials Fig. 2 for the corresponding plot).

3.4. Correlation with interpersonal reactivity index (IRI) score

For exploratory purposes, we examined the relationship between self-reported empathy, as measured by the Interpersonal Reactivity Index (IRI; Davis, 1983), and the amplitude differences in SEPs between Facial Expressions and L-TOC, and Images and L-TOC. These analyses aimed to explore whether changes in SEP amplitude, particularly in response to facial expressions, could be linked to individual differences in empathy. Specifically, we performed Pearson correlation analyses on all subscales of the IRI, which includes Perspective Taking (PT), Empathic Concern (EC), Personal Distress (PD), and Fantasy (FS). To control multiple comparisons, p-values were adjusted using the false discovery rate (FDR; Benjamini and Hochberg, 1995). Among these subscales, the only significant correlation was found between the PT (Perspective Taking) subscale and the SEP amplitude difference in the Facial Expression vs. TOC condition ($r = -0, 42, p = 0.0415$) at the right hemisphere electrodes (Fig. 7). This correlation suggests that higher scores on the PT subscale were associated with a more significant reduction in SEP amplitude in response to the tactile stimulation when concurrently processing facial expressions. Furthermore, although the Images vs TOC condition showed a comparable trend, it did not reveal a significant correlation with the PT subscale ($r = -0.32, p = 0.206$). These findings suggest that empathy, particularly concerning its cognitive component (i.e., PT), is linked with somatosensory resources allocated to emotional stimuli, especially facial expressions of disgust.

4. Discussion

The modulation of the somatosensory cortex by emotional facial expressions has been well-documented, yet the underlying mechanisms remain debated. On the one hand, the *sensorimotor simulation theory* suggests that observing facial expressions activates shared neural circuits involved in both their perception and execution (Adolphs et al., 2002; Fanghella et al., 2022; Pitcher et al., 2008; Sel et al., 2014). However, to convincingly argue that the observed activation reflects a genuine simulative process, it is crucial first to exclude the possibility that such activation merely represents a general emotional reaction to facial expressions (Damasio et al., 2000; Kropf et al., 2018; Straube and Miltner, 2011). In other words, it must be shown that sensory regions are engaged not simply due to a response to the emotional content conveyed by the facial expressions. To address the competing hypotheses and gain deeper insight into the underlying mechanisms, we conducted an experiment that included both disgusted facial expressions and disgusting images as stimuli, examining somatosensory involvement through SEPs. Our findings revealed that when tactile stimulation was delivered 105 ms after the visual stimulus, the P300 SEP component amplitude was significantly, but modestly, reduced for disgusted facial expressions followed by tactile stimulation compared to disgusting images followed by tactile stimulation. This effect was observed in the centro-parietal, central, and centro-frontal electrodes, and was restricted to the right hemisphere. Notably, the absence of significant correlations between SEP amplitude differences and arousal or valence ratings reinforces the interpretation that the observed sensorimotor modulation is not merely a byproduct of generalized emotional reactivity driven by interoceptive mechanisms (Gu et al., 2013; Straube and Miltner, 2011). Instead, it points toward a more selective mechanism, potentially linked to the specific processing demands of facial expressions and their social-communicative relevance. Moreover, our findings revealed a stimulus-specific attenuation of the P300 somatosensory evoked potential (SEP) in response to disgusted facial expressions compared to blank-screen controls. Notably, this attenuation exhibited a robust inverse correlation with Perspective Taking scores on the Interpersonal Reactivity Index, implicating cognitive empathy as a potential modulator of somatosensory cortical engagement during emotional face processing.

While previous studies (Fanghella, et al., 2022; Sel, et al. 2014) have reported modulation in the early and mid-latency components of SEPs, such as P50 and P100—highlighting a specific role of the somatosensory cortex—our findings revealed modulation exclusively in the later P300

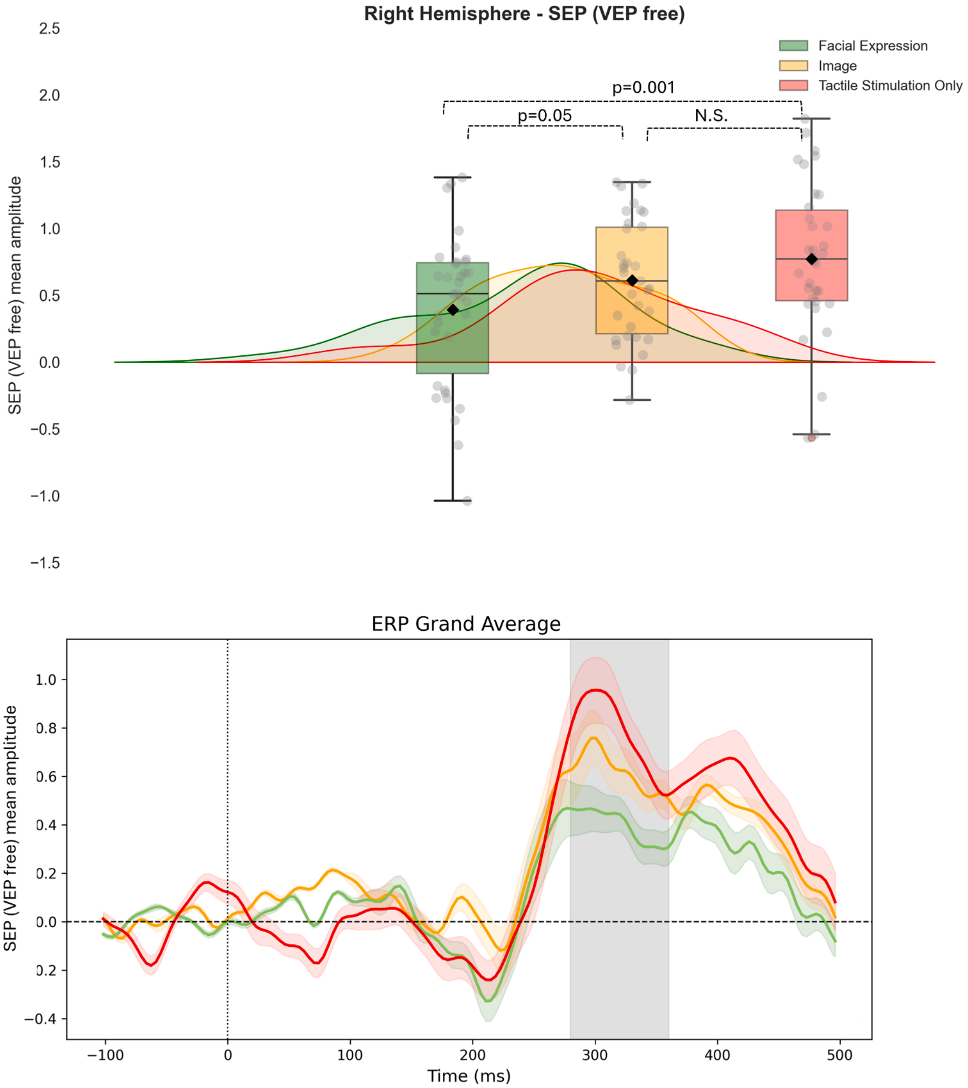

Fig. 6. Comparative SEP Amplitude and ERP Waveform Analysis in the Right Hemisphere Across Facial Expression, Image, and TOC Conditions (105 ms Time Window). (Top) SEP (VEP-Free) mean amplitude comparisons between facial expression (green), images (orange) and tactile stimulation only (TOC) (red) conditions for right hemispheres when the tactile stimulation was delivered in the early time window (105 ms). Density plots show the distribution of amplitudes, with boxplots highlighting the median, interquartile range (IQR), and outliers. The black diamonds represent the mean values for each condition. (Bottom) ERP waveforms comparing facial expression (green), image (orange) and tactile stimulation only (red) conditions in the right hemisphere when the tactile stimulation was delivered in the early time window (105 ms). The plot shows the amplitude (μV) of the SEP signal over time (ms), with shaded areas representing the standard error of the mean. The zero point on the x-axis marks tactile stimulus onset, and the dashed lines indicate the baseline and time reference.

component. This later modulation suggests a more widespread activation of the sensorimotor network, extending beyond the somatosensory cortex to include motor, premotor, and inferior parietal regions (Avanzini et al., 2016). Unlike the early components, which specifically reflect activity in the somatosensory cortex, the later components reflect indeed more diffuse activation involving motor-related areas (Avanzini et al., 2016). The involvement of motor regions in processing emotional facial expressions is well-documented. Recent work by Del Vecchio et al. (2024) specifically identified the Rolandic Operculum as a central hub for motor simulation of facial expressions. Using stereoEEG (sEEG), they demonstrated that this region, situated across the central sulcus between sensory and motor areas responsible for mouth and facial movements, becomes active between 300 ms and 500 ms after the presentation of facial expressions. This timing closely matches the modulation observed in our study and aligns with the well-established phenomenon of facial mimicry—subtle facial movements in observers that mirror the expressions they perceive within 400–500 ms, which are considered a behavioral correlate of sensorimotor simulation (Birch-Hurst et al., 2022; Wood et al., 2016). By integrating the selective response to facial expressions with the coherent timing of motor resonance mechanisms, our findings provide further support for the sensorimotor simulation framework. In line with this framework, studies on both humans and, more extensively, non-human primates have demonstrated the existence of neuroanatomical connections between the secondary somatosensory cortex (SII), premotor regions, and the amygdala (Grezes, et al.; 2014; Rizzo, et al. 2018; Toschi, et al., 2017). This evidence further underscores the complexity of the sensorimotor network, supporting the idea that sensory, motor, and affective components integrate in a highly interconnected system.

The P300 SEP response was significantly reduced when observing facial expressions compared to the P300 SEP response recorded during the blank screen condition, which served as our baseline. This suggests that facial expressions engage the sensorimotor cortex, creating a competitive demand for neural resources that reduces the cortex's ability to process tactile stimuli—its primary function. In contrast, no significant changes in P300 SEP amplitude were observed between the

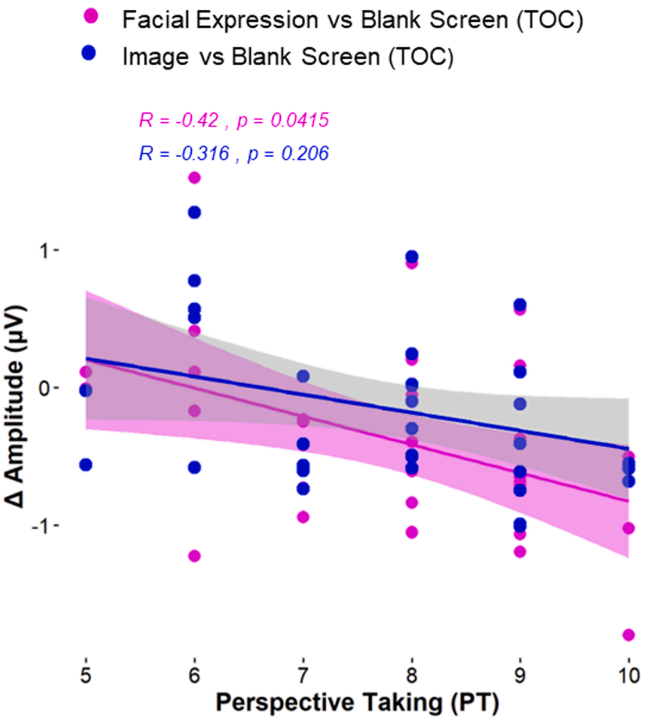

Fig. 7. Empathy and SEP amplitude correlation. Pearson correlations between the Δ amplitude difference for facial expression vs tactile only and image vs tactile only conditions.

blank screen and the observation of disgusting images, indicating that this category of stimuli does not interfere with tactile processing in the same way. The concept of resource sharing aligns with evidence that the activity of the sensorimotor cortex can be modulated by contextual challenges or dispositional factors (Burton et al., 1999). In this vein, recent studies by Al et al. (2020) suggest that internal bodily attention, measured through Heartbeat Event-Related Potentials (HERPs) registered in the central, centro-frontal and centro-parietal electrode, negatively correlates with both early and late SEP components evoked by peripheral tactile stimulation. This indicates that individuals with higher interoceptive awareness, or those who place greater emphasis on internal bodily signals, show reduced sensorimotor resource allocation (as reflected in lower SEP amplitudes) when processing external tactile stimuli. Additionally, the study found that during the systole phase—a critical physiological moment requiring the prioritization of internal resources—the P300 SEP component was reduced, along with a decreased ability to detect tactile stimuli. Taken together, these findings support that sensorimotor processing may operate in a hierarchical or competitive manner, where tactile processing is deprioritized when the sensorimotor regions are engaged in other, or more adaptive, functions. In our context, facial expressions may activate sensorimotor cortices, potentially through a simulative mechanism. This mechanism could allocate a significant portion of sensorimotor resources, directing them in a way that affects the cortical processing of tactile stimuli.

It is important to note that the differential SEP response observed between images and faces cannot be explained solely by arousal and valence, as these factors do not correlate with the differences in SEP amplitude between images and faces.

Research has shown that the activation of sensorimotor regions in response to emotional facial expressions and social stimuli is linked to intersubjectivity mechanisms, which involve both the similarity between others' internal states and our own (Gallese, 2007; Goldman and Sripada, 2005) and the prediction of others' internal states and behaviors (Bonini et al., 2022). In addition, several studies have highlighted a connection between individual empathy traits and sensorimotor processes (Genzer et al., 2022; Woodruff et al., 2011). Consistent with this, our study found a negative correlation between the Perspective Taking (PT) scale of the IRI questionnaire and the amplitude of SEPs elicited by facial expressions, suggesting that individuals with higher PT scores show greater sensorimotor engagement during the processing of emotional facial expressions. As highlighted before, this reduction in activity indicates increased sensorimotor engagement during the processing of emotional facial expressions, with diminished cortical activation reflecting a redistribution of resources between competing mechanisms, such as tactile processing and the simulation of facial expressions. The link between sensorimotor simulation mechanisms and cognitive empathy is documented. Avenanti et al. (2009) demonstrated that higher PT scores were associated with reduced motor-evoked potentials (MEPs) amplitudes, suggesting that individuals with greater cognitive empathy are more tuned to enhanced corticospinal inhibition—an adaptive protective response to pain—even when observing others in pain. Similarly, Cheng et al. (2008) found that somatosensory cortex activity was suppressed while observing others in painful situations, with the degree of suppression correlating with PT scores. Supporting this, Martínez-Jauand et al. (2012) reported a relationship between PT scores and the amplitudes of early SEP components (P50, N70) elicited by touch and pain empathy tasks.

Together, these findings suggest that cognitive empathy, particularly the ability to adopt others' perspectives, could play a critical role in modulating sensorimotor and somatosensory responses during the observation of others' emotional states.

4.1. Limitations and future directions

The present study has some limitations that should be considered when interpreting the results. First, it is important to highlight the small to modest size of the observed effects. While the findings are highly theoretically relevant, the overall magnitude of the effects was limited, although significant. As this is, to our knowledge, the first study to directly contrast these theoretical frameworks using this specific paradigm, the current results should be considered preliminary and need further replication.

A second limitation concerns the emotional content of the visual stimuli, which focused exclusively on disgust. Disgust was intentionally selected because it reliably elicits strong emotional responses in both facial and non-facial formats. Nonetheless, this narrow focus does not allow us to generalize these findings to other emotions and future research should include other discrete emotions (e.g., fear, happiness, anger). Of note, a recent fMRI study found that sensorimotor cortices are involved in a variety of facial expressions (Krautheim et al., 2020).

Finally, the absence of neutral (non-emotional) faces and scenes makes it difficult to determine whether the observed effects are attributable to emotional valence, facial specificity, or broader categorical differences in visual input. While including neutral conditions would have extended the duration of the experiment and increased the risk of participant fatigue, we opted for a more focused and statistically efficient design. Future studies should incorporate neutral faces and scenes to allow for a clearer dissociation of emotional and categorical influences on sensorimotor responses.

In addition to these methodological considerations, future studies may also benefit from examining the current findings through the lens of predictive coding theories. In the context of emotional processing, predictive coding frameworks propose that cortical responses are attenuated when incoming sensory input matches internal expectations (Keysers et al., 2024). From this perspective, the reduced SEP amplitude following facial expressions might reflect the fulfillment of sensorimotor predictions—particularly when tactile stimulation is delivered to a muscle congruent with the observed expression (e.g., the levator labii during the perception of disgusted faces). This interpretation suggests that attenuation may arise not solely from simulation-based mirroring, but also from top-down predictive mechanisms. To test this hypothesis, future studies could directly compare congruent and incongruent tactile stimulation (e.g., stimulating the zygomaticus while observing disgusted expressions). Such an approach would help disentangle predictive coding from simulation-based accounts and provide a more nuanced understanding of the mechanisms underlying sensorimotor modulation during emotion perception.

5. Conclusion

To conclude, our study provides further support for the sensorimotor simulation framework, which suggests that observing an action engages the same sensory and motor regions involved in its execution. In face-to-face interactions, this process appears to rely on a mirror neuron system for facial expressions, similar to the one identified for limb movements (Goldman and Sripada; 2005; Niedenthal et al., 2010; Wood et al., 2016). These simulative mechanisms are thought to play a key role in facial expression recognition, enabling observers to attribute mental states by internally reproducing or enacting a similar state within themselves.

Further evidence of the involvement of sensorimotor regions in this process comes from studies reporting mu rhythm desynchronization in response to facial expressions—an established neural marker of the action-perception mechanism—observed in both adults (Moore et al., 2012) and infants (Marshall and Meltzoff, 2011; Rayson et al., 2016). Additionally, sensorimotor resonance manifests at the peripheral level through facial mimicry, where individuals spontaneously reproduce the motor patterns associated with observed expressions (Dimberg et al., 2000; Rymarczyk et al., 2016; Wood et al., 2016).

Despite accumulating evidence, the precise nature of this phenomenon remains debated. It is unclear whether the observed cortical modulation reflects a true simulation process, relying on the mirror properties of neurons, or whether it instead results from proprioceptive feedback due to behavioral and visceral activation elicited by emotional stimuli (Hess and Fischer, 2013; Wood et al., 2016).

Beyond its nature, its functional role in facial expression recognition is also questioned. While some studies support the sensorimotor simulation framework by showing that individuals with congenital facial palsy or those undergoing transient facial manipulation experience difficulties in recognizing facial expressions—affecting tasks such as emotion labeling or intensity assessment (Schiano Lomoriello et al., 2024; Stefani et al., 2019; Wood et al., 2016)—other findings challenge this view. For instance, Vannuscorps and Caramazza (2020) found no significant impairment in facial expression recognition among individuals with facial palsy, suggesting that sensorimotor activation may not be essential for this process. Instead, their findings propose that such activation may reflect emotional reactivity, potentially driven by emotional contagion or learned social response patterns, rather than a mirroring mechanism strictly necessary for recognizing facial expressions.

Our findings contribute to this debate by suggesting that, regarding its nature, the sensorimotor resonance mechanism is selective for faces, supporting the idea that it relies on the mirror properties of neurons. However, future studies should further investigate the specificity and functional significance of this mechanism, clarifying its role in emotion recognition and social cognition.

CRediT authorship contribution statement

Sara Costa: Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Arianna Schiano Lomoriello:** Writing – review & editing, Visualization, Methodology, Data curation. **Thomas Quettier:** Software. **Fausto Caruana:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Conceptualization. **Pier Francesco Ferrari:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Conceptualization. **Paola Sessa:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

We declare that we have no financial and personal relationship with other people or organization that can inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any service or company that could be construed as influencing the review of the manuscript entitled.

Acknowledgement

The funds assigned to Paola Sessa by the Italian Ministry of Universities and Research have covered the research expenses. We wish to thank Margherita Bagnoli, Gabriele Nobile, Linda Riu, Mattia Taurone for their valuable contribution to data collection.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2025.121322.

Data availability

The data supporting the findings of this study are openly available at : https://osf.io/x8rpg.

References

Adolphs, R., 2002. Recognizing emotion from facial expressions: psychological and neurological mechanisms. Behav. Cogn. Neurosci. Rev. 1 (1), 21–62. https://doi.org/10.1177/1534582302001001003.

Al, E., Iliopoulos, F., Forschack, N., Nierhaus, T., Grund, M., Motyka, P., Villringer, A., 2020. Heart–brain interactions shape somatosensory perception and evoked potentials. Proc. Natl. Acad. Sci. 117 (19), 10575–10584. https://doi.org/10.1073/pnas.191562911.

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 167, 223–234.

Avanzini, P., Abdollahi, R.O., Sartori, I., Caruana, F., Pelliccia, V., Casaceli, G., Orban, G. A., 2016. Four-dimensional maps of the human somatosensory system. Proc. Natl. Acad. Sci. 113 (13), E1936–E1943. https://doi.org/10.1073/pnas.160188911.

Avenanti, A., Minio-Paluello, I., Bufalari, I., Aglioti, S.M., 2009. The pain of a model in the personality of an onlooker: influence of state-reactivity and personality traits on embodied empathy for pain. Neuroimage 44 (1), 275–283. https://doi.org/10.1016/j.neuroimage.2008.08.001.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. R. Stat. Soc. Ser. B Methodol. 57 (1), 289–300.

Birch-Hurst, K., Rychlowska, M., Lewis, M.B., Vanderwert, R.E., 2022. Altering facial movements abolishes neural mirroring of facial expressions. Cogn. Affect. Behav. Neurosci. 22 (2), 316–327. https://doi.org/10.3758/s13415-021-00956-z.

Bonini, L., Rotunno, C., Arcuri, E., Gallese, V., 2022. Mirror neurons 30 years later: implications and applications. Trends Cogn. Sci. 26 (9), 767–781. https://doi.org/10.1016/j.tics.2022.06.0037, 9.

Boudewyn, M.A., Luck, S.J., Farrens, J.L., Kappenman, E.S., 2018. How many trials does it take to get a significant ERP effect? It depends. Psychophysiology 55 (6), e13049.

Burton, H., Abend, N.S., MacLeod, A.M., Sinclair, R.J., Snyder, A.Z., Raichle, M.E., 1999. Tactile attention tasks enhance activation in somatosensory regions of parietal cortex: a positron emission tomography study. Cereb. Cortex. 9 (7), 662–674.

Cheng, Y., Yang, C.Y., Lin, C.P., Lee, P.L., Decety, J., 2008. The perception of pain in others suppresses somatosensory oscillations: a magnetoencephalography study. Neuroimage 40 (4), 1833–1840. https://doi.org/10.1016/j.neuroimage.2008.01.064.

Critchley, H.D., Wiens, S., Rotshtein, P., Öhman, A., Dolan, R.J., 2004. Neural systems supporting interoceptive awareness. Nat. Neurosci. 7 (2), 189–195.

Damasio, A.R., Grabowski, T.J., Bechara, A., Damasio, H., Ponto, L.L., Parvizi, J., Hichwa, R.D., 2000. Subcortical and cortical brain activity during the feeling of self-generated emotions. Nat. Neurosci. 3 (10), 1049–1056.

Davis, M.H., 1983. Measuring individual differences in empathy: evidence for a multidimensional approach. J. Pers. Soc. Psychol. 44 (1), 113–126. https://doi.org/10.1037/0022-3514.44.1.113.

De Stefani, E., Nicolini, Y., Belluardo, M., Ferrari, P.F., 2019. Congenital facial palsy and emotion processing: the case of Moebius syndrome. Genes. Brain Behav. 18 (1), e12548. https://doi.org/10.1111/gbb.12548.

Dell'Acqua, R., Jolicoeur, P., Pesciarelli, F., Job, R., Palomba, D., 2003. Electrophysiological evidence of visual encoding deficits in a cross-modal attentional blink paradigm. Psychophysiology 40 (4), 629–639.

Del, Vecchio, M., Avanzini, P., Gerbella, M., Costa, S., Zauli, F.M., d'Orio, P., Caruana, F., 2024. Anatomo-functional basis of emotional and motor resonance elicited by facial expressions. Brain 147 (9), 3018–3031. https://doi.org/10.1093/brain/awae050.

Dimberg, U., Thunberg, M., Elmehed, K., 2000. Unconscious facial reactions to emotional facial expressions. Psychol. Sci. 11 (1), 86–89. https://doi.org/10.1111/1467-9280.00221.

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 (11), 2298–2312.

Fox, J., Weisberg, S., 2019. An R Companion to Applied Regression. Third edition. Sage, Thousand Oaks CA. https://www.john-fox.ca/Companion/.

Gallese, V., 2007. Before and below 'theory of mind': embodied simulation and the neural correlates of social cognition. Philos. Trans. R. Soc. B 362 (1480), 659–669. https://doi.org/10.1098/rstb.2006.2002.

Genzer, S., Ong, D.C., Zaki, J., Perry, A., 2022. Mu rhythm suppression over sensorimotor regions is associated with greater empathic accuracy. Soc. Cogn. Affect. Neurosci. 17 (9), 788–801.

Goldman, A.I., Sripada, C.S., 2005. Simulationist models of face-based emotion recognition. Cognition 94 (3), 193–213. https://doi.org/10.1016/j.cognition.2004.01.005.

Grezes, J., Valabregue, R., Gholipour, B., Chevallier, C., 2014. A direct amygdala-motor pathway for emotional displays to influence action: a diffusion tensor imaging study. Hum. Brain Mapp. 35 (12), 5974–5983.

Gu, X., Hof, P.R., Friston, K.J., Fan, J., 2013. Anterior insular cortex and emotional awareness. J. Comp. Neurol. 521 (15), 3371–3388. https://doi.org/10.1002/cne.23368.

Hess, U., Fischer, A.H., 2013. Emotional mimicry as social regulation. Pers. Soc. Psychol. Rev. 17 (2), 142–157. https://doi.org/10.1177/1088868312472607.

Keysers, C., Silani, G., Gazzola, V., 2024. Predictive coding for the actions and emotions of others and its deficits in autism spectrum disorders. Neurosci. Biobehav. Rev., 105877

Kragel, P.A., LaBar, K.S., 2016. Somatosensory representations link the perception of emotional expressions and sensory experience. eNeuro 3 (2).

Krautheim, J.T., Steines, M., Dannlowski, U., Neziroğlu, G., Acosta, H., Sommer, J., Straube, B., Kircher, T., 2020. Emotion specific neural activation for the production and perception of facial expressions. Cortex 127, 17–28. https://doi.org/10.1016/j.cortex.2020.01.026.

Kropf, E., Syan, S.K., Minuzzi, L., Frey, B.N., 2018. From anatomy to function: the role of the somatosensory cortex in emotional regulation. Braz. J. Psychiatry 41 (03), 261–269.

Lang, P.J., Bradley, M.M., Cuthbert, B.N., 1997. International affective picture system (IAPS): technical manual and affective ratings. NIMH Cent. Study Emot. Atten. 39–58.

Martínez-Jauand, M., González-Roldán, A.M., Muñoz, M.A., Sitges, C., Cifre, I., Montoya, P., 2012. Somatosensory activity modulation during observation of other's pain and touch. Brain Res. 1467, 48–55.

Marshall, P.J., Young, T., Meltzoff, A.N., 2011. Neural correlates of action observation and execution in 14-month-old infants: an event-related EEG desynchronization study. Dev. Sci. 14 (3), 474–480. https://doi.org/10.1111/j.1467-7687.2010.00991.x.

Marchewka, A., Żurawski, Ł., Jednoróg, K., Grabowska, A., 2014. The Nencki affective picture system (NAPS): introduction to a novel, standardized, wide-range, high-quality, realistic picture database. Behav. Res. Methods 46, 596–610.

Mauersberger, H., Kastendieck, T., Hess, U., 2022. I looked at you, you looked at me, I smiled at you, you smiled at me—the impact of eye contact on emotional mimicry. Front. Psychol. 13, 970954.

Mavratzakis, A., Herbert, C., Walla, P., 2016. Emotional facial expressions evoke faster orienting responses, but weaker emotional responses at neural and behavioural levels compared to scenes: a simultaneous EEG and facial EMG study. Neuroimage 124, 931–946.

Moore, A., Gorodnitsky, I., Pineda, J., 2012. EEG mu component responses to viewing emotional faces. Behav. Brain Res. 226 (1), 309–316. https://doi.org/10.1016/j.bbr.2011.07.048.

Niedenthal, P.M., Mermillod, M., Maringer, M., Hess, U., 2010. The Simulation of Smiles (SIMS) model: embodied simulation and the meaning of facial expression. Behav. Brain Sci. 33 (6), 417–433. https://doi.org/10.1017/S0140525x10000865.

Nummenmaa, L., Glerean, E., Hari, R., Hietanen, J.K., 2014. Bodily maps of emotions. Proc. Natl. Acad. Sci. 111 (2), 646–651. https://doi.org/10.1073/pnas.1321664111.

Pitcher, D., Garrido, L., Walsh, V., Duchaine, B., 2008. Transcranial magnetic stimulation disrupts the perception and embodiment of facial expressions. J. Neurosci. 28 (36), 8929–8933. https://doi.org/10.1523/JNEUROSCI.1450-08.2008.

Pourtois, G., Sander, D., Andres, M., Grandjean, D., Reveret, L., Olivier, E., Vuilleumier, P., 2004. Dissociable roles of the human somatosensory and superior temporal cortices for processing social face signals. Eur. J. Neurosci. 20 (12), 3507–3515.

Rayson, H., Bonaiuto, J.J., Ferrari, P.F., Murray, L., 2016. Mu desynchronization during observation and execution of facial expressions in 30-month-old children. Dev. Cogn. Neurosci. 19, 279–287. https://doi.org/10.1016/j.dcn.2016.05.003.

Rizzo, G., Milardi, D., Bertino, S., Basile, G.A., Di Mauro, D., Calamuneri, A., Cacciola, A., 2018. The limbic and sensorimotor pathways of the human amygdala: a structural connectivity study. Neuroscience 385, 166–180.

Rymarczyk, K., Żurawski, Ł., Jankowiak-Siuda, K., Szatkowska, I., 2016. Emotional empathy and facial mimicry for static and dynamic facial expressions of fear and disgust. Front. Psychol. 7, 1853. https://doi.org/10.3389/fpsyg.2016.01853.

Sel, A., Forster, B., Calvo-Merino, B., 2014. The emotional homunculus: ERP evidence for independent somatosensory responses during facial emotional processing. J. Neurosci. 34 (9), 3263–3267.

Schiano Lomoriello, A., Caperna, G., Carta, A., De Stefani, E., Ferrari, P.F., Sessa, P., 2024. Sensitivity to basic emotional expressions and the emotion perception space in the absence of facial mimicry: the case of individuals with congenital facial palsy. Emotion 24 (3), 602–616. https://doi.org/10.1037/emo0001275.

Straube, T., Miltner, W.H., 2011. Attention to aversive emotion and specific activation of the right insula and right somatosensory cortex. Neuroimage 54 (3), 2534–2538.

Tadel, F., Baillet, S., Mosher, J.C., Pantazis, D., Leahy, R.M., 2011. Brainstorm: a user-friendly application for MEG/EEG analysis. Comput. Intell. Neurosci. 2011, 879716. https://doi.org/10.1155/2011/879716.

Toschi, N., Duggento, A., Passamonti, L., 2017. Functional connectivity in amygdalar-sensory/(pre) motor networks at rest: new evidence from the human connectome project. Eur. J. Neurosci. 45 (9), 1224–1229.

Vannuscorps, G., Andres, M., Caramazza, A., 2020. Efficient recognition of facial expressions does not require motor simulation. Elife 9, e54687. https://doi.org/10.7554/eLife.54687.

Uljarevic, M., Hamilton, A., 2013. Recognition of emotions in autism: a formal meta-analysis. J. Autism. Dev. Disord. 43 (7), 1517–1526. https://doi.org/10.1007/s10803-012-1695-5.

Wood, A., Rychlowska, M., Korb, S., Niedenthal, P., 2016. Fashioning the face: sensorimotor simulation contributes to facial expression recognition. Trends Cogn. Sci. 20 (3), 227–240. https://doi.org/10.1016/j.tics.2015.12.010.

Woodruff, C.C., Martin, T., Bilyk, N., 2011. Differences in self-and other-induced Mu suppression are correlated with empathic abilities. Brain Res. 1405, 69–76. https://doi.org/10.1016/j.brainres.2011.05.046.