



Early motor reactivity to observed human body postures is affected by body expression, not gender

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ARTICLE INFO

Keywords:

Emotional body
Transcranial magnetic stimulation
Motor-evoked potentials
Gender
Orienting motor response

ABSTRACT

The early response to emotional stimuli involves a transient suppression of motor reactivity to favor monitoring of emotionally relevant information. Using transcranial magnetic stimulation (TMS), we have previously shown that viewing emotional body postures induces an early and transient reduction in motor excitability. Yet, it remains unclear whether early motor responses to emotional bodies are automatic or influenced by top-down factors such as task- or gender-related effects. To address these issues, we administered TMS over the right motor cortex (M1) during observation of still pictures of fearful expressions, happy expressions, neutral movements and neutral static body postures, and recorded motor-evoked potentials (MEPs) at an early phase of processing (i.e., at 100–125 ms from stimulus onset). To test gender-related effects, we presented male and female models to male and female participants. To test task-related effects, we asked participants to categorize the different body postures into either four (4AFC: fearful, happy, neutral movements, or static postures) or two distinct categories (2AFC: emotional or neutral postures). Results showed a reduction of MEPs for fearful and happy body postures relative to neutral movements and static postures. This motor suppression was not influenced by the gender of the actor, the gender of the observer, or the task performed. These findings indicate that early motor responses to observed human body postures are affected by the type of expression displayed by the observed model more than by task- or gender-related effects, suggesting these responses may be relatively automatic.

1. Introduction

Bodily expressions convey important information about another person's feelings and intentions. Indeed, emotional body postures represent a powerful, salient stimulus that is efficiently processed by the human visual system (Martinez et al., 2016; Meeren et al., 2005, 2016; Stekelenburg and de Gelder, 2004) and strongly impacts on spatial orienting as shown, for example, by saccade latencies in healthy participants (Bannerman et al., 2010, 2009) and an increase in attentional selection in neglect patients (Tamietto et al., 2007). Processing emotional body expressions recruits a complex neural network which includes visual areas, but also cortical and subcortical regions involved in emotional processing (e.g., the amygdala, anterior insula, and orbitofrontal cortex) and fronto-parietal and cerebellar sensorimotor regions

involved in action planning and execution (de Gelder et al., 2010; Ferrari et al., 2019; Meeren et al., 2016; Tamietto and de Gelder, 2010). Activation of visual areas occurs rapidly when watching emotional bodies as shown by early components of event-related potentials (ERPs), such as the P1, N1, and N190 (Borhani et al., 2016, 2015; Jessen and Kotz, 2011; van Heijnsbergen et al., 2007), suggesting a rapid allocation of cognitive resources for monitoring biologically relevant signals.

The motor system also appears to be rapidly engaged when watching emotional bodies. In a series of transcranial magnetic stimulation (TMS) studies, we explored the chronometry of motor responses to emotional bodies by recording motor-evoked potentials (MEPs) induced by motor cortex (M1) stimulation (Borgomaneri et al., 2017, Borgomaneri et al., 2015a, 2015b, 2015c, 2012). We presented pictures of fearful, happy, and emotionally neutral human body postures to healthy participants

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and tested changes in MEPs in an early time window, i.e., at 70–300 ms from picture onset. We found that emotional bodies decreased early MEP amplitudes (i.e., at 70–150 ms from picture onset; Borgomaneri et al., 2017, Borgomaneri et al., 2015a, 2015b, 2015c), with a tendency for fearful bodies to affect the earliest responses (e.g., Borgomaneri et al., 2015c) and a consistent MEP suppression for both fearful and happy bodies at later times (e.g., Borgomaneri et al., 2015a). Suppression of motor output was detected in both hemispheres (Borgomaneri et al., 2015b), generalized to several muscles of the upper limb (Borgomaneri et al., 2017), and was stronger in participants showing anxiety-related personality traits (Borgomaneri et al., 2017, Borgomaneri et al., 2015a). We interpreted this suppression of motor output as reflecting an orienting/freezing mechanism supporting monitoring of social signals that are relevant for survival (Fanselow, 1994; Frijda, 2010; Graziano, 2016; Hagenaaers et al., 2014; Lang and Bradley, 2010; Löw et al., 2015). Thus, while these early motor responses to emotional bodies appear to reflect automatic responses supporting perception, it remains unclear whether such responses are sensitive to manipulations of social or task-related factors.

A growing body of research has reported gender differences in the neural network involved in processing social and emotional information (Christov-Moore et al., 2014; Dickie and Armony, 2008; Hofer et al., 2006; Kemp et al., 2004; Kret et al., 2011). For example, studies have suggested greater reactivity to emotional stimuli in females, particularly for negatively valenced stimuli (e.g., García-García et al., 2016). Moreover, males and females have been reported to show stronger right and left hemispheric lateralization, respectively, when they are exposed to emotional stimuli (Cahill et al., 2004; Fine et al., 2009; Killgore and Cupp, 2002; Schienle et al., 2005). Additionally, studies have reported that the gender of the person we observe can influence the neural network underlying emotion perception, with male and female models differentially affecting male and female observers (Aleman and Swart, 2008; Fischer et al., 2004; Kret et al., 2011). These findings have typically supported the evolutionary idea that body expressions of threat conveyed by males could signal a larger threat and may thus be more relevant to the observer (e.g., Kret et al., 2011). However, only one prior electrophysiological study used emotional bodies to test gender-related effects (He et al., 2018). This study reported that both the model's and the observer's gender affected the amplitude of the earliest occipito-temporal response to emotional bodies (i.e., the P1 component at ~100–125 ms from stimulus onset). On the other hand, in our previous work investigating MEP responses to emotional bodies, we used only male models and did not test the influence of the observer's gender. Therefore, it remains unclear whether gender-related factors influence early motor responses to emotional bodies.

Another relevant issue for deepening our understanding of early motor reactions to emotional bodies is the conditions under which these motor responses are detected. In our previous series of MEP studies, we observed early motor responses to emotional bodies using an active categorization task, in which participants were asked to categorize still pictures of body postures as a fearful, joyful, or neutral posture with implied motion (i.e., neutral body movement) or a neutral static posture. We used an explicit emotional categorization task because previous imaging (Gur et al., 2002; Habel et al., 2007; Hariri et al., 2003; Winston et al., 2003), TMS (Oliveri et al., 2003) and ERP studies (Mikhailova and Bogomolova, 2000) have shown that active categorization maximizes the chance of detecting emotion-specific modulations in different brain regions, including the motor system. Task demands can affect ERPs evoked by emotional faces (e.g., Itier and Neath-Tavares, 2017; Neath-Tavares and Itier, 2016) and, to date, one study has shown task-related influences on early cortical responses to emotional bodies (i.e., the N100 amplitude; Jessen and Kotz, 2011). However, it remains unclear whether the type of emotional categorization affects the strength of early motor responses to emotional bodies.

Here, we sought to deepen our knowledge about early motor responses to emotional bodies by testing the influence of task and gender

effects using single pulse TMS. To assess early motor responses to emotional bodies, we stimulated the right M1 in an early time window during the presentation of fearful, happy, neutral, and static body postures. We administered TMS pulses at 100–125 ms from picture onset, corresponding to the latencies of the P1 and the N1 (i.e., ERP components that have shown sensitivity to emotion, gender and task-related effects; He et al., 2018; Jessen and Kotz, 2011; van Heijnsbergen et al., 2007), and recorded changes in MEPs. We aimed to expand prior work that investigated motor excitability during the observation of male body postures (e.g., Borgomaneri et al., 2012) by testing male and female participants during exposure to both male and female body postures, in order to investigate the influence of gender-related effects in early motor reactivity. Moreover, to test the influence of task-related effects in early motor reactivity, we asked participants to categorize the different body postures into either four categories (fearful, happy, neutral, or static postures) or two categories (emotional or neutral postures). We hypothesized that emotional body postures would reduce motor excitability relative to emotionally neutral body postures, supporting the notion of an early orienting response for monitoring emotional signals.

To detect a possible effect of gender and/or task, we tested a time window similar to that observed in prior ERP studies on emotional bodies (He et al., 2018; Jessen and Kotz, 2011). However, if early motor responses to emotional bodies reflect early automatic processing, we would expect little or no influence of gender- and task-related factors. Lastly, we expected no MEP differences between the two explored time-points (100 vs. 125 ms) as we assumed these time-points would reflect a similar functional stage (Borgomaneri et al., 2017, 2015c).

2. Methods

2.1. Participants

Twenty-eight healthy participants took part in the study. Participants were randomly assigned to two TMS experiments: 14 participants (6 men, mean age \pm S.D.: 24.1 years \pm 2.3) were assigned to Experiment 1 and another 14 (6 men, 21.2 y \pm 2.5) were assigned to Experiment 2. Two different emotion categorization tasks were used with the same stimuli: a four alternative forced choice (4AFC) task in Experiment 1 and a two alternative forced choice (2AFC) task in Experiment 2. No prior study tested the influence of gender or task demands on MEP responses to emotional bodies. Therefore, sample size was chosen based on two ERP studies testing the influences of gender and task on the early cortical response to emotional bodies. We conducted two power analyses using G*Power 3 (Faul et al., 2007). For gender- and task-related influences, we considered an effect size of *partial eta*² (η_p^2) = 0.1 (He et al., 2018) and η_p^2 = 0.15 (Jessen and Kotz, 2011), respectively. Sample size estimations indicated that 24–26 participants would be necessary to detect significant effects with a power $(1 - \beta) = 0.95$ and $\alpha = 0.05$. Therefore, we decided to test 28 participants divided into subgroups. This sample size is twice the number of participants in previous work on early motor responses to emotional bodies (Borgomaneri et al., 2017, 2015a, 2015b, 2015c), where the median sample size was 14 participants (range: 13–20 participants). All participants were right-handed, had normal or corrected-to-normal vision, and were naïve to the purposes of the experiment. All participants were free from any contraindications to TMS (Rossi et al., 2011). They gave their written informed consent to take part in the study, which was approved by the ethics committee of the University of Bologna and carried out in agreement with legal requirements and international norms of the Declaration of Helsinki (World Medical Association, 2013). No discomfort or adverse effects were reported or noticed during TMS.

2.2. Visual stimuli

Pictures were presented on a 19-inch screen located about 80 cm

away from the participant. Sixteen pictures depicting two male actors and sixteen pictures depicting two female actors in emotional and neutral body postures were selected from a validated database (Borgomaneri et al., 2020, 2015a, 2015c, 2012). The stimuli were well recognized as prototypical representations of the different postures and controlled for emotional variables. To minimize individual differences, all actors wore the same swimming cap and identical black boxers, and all the women wore an elastic band over the breast. Moreover, to focus specifically on body-related information and to ensure that expression recognition was not compromised by morphological differences between males and females, the face was blanked out in all the pictures and the chest of each body was occluded using a black strip (Fig. 1a). 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.

Both experiments presented a total of 64 stimuli (half were the original versions of the stimuli and half were mirror-reflected copies), equally divided into four body posture conditions: 16 fearful postures, 16 happy postures, 16 neutral body movements ("neutral"), and 16 neutral static body postures ("static"). Each expression condition was composed of 8 male and 8 female pictures.

2.3. TMS and electromyography (EMG) recording

MEPs were recorded by stimulating the left first dorsal interosseous (FDI) representation in the right motor cortex. MEPs were induced 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). Pairs of silver-chloride surface electrodes were placed in a belly-tendon montage over the left FDI with ground electrodes on the right wrist (for hand muscles). 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.

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 hand area of the right M1 was defined as the point where stimulation consistently evoked the largest MEP in the left FDI. In both experiments, TMS intensity was set at 120% of the resting motor threshold (rMT), which was defined as the minimal intensity of stimulator output that evoked 5 small responses (~50 μ V) in the relaxed FDI muscle in a series of 10 stimuli (Rossini et al., 2015). Mean motor thresholds (\pm standard deviation) were $37.7\% \pm 6$ and $34.1\% \pm 3.5$ of

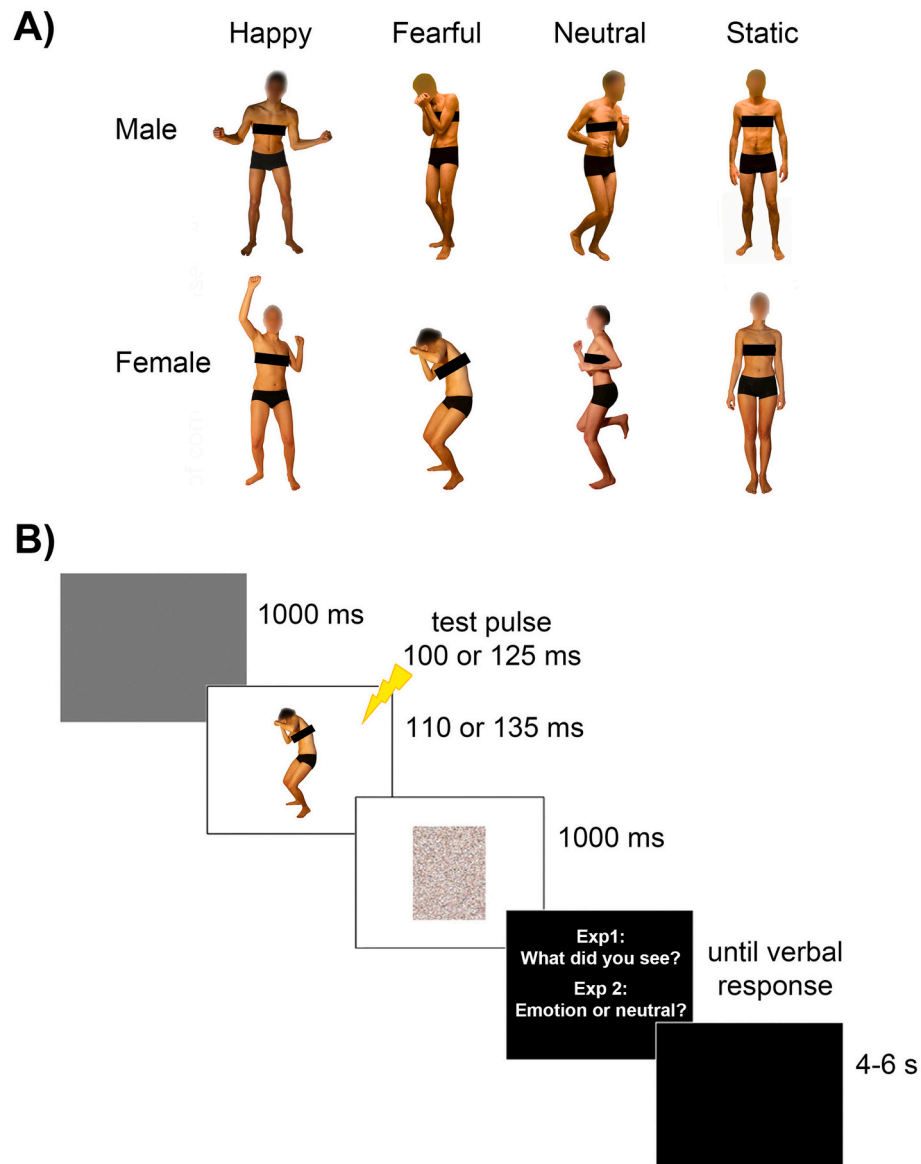


Fig. 1. Stimuli and task. A) Examples of male and female body stimuli showing happy, fearful, neutral, and static body postures. B) Trial example.

the maximum stimulator output in Experiment 1 and 2, respectively. 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

Each experiment consisted of 128 trials divided into 2 blocks. The experiments were programmed using Matlab software to control picture presentation and to trigger TMS pulses. Each trial started with a grey screen (1-s duration), followed by the test picture projected at the center of the screen (Fig. 1b). Then, a random-dot mask (obtained by scrambling the sample stimulus with image segmentation software) lasting 1 s appeared, and, finally, the question “What did you see?” was displayed on the screen. In Experiment 1, participants performed a 4AFC task in which they had to recognize the expression presented by the model out of four alternatives: “happy”, “fearful”, “neutral” (i.e., neutral body movement), or “static” (i.e., neutral static) posture. In Experiment 2, the task was to categorize whether the body expressed an emotion or presented a neutral expression (2AFC task), thus requiring a more abstract cognitive operation. The participants responded verbally (forced choice) and an experimenter collected the answers by pressing a computer key. In order to avoid any effect (influence) of the verbal response on motor excitability, the participants were instructed to answer 2–3 s after the pulse was delivered. After the response, the screen appeared black for 4–6 s, ensuring an inter-pulse interval greater than 10 s and thereby avoiding changes in motor excitability due to TMS per se (Chen et al., 1997).

In half the trials, the stimulus was presented 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. Before and after the experimental session, two blocks of 20 MEPs were recorded to serve as a baseline.

After TMS, participants were presented with all the stimuli (in a randomized order) and asked to judge 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 analyzed offline. For each condition we averaged the MEP amplitude values measured peak to peak. MEPs associated with incorrect answers were removed from the analysis (~3%). We also discarded MEPs with preceding background EMG deviating from the mean by more than 2 SD (~1%), because it is known that background EMG affects motor excitability (Devanne et al., 1997). To normalize the data distribution, a logarithmic transformation was applied to the MEP values [$\log(\text{mean MEP amplitude value} + 1)$]. Then the logarithmic values of MEPs recorded during the baseline were subtracted from the logarithmic values of MEPs recorded during the experimental conditions. MEP contrasts (condition-baseline) were entered in a five-way mixed factors ANOVA with ‘Task’ (2 levels: 4AFC and 2AFC) and ‘Observer gender’ (2 levels: male and female) as between-subjects factors and ‘Time’ (2 levels: 100 and 125 ms), ‘Model gender’ (2 levels: male and female), and ‘Model body expression’ (4 levels: happy, fearful, neutral, and static) as within-subjects factors. Post-hoc comparisons were performed using Duncan’s test. The η_p^2 was computed as a measure of effect size for ANOVA main effects and interactions, whereas repeated measures Cohen’s d was computed for post-hoc comparisons (Cohen, 1992). Accuracy across task and gender groups was assessed using a nonparametric Kruskal-Wallis ANOVA and VAS ratings of arousal, valence, and perceived motion were analyzed through nonparametric Friedman ANOVAs, since these measures were

not normally distributed. Post-hoc comparisons within and between groups were conducted using Bonferroni-corrected Wilcoxon matched pairs tests and Mann-Whitney U tests, respectively.

3. Results

3.1. Neurophysiological data

The Task \times Observer gender \times Model gender \times Model body expression \times Time ANOVA on MEP contrasts showed a significant main effect of Model body expression ($F_{3,72} = 3.10$; $p = 0.03$; $\eta_p^2 = 0.11$) driven by a reduction in MEPs when viewing emotional bodies (Fig. 2). Indeed, post-hoc analyses showed that MEP amplitudes recorded while viewing fearful bodies (mean MEP amplitude \pm SD: $0.021 \text{ mV} \pm 0.076$) were lower compared to neutral bodies ($0.033 \text{ mV} \pm 0.075$; $p = 0.04$; Cohen’s $d = 0.16$) and static bodies ($0.035 \text{ mV} \pm 0.068$; $p = 0.03$; Cohen’s $d = 0.19$) which in turn did not differ from one another ($p = 0.76$). Moreover, happy bodies were associated with smaller MEPs ($0.022 \text{ mV} \pm 0.079$) compared to neutral bodies ($p = 0.04$; Cohen’s $d = 0.15$) and static bodies ($p = 0.03$; Cohen’s $d = 0.18$). MEPs recorded during observation of fearful and happy bodies did not differ from one another ($p = 0.91$).

Thus, the two emotional body postures were associated with lower MEP amplitudes compared to the neutral body postures (mean MEP difference \pm SD: $-0.012 \text{ mV} \pm 0.017$). This effect was comparable across the two tasks (Experiment 1: $-0.014 \text{ mV} \pm 0.013$; Experiment 2: $-0.011 \text{ mV} \pm 0.021$; $F_{3,72} = 0.17$; $p = 0.91$; $\eta_p^2 = 0.07$) and unaffected by the participant’s gender (female: $-0.016 \text{ mV} \pm 0.018$; male: $-0.007 \text{ mV} \pm 0.015$; $F_{3,72} = 0.56$; $p = 0.65$; $\eta_p^2 = 0.02$) or the model’s gender (female: $-0.008 \text{ mV} \pm 0.022$; male: $-0.017 \text{ mV} \pm 0.033$; $F_{3,72} = 1.70$; $p = 0.18$; $\eta_p^2 = 0.07$). No other main effects or interactions were significant in the ANOVA (all $F < 2.17$; $p > 0.10$). See Fig. 3 for an example of raw MEPs from two representative participants.

3.2. Behavioral data

Mean task accuracy was high (mean accuracy \pm standard deviation: $97\% \pm 3$) and comparable across the two tasks and gender groups (Kruskal-Wallis $H = 3.72$, $p = 0.29$).

The Friedman ANOVA on arousal ratings showed significant differences between the models’ body expressions ($\chi^2 = 66.29$; $p < 0.001$). Table 1 shows that arousal for happy and fearful bodies was comparable ($p = 0.64$) and greater than for neutral and static bodies (all $p < 0.001$). Neutral bodies had higher arousal ratings than static bodies ($p < 0.001$). Table S1 shows that, across expressions, no differences in arousal were found between male and female models (all $p > 0.24$), between male and female observers (all $p > 0.57$), or between the two tasks (all $p > 0.41$).

The Friedman ANOVA on valence scores showed significant differences between body expressions ($\chi^2 = 73.66$; $p < 0.001$). Table 1 shows that valence scores were higher for happy body postures compared to all the other expressions (all $p < 0.001$) and lower for the fearful body postures relative to all the other expressions (all $p < 0.001$). Neutral body postures were rated as more positive than static postures ($p < 0.0001$). Table S2 shows that, across expressions, no differences in valence were found between male and female models (all $p > 0.26$), between male and female observers (all $p > 0.63$), or between the two tasks (all $p > 0.15$).

Friedman ANOVA on implied motion scores showed significant differences across body expressions ($\chi^2 = 52.33$; $p < 0.001$). Table 1 shows that still pictures of moving bodies (i.e., fearful, happy and neutral movements) obtained higher scores in implied motion than static body postures (all $p < 0.001$), while no differences were observed across body stimuli with implied motion (all $p > 0.19$). Table S3 shows that across expressions, no differences in implied motion was found between male vs. female models (all $p > 0.08$), male vs. female observers (all $p > 0.38$) or between the two tasks (all $p > 0.76$).

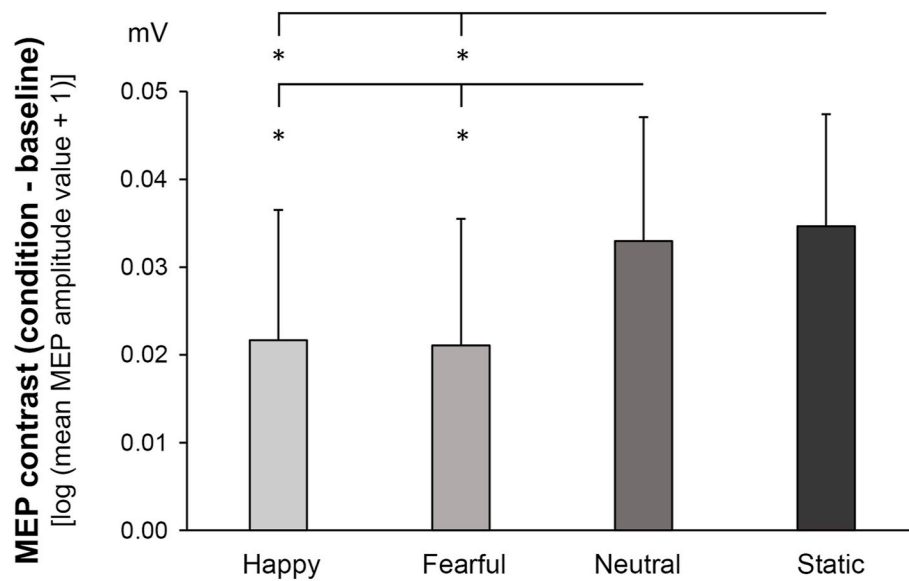


Fig. 2. Mean MEP contrast (condition - baseline) during observation of happy, fearful, neutral, and static body postures. Data represent the main effect of the factor Model body expression (average of the two time points, tasks, model genders, and observer genders) showing a reduction in MEPs for emotional bodies. Error bars indicate SEM. Asterisks (*) denote significant post-hoc comparisons ($p < 0.05$).

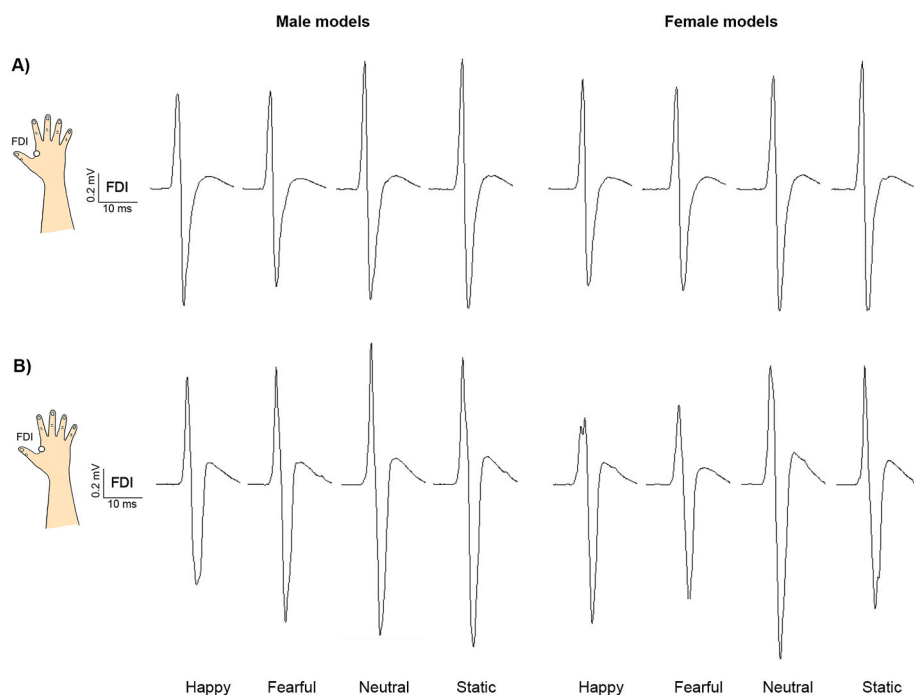


Fig. 3. Examples of raw MEPs recorded from the FDI muscles of two representative participants in Experiment 1 (a male participant, A) and Experiment 2 (a female participant, B) during observation of the different body postures of male models (left) and female models (right). The median MEP from each participant's distribution of MEP amplitudes in each condition (Model gender x Model body expression) is shown.

4. Discussion

In this study, we investigated whether early motor responses to human body postures mainly reflect an automatic process tuned to emotional expressions, or whether they are influenced by social factors (i.e., gender) or the type of task performed by the observer. To this aim we acquired MEPs in an early time window during the observation of emotional and neutral body postures (i.e., at 100–125 ms from stimulus onset, which corresponds to the temporal window of the P1 and N1 components of ERPs). We found that seeing the fearful and happy body

expressions of male and female models reduced motor excitability relative to seeing neutral and static body postures, and that this neurophysiological effect was not affected by any other factors (i.e., gender of the model/observer, type of task). These findings are relevant to computational models of emotional body perception (e.g., Schindler et al., 2008) as they show that, in an early time window, the observer's motor system is primarily engaged in processing emotional features of observed bodies, whereas other attributes (e.g., gender) are likely processed at a later stage or in other brain structures.

These findings confirm and expand previous reports showing that, at

Table 1

Mean arousal, valence, and implied motion ratings of the different body postures (averaged across model gender, observer gender, and task).

	Happy expressions	Fearful expressions	Neutral movements	Static postures
Arousal	3.34 ± 0.76	3.38 ± 0.91	2.36 ± 0.58	1.21 ± 0.37
Valence	4.39 ± 0.39	1.50 ± 0.53	2.87 ± 0.61	2.53 ± 0.73
Implied motion	3.29 ± 0.70	3.29 ± 0.79	3.13 ± 0.50	1.09 ± 0.33

a similar latency (e.g., 150 ms from stimulus onset), motor excitability is reduced during observation of emotional (male) body postures (Borgomaneri et al., 2015a). These findings support the hypothesis of an orienting/freezing mechanism that suppresses motor output to favor monitoring of biologically relevant signals (Fanselow, 1994; Frijda, 2010; Graziano, 2016; Hagenaaers et al., 2014; Lang and Bradley, 2010; Löw et al., 2015). Our findings are in line with previous behavioral work showing reduced motor output during monitoring of arousing stimuli (e.g., Hagenaaers et al., 2014). They are also in line with prior TMS experiments that have documented fast and transient reductions in motor excitability following salient stimuli, such as strong, unexpected, or rapidly approaching auditory or visual stimuli (Avenanti et al., 2012; Cantello et al., 2000; Furubayashi et al., 2000; Makin et al., 2009; Serino et al., 2009). Similar results have been found with emotionally negative stimuli, such as pictures showing revulsive foods, highly disapproved moral violations (Vicario et al., 2020, 2017b; 2017a), or painful stimuli, either self-experienced (Farina et al., 2003, 2001; Urban et al., 2004) or observed in others (Avenanti et al., 2009b, 2009a, 2006) – particularly when the observed painful stimuli are presented near the participant's body (Mahayana et al., 2014 i.e., within the boundaries of peripersonal space; see di Pellegrino and Ladavas, 2015; Serino, 2019).

In keeping with these prior studies, the present findings support theoretical models of emotion that assume a critical link between emotion and motor systems (Blair, 2003; Frijda, 1986; Lang et al., 1990; Tamietto and de Gelder, 2010). Emotional body postures serve a key communicatory role by allowing rapid transmission of emotional information from one individual to another (Blair, 2003; de Gelder et al., 2010). Emotional body postures represent biologically relevant stimuli that could signal important information to the observer. For example, happy expressions could signal a positive attitude, whereas fearful expressions could signal potential threats in the surrounding environment (Davis and Whalen, 2001; Kret et al., 2013; Lee et al., 2013; Phelps et al., 2006; Whalen et al., 1998). Thus, a reduction in motor output would support the attempt to garner more sensory information about positive social stimuli or potential threats. In line with the hypothesis that MEP suppression reflects a motor response supporting sensory processing, we have previously reported that the MEP suppression detected by probing the right motor cortex (at 150 ms from stimulus onset) was associated with impaired recognition of body postures, suggesting this region was functionally relevant to perceptual recognition (Borgomaneri et al., 2015a).

While we focused on the human motor cortex, prior magnetoencephalography evidence has shown that posterior parietal areas are also active in the same time window (Meeren et al., 2016) and TMS targeting of these parietal areas affects perception of emotional bodies (Engelen et al., 2015; Mazzoni et al., 2017). Taken together, these findings suggest that extended fronto-parietal networks dynamically interact for perceiving and preparing adaptive responses to social and emotional signals (Avenanti et al., 2013; Engelen et al., 2018; Paracampo et al., 2018a, 2018b, 2017; Pitcher et al., 2008).

Importantly, our design allowed us to test whether adaptive motor responses are affected by gender-related influences. Participant gender is a well-documented moderator of both psychological and neurophysiological effects, with men and women consistently differing on mean

levels of emotional intelligence (Salguero et al., 2012), the tendency to display emotions (in terms of frequency rather than intensity; Kring and Gordon, 1998), and laterality of brain activations during cognitive and affective tasks (Cahill, 2006; Cahill et al., 2004; Canli et al., 2002). ERP studies have reported that early components reflecting attention (e.g., the N1) are larger for negatively valenced or unpredictably threatening stimuli in women relative to men (Jin et al., 2013; Lithari et al., 2010), whereas men showed larger P3 amplitudes for the faces of attractive females relative to attractive males (Oliver-Rodríguez et al., 1999). Similar findings were recently reported for emotional bodies, with larger P1 responses to threatening male bodies in women and larger P3 amplitudes for female bodies in male observers (He et al., 2018). Despite these reports of gender-related modulations, we found no gender-related effects on early motor responses to emotional bodies. Indeed, MEPs were consistently suppressed when seeing happy and fearful body postures, and this modulation appeared similar for both male and female models and across male and female observers.

These findings suggest that at an early phase of processing – i.e., at 100–125 ms from stimulus onset – the observer's M1 is sensitive to emotion but not gender information and shows no difference between male and female observers, in contrast to the visual system which appears sensitive to both effects (He et al., 2018). These findings can therefore inform models of emotional body perception (e.g., Schindler et al., 2008) by suggesting that, while emotion information is processed by both visual and motor systems, in an early stage, body attributes like gender are mostly processed within the visual system (i.e., He et al., 2018). It is possible that the observer's M1 might process gender attributes at a later time window. However, the lack of sensitivity to gender information appears to be in line with prior imaging work showing that dancers' motor systems are more sensitive to the specific bodily movements performed by an observed agent than to her/his gender (Calvo-Merino et al., 2006, 2005) and with TMS evidence that interference with the motor system disrupts the ability to discriminate between two observed actions, but not the ability to discriminate between two bodies making similar actions (Urgesi et al., 2007a, 2007b).

Motor responses to emotional bodies appeared very similar across the 4AFC and 2AFC tasks performed by participants. This finding would further support the idea that early motor reactivity reflects an automatic response favoring monitoring of body expressions. It is also possible that, later in time, task demands could have a larger impact on the motor system. This would be in line with prior work showing that stimulus-driven motor responses can be detected when testing MEPs in a time range similar to that used here, whereas task-related influences can be traced at later time windows (e.g., Ubaldi et al., 2015). On the other hand, it should be noted that both our tasks involved explicit categorization of the observed body postures, so the differences in the types of cognitive processes involved (i.e., direct recognition of the observed expressions in the 4AFC task vs. a more abstract categorization in the 2AFC task) may be minimal. Thus, future work is needed to test additional types of tasks and contrast explicit categorization with the recognition of other body attributes (e.g., identity/gender).

Our study has further limitations. First, the sample size was not large and this may have limited the possibility of observing weak effects of gender or task. However, the sample size was chosen based on prior ERP work showing such effects during observation of emotional bodies (He et al., 2018; Jessen and Kotz, 2011). Moreover, we observed an influence of body posture, ruling out the possibility that MEPs are simply not a sensitive measure. Second, we recorded MEPs by targeting M1 with only a single pulse of TMS. This method allowed us to assess global changes in corticospinal motor excitability. Yet, previous work has suggested that MEPs induced by paired-pulse TMS – which assesses changes in intracortical excitatory circuits mediated by glutamate (Di Lazzaro et al., 2000; Kujirai et al., 1993) – may be a more sensitive measure during perception of emotional signals (e.g., Borgomaneri et al., 2017, 2015b). Moreover, we only tested the left FDI/right M1 and future studies could investigate other sectors of the motor system, to verify whether similar

effects would be observed in both hemispheres or in different muscles, as an orienting/freezing interpretation would suggest. Lastly, our study does not clarify the neural pathways through which early motor responses to emotional bodies can be implemented. In principle, both cortical (occipito-temporal, parieto-frontal) and subcortical (amygdala, periaqueductal grey, superior colliculus) networks are connected with different segments of the motor pathway and could provide signals to M1 during the processing of emotional bodies (de Gelder et al., 2010; Ferrari et al., 2019; Grèzes et al., 2014; Tamietto and de Gelder, 2010).

In conclusion, we observed an early reduction in motor excitability for fearful and happy body postures relative to neutral postures. This motor suppression was not influenced by the gender of the actor, the gender of the observer, or the task performed. These findings indicate that early motor responses to observed human body postures are more affected by the type of expression displayed by the observed model than by task- or gender-related effects, suggesting these responses may be automatic.

Declaration of competing interests

The authors declare no competing interests.

CRediT authorship contribution statement

Sara Borgomaneri: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Software, Writing - review & editing. **Francesca Vitale:** Data curation, Formal analysis, Visualization, Writing - review & editing. **Alessio Avenanti:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Resources, Supervision, Writing - original draft.

Acknowledgments

This work was supported by grants from the Bial Foundation, Portugal [347/18], Fondazione del Monte di Bologna e Ravenna, Italy [339bis/2017] and Ministero Istruzione, Università e Ricerca, Italy [2017N7WCLP] awarded to A.A., and by grants from the Ministero della Salute, Italy [GR-2018-12365733] awarded to S.B. The authors thank Brianna Beck for proofreading the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuropsychologia.2020.107541>.

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