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Research Report

Task-related modulation of motor response to emotional bodies: A TMS motor-evoked potential study

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ABSTRACT

Exposure to emotional body postures during perceptual decision-making tasks has been linked to transient suppression of motor reactivity, supporting the monitoring of emotionally relevant information. However, it remains unclear whether this effect occurs implicitly, i.e., when emotional information is irrelevant to the task. To investigate this issue, we used single-pulse transcranial magnetic stimulation (TMS) to assess motor excitability while healthy participants were asked to categorize pictures of body expressions as emotional or neutral (emotion recognition task) or as belonging to a male or a female actor (gender recognition task) while receiving TMS over the motor cortex at 100 and 125 ms after picture onset. Results demonstrated that motor-evoked potentials (MEPs) were reduced for emotional body postures relative to neutral postures during the emotion recognition task. Conversely, MEPs increased for emotional body postures relative to neutral postures during the gender recognition task. These findings indicate that motor inhibition, contingent upon observing emotional body postures, is selectively associated with actively monitoring emotional features. In contrast, observing emotional body postures prompts motor facilitation when task-relevant features are non-emotional. These findings contribute to embodied cognition models that link emotion perception and action tendencies.

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1. Introduction

Substantial neurophysiological evidence indicates that emotional stimuli, such as emotional body postures, benefit from enhanced processing, which is reflected in the early modulation of visual components of event-related potentials (ERPs), like the P1, N1, and N190 (Borhani, Borgomaneri, Làdavas, & Bertini, 2016; Jessen & Kotz, 2011; van Heijnsbergen, Meeren, Grèzes, & de Gelder, 2007), and the modulation of fronto-central ERP components and beta oscillations within the same early temporal window (Botta et al., 2024). Behavioral studies also demonstrate fast motor responses to emotional bodies, suggesting that enhanced perceptual processing is coupled with increased motor reactivity (Borgomaneri, Vitale, & Avenanti, 2020; Botta, Lagravinese, Bove, Avenanti, & Avanzino, 2021). In a series of transcranial magnetic stimulation (TMS) studies (Borgomaneri, Vitale, & Avenanti, 2015; Borgomaneri, Vitale, & Avenanti, 2017; Borgomaneri, Vitale, et al., 2020; Botta et al., 2022; Borgomaneri, Vitale, Gazzola, Avenanti, 2015), we have demonstrated that the perception of emotional bodies quickly modulates the motor system shortly after the stimulus is presented. This is evidenced by a consistent reduction of TMS-induced motor-evoked potentials (MEPs), which provide a reliable measure of motor excitability. In these studies, TMS was administered over the primary motor cortex (M1) within the same temporal window as the P1 and N1 components of ERPs, and MEP suppression within this temporal window suggests a coupling between enhanced perceptual and action processing (Borgomaneri, Vitale, & Avenanti, 2015, Borgomaneri, Gazzola, Avenanti, 2015, Borgomaneri et al., 2017; Borgomaneri, Vitale, et al., 2020). MEP suppression was observed in both hemispheres (Borgomaneri, Vitale, Avenanti, 2015), across different muscles of the upper limb (Borgomaneri et al., 2017), and was stronger in individuals with higher scores in anxiety-related personality traits (Borgomaneri et al., 2017; Borgomaneri, Gazzola, et al., 2015). This MEP suppression was transient, consistently observed in an early temporal window (e.g., at 100–150 ms from stimulus presentation) (Borgomaneri, Gazzola, et al., 2015; Borgomaneri, et al., 2017; Borgomaneri, Vitale, et al., 2020; Borgomaneri, Vitale, Gazzola, et al., 2015), while at later timing (e.g., 300 ms) it transitioned into MEP facilitation (Borgomaneri, Gazzola, & Avenanti, 2012; Borgomaneri, Gazzola, et al., 2015; Botta et al., 2022). Based on these findings, we previously interpreted the transient reduction of motor output for emotional bodies as an orienting/freezing mechanism that supports the monitoring of emotional and salient signals (Fanselow, 1994; Frijda, 2010; Graziano, 2016; Hagenaars, Oitzl, & Roelofs, 2014; Lang & Bradley, 2010). Recently, however, we found no MEP inhibition when participants had to recognize emotional faces (Borgomaneri, Vitale, Battaglia, & Avenanti, 2021) or emotional scenes (Borgomaneri, Gazzola, & Avenanti, 2014), and MEPs were recorded in a similar early temporal window (e.g., at 150 ms). Instead, these emotional stimuli facilitated MEPs (Borgomaneri et al., 2014, 2021). Likewise, consistent MEP facilitation to emotional faces or scenes was observed in various studies using passive viewing or other tasks, exploring MEPs across different time windows (Coelho, Lipp, Marinovic, Wallis, & Riek, 2010; Coombes et al., 2009; Fiori, Ciricugno, Cattaneo, & Ferrari, 2023; Hajcak et al., 2007). This motor facilitation has been interpreted in terms of increased action readiness in response to emotionally salient stimuli. These findings suggest that the early transient inhibitory response to emotional bodies is not a general orienting mechanism but rather a stimulus-specific response. Interestingly, motor processes associated with early motor inhibition could reflect critical computations for visual recognition: TMS over M1 at 150 ms (but not at 300 ms) from stimulus onset also interfered with the recognition of emotional bodies (Borgomaneri, Gazzola, et al., 2015).

It should be noted, however, that in all the above-mentioned MEP studies on emotional bodies, participants were required to perform explicit emotion recognition tasks. These tasks involved identifying specific emotions expressed by observed bodies (Borgomaneri et al., 2012; Borgomaneri et al., 2017; Borgomaneri, Gazzola, et al., 2015; Borgomaneri, Vitale, & Avenanti, 2015; Borgomaneri, Vitale, et al., 2020; Borgomaneri, Vitale, Gazzola, et al., 2015) or categorizing them as neutral versus emotional (Borgomaneri, Vitale, et al., 2020). As a result, it remains unclear whether the stimulus-specific MEP suppression observed during the presentation of emotional bodies is a response specific to explicit emotion recognition or a more automatic response independent of the current task. The present study aims to address this question, as clarifying whether MEP modulation is task-specific can provide important insights into the neural mechanisms underlying the perception of emotional body language.

To understand the effect of task instruction on brain activation during emotion processing, a recent meta-analysis examined 180 neuroimaging studies that investigated explicit evaluation, passive perception, and incidental perception of emotions using visual stimuli like facial, vocal, and body expressions (Dricu & Frühholz, 2016). The meta-analysis revealed shared amygdala and fusiform gyrus activation across different tasks. Explicit emotion evaluation recruited the amygdala, visual-related areas (i.e., the inferior occipital gyrus, middle fusiform gyrus, the superior temporal gyrus, and the posterior superior temporal sulcus), and brain regions involved in mindreading and action processing (i.e., dorsomedial and inferior frontal cortex) to a greater extent compared to implicit tasks such as gender recognition. Implicit tasks, on the other hand, tended to activate subcortical regions in the claustrum and the hippocampus, while passive tasks primarily activated sensory regions (Dricu & Frühholz, 2016).

However, it is important to note that only a few studies included in this meta-analysis focused on brain activations during the perception of emotional body postures (Grèzes, Pichon, & de Gelder, 2007; Jessen & Kotz, 2011; Peelen & Downing, 2007; Pichon, de Gelder, & Grezes, 2008, 2009; Pouga et al., 2010; Sinke, Sorger, Goebel, Gelder, & de Gelder, 2010) with most studies focusing on facial and voice stimuli (Dricu & Frühholz, 2016). These studies reported activation in various portions of the motor system during both passive and explicit tasks. Still, they did not directly investigate neural activations during explicit versus implicit evaluation of emotional bodies.

The critical involvement of motor areas in recognition of emotional bodies has been demonstrated in a few TMS studies targeting the right M1 (Borgomaneri, Gazzola, et al., 2015), right anterior intraparietal sulcus (Mazzoni, Jacobs, Venuti, Silvanto, & Cattaneo, 2017), and the cerebellum (Ferrari, Ciricugno, Urgesi, & Cattaneo, 2019). Moreover, interference with the inferior frontal cortex affected the discrimination of bodies based on body postures/expressions but not on morphological cues (Candidi, Urgesi, Ionta, & Aglioti, 2008; Urgesi, Candidi, Ionta, & Aglioti, 2007), supporting the involvement of sensorimotor regions in emotion and action perception (Avenanti, Candidi, & Urgesi, 2013; Avenanti & Urgesi, 2011; Paracampo, Tidoni, Borgomaneri, di Pellegrino, & Avenanti, 2017; Paracampo, Pirruccio, Costa, Borgomaneri, & Avenanti, 2018). Together, these findings suggest a crucial involvement of the human motor cortex in the explicit recognition of emotional bodies. However, whether M1 differentially responds to emotional bodies depending on the specific task at stake remains an interesting and so far unanswered question.

To address this issue, we conducted a study that tested whether M1 responses to others' emotional body expressions can be observed not only during explicit emotion recognition tasks, but also during implicit tasks, when emotion information is irrelevant to the perceptual task. Building on a recent study that examined MEPs during an explicit emotion recognition task of body postures of male and female actors (Borgomaneri, Vitale, et al., 2020), we stimulated the right M1 while presenting fearful, happy, neutral dynamic, and neutral static body postures. We administered TMS pulses at 100–125 ms from picture onset, corresponding to the latencies of the P1 and the N1 components of ERPs that have shown sensitivity to emotion and task-related effects (He, Liu, Wang, & Zhang, 2018; Jessen & Kotz, 2011; van Heijnsbergen, Meeren , Grèzes, & de Gelder B, 2007). Changes in MEPs were recorded within this early time window (Borgomaneri, Vitale, & Avenanti 2017; Borgomaneri, Vitale, et al., 2020). We aimed to expand previous work by assessing the influence of task-related effects on early motor reactivity. We hypothesized that emotional body postures would reduce motor excitability during explicit emotion recognition tasks, replicating prior findings (Borgomaneri, Gazzola, et al., 2015; Borgomaneri, Vitale, & Avenanti, 2015; Borgomaneri et al., 2017; Borgomaneri, Vitale, et al., 2020). If early motor responses to emotional bodies reflect an automatic process, we would expect little or no influence of task-related factors, resulting in comparable MEP inhibition for emotional bodies regardless of the task demands. On the other hand, as an implicit task, we employed a gender recognition task which requires discrimination of bodies based on morphological cues and should in principle mostly rely on visual areas in the ventral stream (Kanwisher & Yovel, 2006; Tsantani et al., 2021; Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007; Wiese, Kloth, Güllmar, Reichenbach, & Schweinberger, 2012). Therefore, based on previous work that directly compared brain areas involved in the discrimination of body posture/expression vs body form (Urgesi, Candidi, et al., 2007), we would expect the motor system to be mostly engaged in the explicit task, and thus greater MEP inhibition during perception of emotional bodies in the emotion recognition task. In this vein, M1 engagement in the explicit task would reflect processes supporting visual discrimination based on body postures.

Both male and female actors were used in both tasks; moreover, we tested both male and female participants, allowing for an investigation of potential gender-related effects on early motor reactivity. However, based on prior work (Borgomaneri, Vitale, et al., 2020), we did not expect consistent gender-related modulations of MEPs.

2. Materials and methods

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. Materials and data for the study are available at https://osf.io/3zehm/. No part of the study procedures or analyses was preregistered prior to the research being conducted.

2.1. *Participants*

Sixteen healthy participants (6 males, mean age ± S.D.: 21.3 years ± 2.5) took part in this study after signing informed consent. The number of participants was determined using G*Power software (Faul, Erdfelder, Lang, & Buchner, 2007) to conduct a power analysis aiming for a robust power ($1 - \beta$) of .95, while maintaining a significance level (α) of .05. Drawing upon the MEP modulations observed across our prior investigations (Borgomaneri et al., 2012; Borgomaneri et al., 2017; Borgomaneri, Gazzola, et al., 2015; Borgomaneri, Vitale, & Avenanti, 2015; Borgomaneri, Vitale, et al., 2020; Borgomaneri, Vitale, Gazzola, et al., 2015), we expected a substantial MEP suppression in response to emotional bodies during the emotion task, with a large effect size ($f = .4$), and a notably high degree of correlation among the measured variables ($r > .9$). However, when considering the expected interaction between the task and the observed body expression, we conservatively expected a more modest effect size ($f = .25$) and correlation coefficient ($r = .8$) and this led to the determination that a sample of 16 participants was necessary for our study. This sample size also aligned with the typical sample employed across ten experimental groups in the aforementioned studies, where the mean participant count was 15 per group.

All participants were right-handed, were naïve to the purposes of the experiment, and did not report any neurological or psychiatric disease, visual problems, medicine intake, or any contraindication to TMS (Rossi, Hallett, Rossini, & Pascual-Leone, 2011). The study was approved by the Bioethics Committee of the University of Bologna and was carried out in agreement with legal requirements and international norms (Declaration of Helsinki, 2013). No discomfort or adverse effects during TMS were reported or noticed.

2.2. Visual stimuli

Different types of pictures were presented on a 19-inch screen located about 80 cm away from the participant. The stimuli included pictures of an actor in emotional and neutral body postures. There were sixteen pictures depicting two male actors and sixteen pictures depicting two female actors. Stimuli were selected from a validated database used in prior work (Borgomaneri, Bolloni, Sessa, & Avenanti, 2020; Borgomaneri et al., 2012; Borgomaneri, Gazzola, et al., 2015; Borgomaneri, Vitale, et al., 2020; Borgomaneri, Vitale, Gazzola, et al., 2015). To minimize the individual differences among the actors, all of them wore the same swimming cap and identical black boxer shorts. In addition, the faces of the actors were blanked out in all the pictures. Moreover, although all the women wore an elastic band over the breast, the chest of each body was occluded using a black strip (Fig. 1). These changes ensure that attention is focused explicitly on body-related information and that any morphological differences between males and females did not compromise the recognition of body expressions. To rule out the possibility that changes in M1 excitability might be due to differing amounts of implied motion in the models' left or right body parts, mirror-reflected copies of the stimuli were also created. A total of 64 stimuli were used in the experiment, equally divided into 16 fearful postures, 16 happy postures, 16 neutral body movements ("neutral dynamic"), and 16 neutral static body postures ("neutral static") for a total pool of 64 stimuli.

2.3. Transcranial magnetic stimulation and electromyography recording

The experiment began with the electrode montage setup, detection of the optimal scalp position, and measurement of the resting motor threshold (rMT). To explore motor excitability, MEPs were recorded by stimulating the left first dorsal interosseous (FDI) representation in the right motor cortex, using a Magstim 200 magnetic stimulator (Magstim, Whiteland, Dyfed, UK) and a figure-of-eight magnetic coil (70 mm outer diameter; peak magnetic field 2.2 T). Surface electromyograms (EMG) from the left FDI were recorded with a Biopac MP-35 (Biopac, U.S.A.), band-pass filtered (30–500 Hz), sampled at 5 kHz, digitized, and stored on a computer for offline analysis. Pairs of silver-chloride surface electrodes were placed in a belly-tendon montage over the left FDI with ground electrodes on the right wrist. The intersection of the coil was placed tangentially to the scalp at a 45° angle to the mid-line to induce a posterior–anterior current flow across the central sulcus. The optimal position of the coil was defined as the point where stimulation consistently evoked the largest MEP in the left FDI. The rMT was defined as the minimal stimulator output intensity that evoked 5 small responses (~50 μV) in the relaxed FDI muscle in a series of 10 stimuli (Rossini et al., 2015). During the experiment, TMS intensity was set at 120% of rMT. Mean motor thresholds (± standard deviation) were 34.7 ± 3.7% of the maximum stimulator output. The experimenter visually verified the absence of voluntary contractions continuously throughout the experiment. When muscle tension was detected, the experiment was briefly interrupted, and the participant was invited to relax.

2.4. Procedure and experimental design

The experiment was programmed using MATLAB software to control picture presentation and trigger TMS pulses. Before and after the experimental session, two blocks of 10 MEPs were recorded and served as a baseline. The participants performed two different tasks. In each one, 128 pictures divided into 2 blocks were presented to the participants. Each trial consisted of a grey screen (1-sec duration), followed by the test picture projected at the center of the screen (Fig. 1b). In half of the trials, the stimulus was shown for 110 ms and the single pulse of TMS was delivered at 100 ms from stimulus onset. In the remaining trials, the stimulus was presented for 135 ms and the pulse was delivered at 125 ms from stimulus onset. We recorded MEPs at the 100 and 125 ms time points to introduce temporal variability in the occurrence of the TMS pulse and thus reduce potential priming effects. In line with prior research (Borgomaneri, Vitale, et al., 2020), we did not

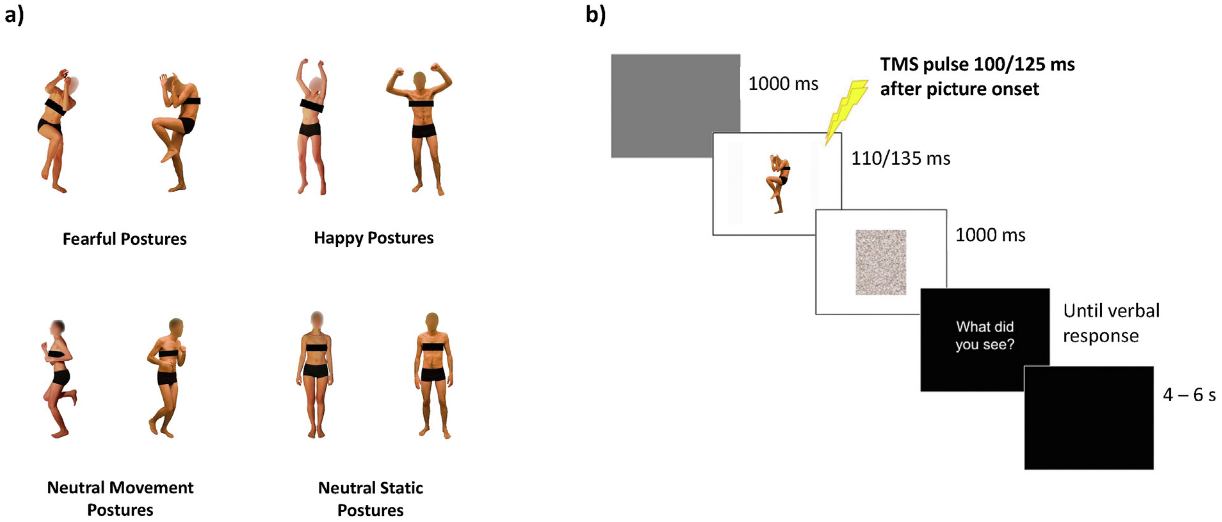

Fig. 1 – a. Examples of visual body stimuli. b Trial sequence.

expect MEP differences, considering that these two time points likely correspond to the same stage of information processing.

After the picture, a random-dot mask (obtained by scrambling the sample stimulus with image segmentation software) lasting 1 sec appeared, and, finally, the question “What did you see?” was displayed on the screen. In the gender recognition task, participants were asked to recognize whether the actor appearing in the picture was a male or a female. Instead, in the emotion recognition task, they had to categorize whether the body expressed emotion or presented a neutral expression. In both tasks, participants provided a verbal response (forced choice), and an experimenter collected the answer by pressing a computer key. To avoid changes in motor excitability due to the verbal response (Meister et al., 2003; Tokimura, Tokimura, Oliviero, Asakura, & Rothwell, 1996), participants were instructed to answer only during the question screen 2–3 s after the TMS pulse was delivered. After the response, a black screen appeared for 4–6 s, ensuring an inter-pulse interval greater than 10 s, thereby avoiding changes in motor excitability due to the TMS *per se* (Chen et al., 1997). At the end of the TMS session, participants viewed all the stimuli again (presented in a randomized order) and judged the arousal, valence, and perceived movement using a 5-point Likert scale. To avoid building up artificial correlations between the different judgments, each rating was collected separately during successive presentations of the whole set of stimuli.

2.5. *Data analysis*

Neurophysiological data were recorded and processed offline. For each condition, the mean peak-to-peak amplitude, measured in mV, was calculated and normalized by a logarithmic transformation [log (mean MEP amplitude value + 1)]. MEPs associated with an incorrect response were removed from the analysis (~7%). Although the mean accuracy in both tasks was considerably high (gender recognition task: mean accuracy ± SD: 90 ± 6%; emotion recognition task: 96 ± 3%), discriminating the gender of the model in the pictures was overall more difficult compared to the recognition of the emotion expressed by the model ($p < .01$; see Supplementary Data for a discussion of the relation between classification accuracy and motor excitability). Moreover, since EMG background can influence motor excitability (Devanne, Lavoie, & Capaday, 1997), we eliminated MEPs with preceding background EMG of 100 ms deviating from the mean by more than 2 SD (~5%). Normalized MEPs were submitted to a five-way mixed factors ANOVA with ‘Observer gender’ (2 levels: male and female) as a between-subjects factor and ‘Task’ (2 levels: Gender and Emotion), ‘Time’ (2 levels: 100 and 125 ms), ‘Model gender’ (2 levels: male and female), and ‘Model body expression’ (2 levels: emotion, neutral) as within-subjects factors. All post-hoc comparisons were performed using the Newman–Keuls test. Effect size indices for main effects and interactions were computed using partial eta^2 (η_p^2), whereas Cohen's *d* was calculated for post-hoc comparisons (Cohen, 1992).

Since the mean VAS rating for arousal, valence, and implied motion were not normally distributed, they were analyzed with non-parametric Friedman ANOVAs. For the same reason, the accuracy (% of correct response) across gender groups was assessed using the nonparametric Kruskal–Wallis ANOVA. Bonferroni-corrected Wilcoxon matched pairs tests, and Mann–Whitney *U* tests were carried out for post-hoc within- and between-group comparisons, respectively.

3. Results

3.1. *Subjective measures*

The Friedman ANOVA on arousal scores showed a significant difference between the models’ body expressions ($\chi2 = 35.23$; $p < .001$; Table 1). Arousal for happy and fearful was comparable ($p = .82$) and greater than for neutral dynamic and neutral static bodies (all $p < .001$). Neutral dynamic bodies had higher arousal ratings than neutral static bodies ($p < .001$).

The Friedman ANOVA on valence was significant ($\chi2 = 45.46$; $p < .001$; Table 1), showing that happy body postures were judged more positive compared to all the other expressions (all $p < .001$), while the fearful body postures were considered more negative compared to all the other expressions (all $p < .001$). Also, the valence scores for the neutral dynamic body postures were higher than the neutral static postures ($p < .001$).

The Friedman ANOVA on implied motion scores revealed significant differences across bodily expressions ($\chi2 = 32.40$; $p < .001$; Table 1). The scores of pictures representing all bodily movements (i.e., happy, fearful, and neutral dynamic) were higher compared to pictures showing static postures (all $p < .001$). In addition, the amount of implied motion for neutral dynamic body movement was comparable to the happy postures ($p = .88$), although it was significantly different relative to the pictures of fearful bodies ($p = .05$).

3.2. *Neurophysiological data*

The Observer gender x Task x Time x Model gender x Model body expression ANOVA on normalized MEP revealed a significant main effect of Observer gender ($F_{1,14} = 9.10$; $p < .01$; $\eta_p^2 = .39$), accounted for by the lower MEP for female participants (mean MEP amplitudes ± SD: .319 ± .094) compared to

Table 1 – Mean (± standard deviation) arousal, valence, and implied motion ratings of the different body postures (averaged across tasks, model gender and observer gender).

	Happy	Fearful	Neutral Dynamic	Neutral Static
Valence	4.31 ± .29	1.47 ± .41	2.92 ± .68	2.57 ± .66
Arousal	3.30 ± .66	3.34 ± .87	2.61 ± .51	1.29 ± .46
Implied Motion	3.13 ± .62	3.49 ± .75	3.11 ± .48	1.01 ± .02

male participants (.495 ± .142). More importantly, the two-way Task x Model body expression interaction was also significant ($F_{1,14} = 21.89$; $p < .001$; $\eta_p^2 = .61$; Fig. 2; Table S2). Such interaction indicates that, when participants had to categorize the type of expression conveyed by the model body (emotion recognition task), the MEPs were smaller for emotion expressions (.372 ± .144) with respect to neutral expressions (.381 ± .143; $p < .01$, Cohen $d' = .49$). On the contrary, when participants were asked to recognize the gender of the model (gender recognition task), MEPs associated with the emotion expressions (.399 ± .143) were larger than those associated with neutral dynamic expression (.387 ± .145; $p < .01$, Cohen $d' = .61$). See Table 2 for a breakdown of MEP data across the four types of emotional body expressions. The ANOVA showed no other significant main effects or interactions (all $F \leq 3.12$; all $p \geq .10$).

4. Discussion

The ability to rapidly perceive and respond appropriately to emotional stimuli represents a crucial capacity in a social environment. Similarly to the observation of emotional faces (Borgomaneri et al., 2021; Schutter, Hofman, & Van Honk, 2008), the observation of emotional bodies was found to rapidly influence the observer's motor system, as shown by a consistent MEP suppression during tasks requiring explicit identification or categorization of the observed emotional expressions (Borgomaneri et al., 2017; Borgomaneri, Gazzola, et al., 2015; Borgomaneri, Vitale, & Avenanti, 2015; Borgomaneri, Vitale, et al., 2020; Borgomaneri, Vitale, Gazzola, et al., 2015). However, to date, it was still unclear whether such motor suppression reflected an automatic process that is not influenced by the task at hand, or rather a more controlled process specifically associated with explicit recognition of emotion bodies. In the present study, we addressed this issue to provide novel insights into the neural mechanisms underlying the perception of emotional body expressions.

The results of this study revealed that participants showed MEP suppression for emotional compared to neutral bodies, selectively when asked to perform the emotion recognition task. In contrast, MEP amplitudes increased during the gender recognition task for emotional body postures compared to neutral body postures. Neither neurophysiological effect was influenced by any other factors (i.e., gender of the observer, gender of the models, time of the stimulation). These results demonstrated that attention directed toward the emotional content of body postures triggered an inhibitory MEP response

Fig. 2 – Task-related modulations of MEP amplitudes during perception of emotional and neutral body expressions. Split violin plots reporting the distribution of logarithmic MEP amplitude for both tasks and stimuli presented. Within the inner box, the solid line represents the median, while the boundary lines represent the 25th and the 75th percentile. Dots represent the individual mean MEP values. Asterisks (*) Indicate significant differences between experimental conditions ($p \leq .05$). Results show that during the emotion discrimination task, we observed a reduction of MEPs for emotional body expressions relative to neutral expressions, whereas, during the gender discrimination task, emotional bodies increased MEPs relative to neutral expressions.

Table 2 – Mean MEP amplitudes (± standard deviation) during the perception of the different body postures (averaged across times, model gender and observer gender).

	Happy	Fearful	Neutral Dynamic	Neutral Static
Emotion Task	.367 ± .147	.373 ± .143	.380 ± .145	.382 ± .144
Gender Task	.396 ± .146	.401 ± .143	.386 ± .142	.386 ± .150

to emotional bodies, replicating the results in previous studies with similar task demands (Borgomaneri et al., 2017; Borgomaneri, Gazzola, et al., 2015; Borgomaneri, Vitale, & Avenanti, 2015; Borgomaneri, Vitale, et al., 2020; Borgomaneri, Vitale, Gazzola, et al., 2015). Such effect was not observed when participants' attention was not directed towards stimulus emotional features (i.e., during a gender recognition task). Thus, our study allows us to establish that MEP modulation during the perception of emotional bodies is task-dependent.

Why was motor inhibition observed only in the explicit emotion recognition task, whereas in the implicit task, we observed MEP facilitation? It should be noted that the vast majority of TMS-MEP studies have reported motor facilitation when participants perceived emotional stimuli such as emotional scenes, faces, or even sounds (Baumgartner, Willi, & Jäncke, 2007; Coelho, Lipp, Marinovic, Wallis, & Riek, 2010; Coombes et al., 2009; Ferrari, Fiori, Suchan, Plow, & Cattaneo, 2021; Fiori, Ciricugno, Cattaneo, & Ferrari, 2023; Giovannelli et al., 2013; Hajcak et al., 2007; Oliveri et al., 2003), a phenomenon that has been related to increased motor readiness and action preparation. Notably, similar MEP facilitations were found during explicit tasks requiring the identification/categorization of emotional faces or scenes (Borgomaneri et al., 2014, 2021). On the other hand, during observation and explicit recognition of emotional bodies, a transient early MEP inhibition is found, followed by facilitation at a later time (Borgomaneri et al., 2012; Borgomaneri, Gazzola, et al., 2015, Botta et al., 2022).

Visual recognition of emotional body postures may require an internal simulation of the observed body expression, as suggested by embodied cognition theories (Bastiaansen, Thioux, & Keysers, 2009; Gallese & Caruana, 2016; Ross & Atkinson, 2020; Wood, Rychlowska, Korb, & Niedenthal, 2016). Covert emotional states (e.g., happiness) frequently manifest in overt motor behaviors (e.g., smiling, joyful body postures, and gestures). Based on this, observers can understand the unobservable emotional state of others by embodying their observable motor behavior (Borgomaneri, Bolloni, et al., 2020; Niedenthal, Mermillod, Maringer, & Hess, 2010; Oberman, Winkielman, & Ramachandran, 2007; Oberman & Ramachandran, 2007). This process has been related to the phenomenon of motor resonance, i.e., the activation of the motor cortex when facing the actions of others, which can support action understanding and prediction (Avenanti, Candidi, & Urgesi, 2013, Avenanti, Paracampo, Annella, Tidoni, & Aglioti, 2018; Paracampo, Montemurro, de Vega, & Avenanti, 2018). However, motor resonance does not necessarily imply excitatory processes (Avenanti, Minio-Paluello, Bufalari, & Aglioti, 2009; Bonini, Maranesi, Livi, Fogassi, & Rizzolatti, 2014; Kraskov, Dancause, Quallo, Shepherd, & Lemon, 2009; Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010; Vicario et al., 2017).

Interestingly, studies on action language have commonly reported motor activations when processing words or sentences involving action verbs (Tettamanti et al., 2005; de Vega et al., 2014; Vigliocco, Vinson, Druks, Barber, & Cappa, 2011; Vitale, Padrón, Avenanti, & de Vega, 2021). However, they have also reported behavioral interference, attenuated electrocortical beta power suppression, and reduction of MEP amplitudes in specific temporal windows during the listening of action verbs (Buccino et al., 2005; de Vega, Moreno, & Castillo, 2013; García & Ibáñez, 2016; Visani et al., 2022), an effect that has been related to the competition of motor resources involved action verb semantic processing with M1 motor output.

In this vein, our emotion recognition task, involving a semantic judgment that could share emotional and sensorimotor networks (including M1) with the perception of body expressions, might compete for neural resources with the perception of body expressions itself, thus inducing inhibition of M1 motor output, observed in MEPs. On the other hand, the gender discrimination task involves the processing of morphological cues that mostly tap into the ventral visual stream (Kanwisher, McDermott, & Chun, 1997; Tsantani et al., 2021; Urgesi, Candidi, et al., 2007; Wiese et al., 2012) and therefore this task does not demand the same emotional and sensorimotor resources required for processing body expressions. In this vein, the perception process of emotional bodies could occur freely by emotion and sensorimotor networks, in parallel with the semantic process of gender discrimination. Thus, the facilitation of M1 observed in the gender task could be representative of the ordinary processing of emotional signals observed when there is no interference or competition from another task. This proposal finds support in several MEP studies that have investigated the effects of passive viewing of emotional faces and scenes (Coelho, Lipp, Marinovic, Wallis, & Riek, 2010; Ferrari, Fiori, Suchan, Plow, & Cattaneo, 2021; Fiori, Ciricugno, Cattaneo, & Ferrari, 2023; Hajcak et al., 2007; Oliveri et al., 2003; Schutter, Hofman, & Van Honk, 2008). However, to draw firm conclusions about spontaneous motor modulations in the absence of instruction-driven attentional influences, direct evidence with passive viewing of emotional bodies is needed.

Our results support and extend previous evidence on hand motor control, by demonstrating that early motor physiological responses to emotional bodies, not just behavioral responses, can be modulated by task demands (Calbi et al., 2022). This is consistent with findings from early-mid ERP responses to emotional faces (i.e., N170), which show different modulations during explicit vs. implicit emotion perception tasks (Ashley, Vuilleumier, & Swick, 2004; Balconi & Lucchiari, 2005; Eimer & Holmes, 2002; Herrmann et al., 2002; Holmes, Vuilleumier, & Eimer, 2003; Santesso et al., 2008). Taken together, these findings indicate that both visual and motor responses to emotion are susceptible to top-down factors even at an early time window, in contrast with other MEP studies that have suggested that task-related influences can be traced only at later time windows (e.g., Ubaldi, Barchiesi, & Cattaneo, 2015).

Thus, while in previous studies (Borgomaneri, Gazzola, et al., 2015; Borgomaneri, Vitale, et al., 2020) we suggested interpreting MEP suppression as a process supporting the monitoring of salient signals (Fanselow, 1994; Frijda, 2010; Graziano, 2016; Hagenaars, Oitzl, & Roelofs, 2014; Lang & Bradley, 2010; Löw, Weymar, & Hamm, 2015), the present task-dependent findings suggest that MEP suppression could instead reflect a competing mechanism of interference/inhibition of body sensorimotor representations specific to explicit emotional judgments of emotional bodies.

MEP suppression is unlikely to be due to non-specific factors, such as task difficulty. If resource demands were a factor underlying a competing mechanism, the most difficult task (i.e., gender recognition) would have induced greater MEP suppression; however this was not the case. Additionally, the inhibitory and facilitatory influences exerted by the two tasks on MEPs remained even when task accuracy was matched (Table S2). This supports the interpretation that the observed MEP suppression reflects a specific sensorimotor mechanism of interference between an explicit semantic judgment and the inherent cortical processing of emotional body expressions.

One might wonder about the neural network underlying our findings. While the methodology employed in this study does not provide a direct answer, previous neuroimaging research has identified an extended network of brain regions that are active when observing emotional bodies, including visual, limbic, and parieto-frontal motor regions (de Gelder, Snyder, Greve, Gerard & Hadjikhani, 2004, de Gelder, de Borst & Watson, 2015). These frontal and subcortical regions have established connections with M1, either through direct projections or via premotor and supplementary motor areas (Cavada, Compañy, Tejedor, Cruz-Rizzolo, & Reinoso-Suárez, 2000; Grèzes, Valabrègue, Gholipour, & Chevallier, 2014; Morecraft & van Hoesen, 1998). These connections suggest a potential cortical pathway through which these regions may influence M1 during the perception of emotional bodies (Oliveri et al., 2003; Pessoa & Adolphs, 2010). During implicit emotional tasks, there is no notable additional activation within the network engaged during emotion perception compared to passive viewing (Dricu & Frühholz, 2016). Conversely, in explicit emotion recognition tasks, the network displays heightened activity, particularly within the occipitotemporal cortex, the amygdala and specific frontal areas such as the dorsomedial and inferior frontal cortex (Dricu & Frühholz, 2016), which also send projections to the M1 either directly and indirectly (Cavada et al., 2000; Grèzes, Valabrègue, Gholipour & Chevallier, 2014; Morecraft & van Hoesen, 1998; Oliveri et al., 2003) and could provide a substrate for the hypothesized competing mechanism during explicit recognition of emotional body expressions. Future studies using the dual-coil TMS procedures to map connectivity (Chiappini et al., 2020; Fiori et al., 2016, 2017) and/or to influence it (Borgomaneri et al., 2023; Fiori, Chiappini, & Avenanti, 2018; Turrini, Bevacqua, et al., 2023; Turrini et al., 2022; Turrini, Fiori, et al., 2023) could provide more direct evidence of cortico–cortical interactions between premotor regions and M1 during the perception of emotional body postures.

Prior studies on action observation (Avenanti, Bolognini, Maravita, & Aglioti, 2007; Tidoni, Borgomaneri, di Pellegrino, & Avenanti, 2013; Vicario et al., 2017) have reported that motor resonance effects are effector-specific. Our findings are in line with the idea that emotional stimuli induce effector-specific modulation of MEPs. Indeed, the emotional stimuli we have employed in the present study depict full body postures, and the upper limbs of the actors provide particularly useful information to discriminate between the different postures. It is important to note that we found hand MEP inhibition when participants explicitly had to recognize emotional bodies, and a prior work showed that MEP inhibition extended to several muscles of the upper limb (Borgomaneri et al., 2017); on the other hand, we found no hand MEP inhibition during explicit categorization of emotional faces (Borgomaneri et al., 2021). Future studies are needed to systematically test whether MEPs from facial and upper limb muscles would show effector-specific modulations when observing facial and body expressions.

It is worth mentioning that we specifically targeted the M1 in the right hemisphere, which is traditionally associated with emotion perception and attention (Borod, 2000; Gainotti, 2019; Hervé, Zago, Petit, Mazoyer, & Tzourio-Mazoyer, 2013; Toga & Thompson, 2003). This choice stems from our earlier research (Borgomaneri, Vitale, et al., 2020), which demonstrated that when stimulating the right M1 at this early temporal window (100–125 ms), we observed a reduction of MEP amplitudes when participants viewed emotional body postures (both fearful and happy) of male and female models, in comparisons to their neutral movements and static postures. Our current study aimed to explore how this MEP modulation, observed through right M1 stimulation, was influenced by the specific task being performed. While our conclusions are firmly rooted in observations related to the right M1, it is noteworthy that signs of motor suppression can indeed be identified in a similar early time window in both hemispheres (Borgomaneri, Vitale, Gazzola, et al., 2015), which may suggest that the current findings could in principle extent to the left M1 as well.

Lastly, our investigation revealed no discernible gender differences, despite prior studies having identified such differences in other aspects of motor reactivity, such as facial mimicry (e.g., Dimberg & Lundquist, 1990) and brain activity related to the processing of social and emotional information (Christov-Moore et al., 2014). While our sample size was adequate to detect the combined impact of the task and observed body expressions on MEPs, it is plausible that larger sample sizes may be necessary to detect potential gender-related effects. Conversely, though not definitively conclusive, the absence of gender-related effects in our current study aligns with the null findings we reported in our previous research, where the same set of stimuli and TMS parameters were employed (Borgomaneri, Vitale, et al., 2020).

5. Conclusions

In summary, our study demonstrates that observing emotional bodies elicits opposite effects on motor excitability, depending on the specific task being performed. Attending to emotional features was linked to early motor inhibition, whereas attending to non-emotional features was associated with early motor facilitation. These results point to a competing mechanism involving interference or inhibition of body sensorimotor representations that is specific to emotional bodies when attention is directed towards their emotional features. Our research contributes to understanding embodied cognition mechanisms that link perception of emotions and action tendencies.

Credit author statement

Conceptualization: Avenanti; Methodology: Borgomaneri, Avenanti; Software: Borgomaneri; Formal analysis:

Borgomaneri, Vitale; Investigation: Borgomaneri, Vitale; Resources: Avenanti; Data curation: Borgomaneri, Vitale; Visualization: Battaglia; Writing-original draft: Borgomaneri, Vitale, Avenanti; Writing-review and editing: Borgomaneri, Vitale, Battaglia, de Vega, Avenanti; Supervision: de Vega, Avenanti; Funding acquisition: Avenanti, Borgomaneri. All authors have read and agreed to the published version of the manuscript.

Open practices section

The study in this article earned Open Data and Open Material badges for transparent practices. The data and material that support the findings of this study are openly available at: https://osf.io/3zehm/

No analysis code was used.

Declaration of competing interest

Authors have nothing to declare.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2023.10.013.

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