Seeing fearful body language rapidly freezes the observer's motor cortex.

Seeing fearful body language rapidly freezes the observer's motor cortex

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Abstract

Fearful body language is a salient signal alerting the observer to the presence of a potential threat in the surrounding environment. Although detecting potential threats may trigger an immediate reduction of motor output in animals (i.e., freezing behavior), it is unclear at what point in time similar reductions occur in the human motor cortex and whether they originate from excitatory or inhibitory processes. Using single-pulse and paired-pulse transcranial magnetic stimulation (TMS), here we tested the hypothesis that the observer's motor cortex implements extremely fast suppression of motor readiness when seeing emotional bodies – and fearful body expressions in particular. Participants observed pictures of body postures and categorized them as happy, fearful or neutral while receiving TMS over the right or left motor cortex at 100–125 msec after picture onset. In three different sessions, we assessed corticospinal excitability, short intracortical inhibition (SICI) and intracortical facilitation (ICF). Independently of the stimulated hemisphere and the time of the stimulation, watching fearful bodies suppressed ICF relative to happy and neutral body expressions. Moreover, happy expressions reduced ICF relative to neutral actions. No changes in corticospinal excitability or SICI were found during the task. These findings show extremely rapid bilateral modulation of the motor cortices when seeing emotional bodies, with stronger suppression of motor readiness when seeing fearful bodies. Our results provide neurophysiological support for the evolutionary notions that emotion perception is inherently linked to action systems and that fear-related cues induce an urgent mobilization of motor reactions.

1. Introduction

Different lines of evidence suggest that threat-related signals are rapidly and efficiently processed in the central nervous system (Adolphs and Tranel, 2003, LeDoux, 1996, Öhman and Mineka, 2001) and that attention tends to be prioritized towards threatening stimuli (Fox et al., 2000, Vuilleumier, 2002).
Fearful body language is a salient emotional signal, easily observable from a distance that alerts the observer to the presence of a potential threat (de Gelder et al., 2004, Tamietto et al., 2007). Perceiving fearful expressions in others requires specific processing in an attempt to garner more information about the source of the threat in the surrounding environment (Whalen et al., 1998). Indeed, behavioral studies have shown enhanced sensory acquisition (Lee, Susskind, & Anderson, 2013), perceptual processing (Phelps, Ling, & Carrasco, 2006) and attention (Davis and Whalen, 2001, Kret et al., 2013) when exposed to fearful expressions. Notably, electrophysiological studies have also reported a rapid bias in visual attention allocation with greater resources devoted to fearful expressions; they reported increased amplitudes or shorter latencies of early (100–200 msec) occipito-temporal event-related potential (ERP) components when viewing fearful body expressions (Jessen and Kotz, 2011, Van Heijnsbergen et al., 2007) and facial expressions (Pourtois et al., 2005, Righart and de Gelder, 2006, Williams et al., 2006) relative to emotionally positive and neutral expressions.
Besides increasing sensory vigilance for monitoring potential threats, the sight of fearful expressions may affect the motor system. Animal research has shown that initial reactions to sudden stimuli - and potential threats, in particular - involve reducing motor output, i.e., implementing freezing behavior or orienting immobility while monitoring the source of danger (Fanselow, 1994; Hagenaars, Oitzl, & Roelofs, 2014). Similar phenomena have been suggested in humans (Fanselow, 1994, Frijda, 2010, Hagenaars et al., 2014, Lang and Bradley, 2010). In keeping with this notion, transcranial magnetic stimulation (TMS) studies have

documented fast reductions in motor excitability following salient and potentially noxious stimuli like 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), and painful stimuli self-experienced (Farina et al., 2003, Farina et al., 2001, Urban et al., 2004) or observed in others (Avenanti et al., 2006, Avenanti, Minio-Paluello, Bufalari, et al., 2009a, Avenanti, Minio-Paluello, Sforza, et al., 2009b). Moreover, a reduction of activity in primary motor cortex (M1) has been reported during periods in which participants expect to receive painful stimuli relative to conditions without pain expectation (Butler et al., 2007). Remarkably, imaging studies have shown that observing fearful expressions in others activates subcortical (e.g., amygdala, superior colliculus) and cortical regions (e.g., cingulate cortex and supplementary motor area, SMA) known to be involved in emotional processing and motor control (de Gelder et al., 2004, de Gelder et al., 2010, Grèzes et al., 2007, Hadjikhani and de Gelder, 2003, Kret et al., 2011, Thielscher and Pessoa, 2007, Vuilleumier et al., 2001, Vuilleumier and Pourtois, 2007). However, the nature of such activations is ambiguous because imaging can hardly distinguish between motor inhibition (which would support freezing-like body immobilizations) and excitation (which would reflect increased action readiness) and cannot precisely determine when these modulations occur. On the other hand, the high temporal resolution of TMS and its ability to distinguish between excitatory and inhibitory activity in motor areas allow effective exploration of motor dynamics during emotion perception.

The goal of this study was to test whether exposure to fearful body postures rapidly reduces excitability in the observer's M1. To this aim, we used TMS over M1 to non-invasively assess motor excitability during perception of emotional body expressions. In previous studies, we started to investigate the dynamics of the human motor system by assessing corticospinal excitability in the observers' left and right M1 during an emotion recognition task (Borgomaneri et al., 2012, Borgomaneri et al., 2014b). We recorded motor-evoked potentials (MEPs) at 150 and 300 msec after the presentation of fearful, happy and neutral expressions in which the body posture was presented in isolation, with no contextual or facial cues. In the earlier time window (150 msec) we found a weak increase in corticospinal excitability in the left hemisphere in response to fearful body postures, suggesting action preparation activity in the motor representation of the dominant hand (see also Borgomaneri et al., 2013, Schutter et al., 2008 for similar findings using fearful facial expressions and negative natural complex scenes). Remarkably, in the same time window, we found a consistent reduction of corticospinal excitability in the right hemisphere for both fearful and happy body postures (Borgomaneri et al., 2014b). This reduction in motor excitability also appeared to be causally related to visual recognition of body postures. TMS over right M1 (but not left M1) at 150 msec after visual stimulus onset also decreased the ability to recognize the observed body postures. The decrease in performance additionally correlated with the reduction in corticospinal excitability, suggesting a close link between motor suppression in the right M1 and perceptual processing of body postures.

At the later stage (300 msec), greater MEP amplitudes were measured when viewing fearful, happy and emotionally neutral dynamic body postures relative to emotionally neutral static body postures. This later increase in motor excitability was similar in the two hemispheres. Moreover, it was comparable for the three dynamic postures (see also Borgomaneri et al., 2012) and likely reflected motor resonance, i.e., the embodiment of the actor's movements into one's own motor system (Bastiaansen et al., 2009, Gallese et al., 2004, Gallese and Sinigaglia, 2011, Keysers and Gazzola, 2009, Niedenthal et al., 2010, Oberman et al., 2007, Rizzolatti and Sinigaglia, 2010) that is typically detected in similar time windows (200–400 msec) according to TMS and MEG evidence (Barchiesi and Cattaneo, 2013, Cavallo et al., 2014, Naish et al., 2014, Nishitani et al., 2004). Consistent with this interpretation, the magnitude of the later motor facilitation also correlated with dispositional cognitive empathy scores (Borgomaneri et al., 2014b), as previously shown in a number of studies investigating motor resonance (e.g., Avenanti, Minio-Paluello, Sforza, et al., 2009b, Avenanti et al., 2010, Gazzola et al., 2006, Lepage et al., 2010, Minio-Paluello et al., 2009). In contrast to the effect reported at 150 msec, neither stimulation of the right nor the left M1 at 300 msec affected visual recognition of body postures. These findings indicated that, at this stage of processing (300 msec), neural activity reflecting motor resonance was stronger in highly empathetic participants who tend to take the psychological perspectives of others in daily life, but was not critical for visual recognition of emotional body postures. These results revealed two distinct functional stages of motor cortex involvement during perception of emotional body language: an initial stage (∼150 msec) reflecting increased motor readiness

in the left hemisphere and perceptual mechanisms in the right hemisphere, and a later stage (~300 msec) in which the motor cortices bilaterally implement motor resonance, which may reflect a more sophisticated and empathy-related reading of the observed body expression "from the inside" (Avenanti, Candidi, et al., 2013b, Avenanti and Urgesi, 2011, Gazzola et al., 2006, Rizzolatti and Sinigaglia, 2010).

In the present study, we sought to further investigate motor responses to emotional bodies in the right and left hemispheres and to test the possible existence of an earlier additional stage of M1 involvement during perception of emotional bodies. Our previous studies suggested comparable motor reactivity in response to happy and fearful body expressions when motor excitability was tested in the 150–300 msec temporal window after visual stimulus onset (Borgomaneri et al., 2012, Borgomaneri et al., 2014b). Here, based on the evolutionary contentions that i) emotional and, in particular, threat-related stimuli should evoke extremely rapid motor reactions (Carretié et al., 2001, Costa et al., 2013, Frijda, 2009, Lang et al., 2000, Öhman and Mineka, 2001); and ii) fear-related signals might reduce motor readiness (as in orienting immobility and freezing responses) to allow environmental monitoring for the source of danger (Fanselow, 1994, Frijda, 2010, Hagenaars et al., 2014, Lang and Bradley, 2010, Whalen et al., 1998), we tested the hypothesis that a transient suppression of motor reactivity would be detected at a very early time window when viewing fearful bodies. To this aim, we investigated motor excitability in the right and left M1 within the same temporal window in which fearful faces and bodies are known to induce the earliest modulation of occipito-temporal cortices (i.e., at 100–125 msec, corresponding to the timing of the P1 component; Pourtois et al., 2005, Righart and de Gelder, 2006, Van Heijnsbergen et al., 2007, Vuilleumier and Pourtois, 2007, Williams et al., 2006).

Similarly to previous research on emotion perception, we used single-pulse TMS over M1 in order to record MEPs from the hand muscles and thus assess how visual perception affects the functional state of the observer's corticospinal system. However, it should be noted that the MEP amplitude obtained with single-pulse TMS reflects the net effect of excitatory and inhibitory inputs to the corticospinal pathway, providing a measure of both cortical and spinal excitability (Di Lazzaro et al., 2001). To directly assess modulations of intracortical excitability within the right and left M1, in the present study, we used for the first time in emotion perception research the paired-pulse protocol, in which pairs of TMS stimuli are administered through a single coil placed over the target M1. In paired-pulse TMS, a conditioning stimulus (CS) below the threshold intensity needed to elicit a MEP is followed at short interstimulus intervals (ISIs) by a suprathreshold test stimulus (TS). At ISIs of 1–5 msec, the CS results in MEP inhibition (i.e., "short intracortical inhibition", SICI), while longer ISIs of 7–20 msec produce MEP facilitation ("intracortical facilitation", ICF). This modulation of MEP size takes place at the cortical level and is thought to reflect the activation of separate populations of inhibitory and excitatory cortical interneurons without affecting spinal circuits (Kujirai et al., 1993). In particular it is held that SICI and ICF mainly reflect the activation of low threshold inhibitory interneurons mediated by gamma-aminobutyric acid (GABA) (Di Lazzaro et al., 2000, Ilić et al., 2002, Ziemann et al., 1996aa) and glutamatergic interneurons (Nakamura et al., 1997, Ziemann, 2003), respectively. Therefore, paired-pulse TMS provides reliable indices of motor cortical activations. Here, taking advantage of these paired-pulse paradigms, we aimed to further investigate whether the excitatory or inhibitory intracortical neural circuits within the right and left M1 are modulated during observation of emotional body expressions. By comparing neurophysiological indices of intracortical and corticospinal excitability, we tested whether the sight of emotional bodies at an early time window (100–125 msec) affected the observers' M1, descending corticospinal pathways or both. This allowed us to demonstrate that, before perceptual- and action-related processing at 150 and 300 msec (see Borgomaneri et al., 2012, Borgomaneri et al., 2014b), the motor system in both hemispheres implements fast suppression of motor reactions to emotional bodies with stronger suppression for fearful body expressions.

2. Methods

2.1. Participants

Twenty-eight healthy subjects took part in the study. Fourteen participants (6 men, mean age ± S.D.: 22.8 y ± 2.6) were tested in a first experiment in which the right M1 was stimulated (Exp1M1right), whereas the remaining 14 participants (7 men, mean age ± S.D.: 23.3 y ± 2.6) were tested in a second experiment in which the left M1 was stimulated (Exp2M1left). All participants were right-handed according to a standard

handedness inventory (Oldfield, 1971) and free from any contraindication to TMS (Rossi et al., 2009). They gave their written informed consent to take part in the study which was approved by the Department of Psychology ethics committee at the University of Bologna and was carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki. No discomfort or adverse effects were reported or noticed during TMS.

2.2. Visual stimuli

Different types of pictures were presented on a 19-inch screen located 80 cm away from the participants. Forty-five pictures were selected from a validated database (Borgomaneri et al., 2012, Borgomaneri et al., 2014b). Pictures depicted four different actors in emotional and neutral postures (Fig. 1a). To focus specifically on body-related information, the face was blanked out in all pictures. Stimuli included pictures of emotionally positive (happy) and negative (fearful) movements and neutral movements (i.e., actions with implied movement comparable to emotional body expressions but with no emotional meaning).

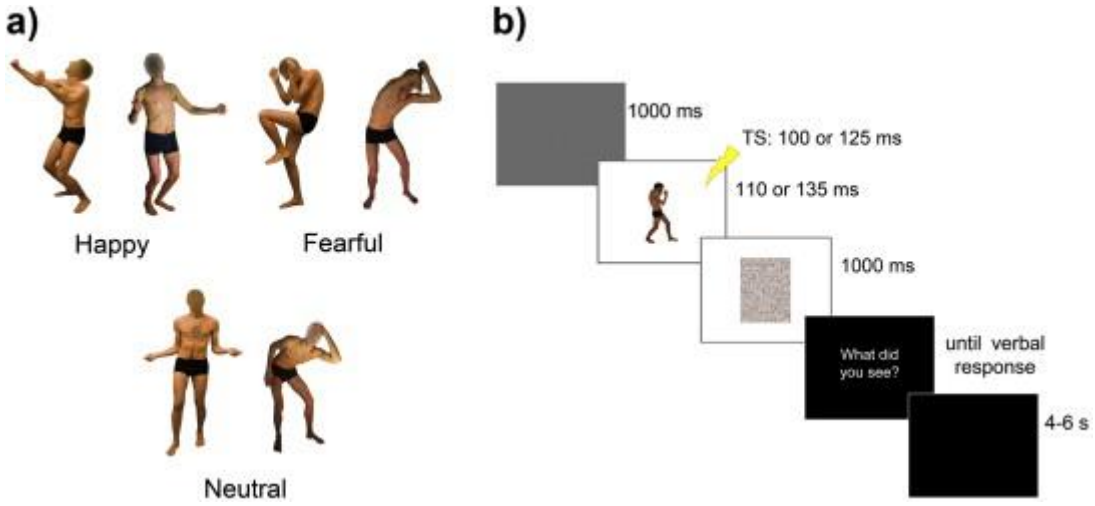

Fig. 1. (a) Examples of visual body stimuli. (b) Trial sequence.

During the recording of neutral movements, instructions to the actors specified the action to be performed (e.g., jump rope). For emotional expressions, instructions specified a familiar scenario (e.g., you have just won the lottery) or involved a potential threat (e.g., a tennis ball was thrown at the actor). Stimuli were selected from an initial sample of about 1000 images based on two pilot studies in which emotional ratings and emotion recognition data were collected, resulting in a final selection of 15 fearful body expressions, 15 happy body expressions and 15 neutral movements that were well recognized as prototypical representations of the different expressions (see Borgomaneri et al., 2012 for details). All the emotional and neutral movement stimuli represented a whole-body movement with a clear involvement of upper-limbs (implied motion stimuli). In none of the stimuli did the model interact with objects or other individuals. To rule out the possibility that changes in right M1 excitability might be due to differences in the amount of implied motion of the models' left or right hands, mirror-reflected copies of the selected stimuli were also created. Within each experiment, half the participants were tested with the original version of the stimuli, and the remaining half were tested with mirror-reflected copies.

2.3. TMS and electromyography recordings

Both Exp1M1right and Exp2M1left started with the electrode montage setup, detection of optimal scalp position and measurement of resting motor threshold (rMT). To explore motor excitability, MEPs induced by TMS of the right and left M1 were recorded from the left and right first dorsal interosseus (FDI) muscle, respectively (contralateral to the stimulated hemisphere), using a Biopac MP-35 (Biopac, U.S.A.)

electromyograph. EMG signals were band-pass filtered (30–500 Hz), sampled at 5 kHz, digitized and stored on a computer for off-line analysis. Pairs of silver-chloride surface electrodes were placed in a belly-tendon montage with ground electrodes on the wrist. A figure-of-eight coil connected to a Magstim Bistim2 stimulator (Magstim, Whitland, Dyfed, U.K.) was placed over the target M1. The intersection of the coil was placed tangentially to the scalp with the handle pointing backward and laterally at a 45° angle away from the midline. In this way, the current induced in the neural tissue was directed approximately perpendicular to the line of the central sulcus, optimal for trans-synaptic activation of the corticospinal pathways (Brasil-Neto et al., 1992, Mills et al., 1992). Using a slightly suprathreshold stimulus intensity, the coil was moved over the target hemisphere to determine the optimal position from which maximal MEP amplitudes were elicited in the controlateral FDI muscle. The optimal position of the coil was then marked on the scalp with a pen to ensure correct coil placement throughout the experiment. The rMT was defined as the minimal intensity of stimulator output that produced MEPs with an amplitude of at least 50 μV with 50% probability (using about 20 pulses) (Rossini et al., 1994). The absence of voluntary contraction was visually verified throughout the experiment. When muscle tension was detected, the experiment was briefly interrupted and the subject was invited to relax.

In both experiments, MEPs were recorded in three sessions: Single pulse (SP), Short-interval intracortical inhibition (SICI) and Intracortical facilitation (ICF). During the SP session, intensity was set to evoke MEPs with a peak-to-peak amplitude of ∼1.0 mV. During the paired-pulse TMS paradigm, SICI and ICF were measured using an established protocol (Kujirai et al., 1993, Ziemann et al., 1996bb). The conditioning (CS) and test (TS) stimuli were given through the same coil. The intensity of the CS was 80% of the rMT, a level at which we confirmed that MEPs were never induced. TS intensity was the same as that used in the SP session. We selected two ISIs, 3 msec and 12 msec, which are typically used to investigate SICI and ICF circuits, respectively (Kujirai et al., 1993, Ziemann et al., 1996b).

2.4. Procedure and experimental design

The experiments were programmed using Matlab software to control picture presentation and to trigger TMS pulses. In each experiment, MEPs were collected in three experimental sessions (SP, SICI and ICF). Before and after these sessions, additional SP blocks were recorded and served as baselines: subjects held their eyes closed with the instruction to imagine watching a sunset at the beach (Borgomaneri et al., 2012, Fourkas et al., 2008) while receiving TMS over the right motor cortex (inter-pulse interval ∼10 sec). Ten trials were recorded for each of the baseline blocks. In the other three experimental sessions, subjects performed an emotion recognition task, in which they were presented with body postures, and asked to categorize them as happy, fearful or neutral. Each emotion evaluation block included 90 trials (270 trials in total), and each trial consisted of a gray screen (1 sec duration) indicating the beginning of the trial, followed by the test picture presented at the center of the screen (Fig. 1b). In half the trials, stimuli were presented for 110 msec and the SP (or TS in the paired-pulse sessions) was delivered at 100 msec from stimulus onset. In the remaining trails, stimuli were presented for 135 msec and the SP/TS was delivered at 125 msec from stimulus onset. Stimulus duration was randomly distributed in the two blocks and the session order was counterbalanced across participants. The picture was followed by a random-dot mask (obtained by scrambling the corresponding sample stimulus using a custom-made image segmentation software) lasting 1 sec. Then the question “What did you see?” appeared on the screen, and the subject provided a verbal response (forced choice). Possible choices were happy, fear, or neutral. An experimenter collected the answer by pressing a computer key. To avoid changes in excitability due to the verbal response (Meister et al., 2003, Tokimura et al., 1996), participants were invited to answer only during the question screen, a few seconds after the TMS pulse (Tidoni, Borgomaneri, di Pellegrino, & Avenanti, 2013). After the response, the screen appeared black for 4–6 sec, ensuring an inter-pulse interval greater than 10 sec and thereby avoiding changes in motor excitability due to TMS per se (Chen et al., 1997). To reduce the initial transient-state increase in motor excitability, before each block two single-pulses (or two paired-pulses) were delivered over M1 (inter-pulse interval >10 sec). Each baseline and experimental block lasted about 2 and 10 min respectively. After TMS, subjects were presented with all the stimuli (shown 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 presentation of the whole set of stimuli.

2.5. Data analysis

Neurophysiological and behavioral data were processed off-line. Mean MEP amplitudes in each condition were measured peak-to-peak (in mV). MEPs associated with incorrect answers (less than 10% in both experiments) were discarded from the analysis. Since background EMG is known to affect motor excitability (Devanne, Lavoie, & Capaday, 1997), MEPs preceded by background EMG deviating from the mean by more than 2 SD were removed from further analysis (less than 6% in both experiments).

In a first analysis, MEPs recorded in the SP, ICF and SICI sessions were expressed relative to the baseline (% of the average of the two baseline blocks) and analyzed by means of a mixed-model four-way ANOVA with Experiment (2 levels: Exp1M1right and Exp2M1left) as a between-subjects factor and Session (3 levels: SP, ICF and SICI), Time (2 levels: 100 and 125 msec) and Movement type (3 levels: happy, fearful and neutral) as within-subjects factors.

Moreover, to quantify ICF and SICI effects, we expressed MEPs in the paired-pulse sessions relative to the SP session (to estimate the effects of the subthreshold CS on the MEP elicited by the suprathreshold TS). For each experimental condition we calculated the ratio of the mean conditioned MEP over the mean unconditioned test MEP (Kujirai et al., 1993, Ziemann et al., 1996b). These data were analyzed by means of an Experiment × Session × Time × Movement type mixed-model ANOVA as in the previous analysis, but the factor Session had only 2 levels (ICF and SICI). Mean ratings of arousal, valence and implied movement were analyzed by means a two-way mixed-model ANOVA with Experiment (2 levels: Exp1M1right and Exp2M1left) as a between-subjects factor and Movement type as a within-subjects factor (3 levels: happy, fearful and neutral). Accuracy in the emotion recognition task was analyzed by means of a two-way mixed-model ANOVA with Experiment (2 levels: Exp1M1right and Exp2M1left) as a between-subjects factor and Session as a within-subjects factor (3 levels: SP, ICF and SICI). In all the ANOVAs, post-hoc comparisons were carried out by means of the Newman–Keuls test. Moreover, effect size indices for main effects and interactions were computed using partial eta2, whereas repeated measures Cohen's d values were computed for post-hoc comparisons (Cohen, 1977, Wolf, 1986).

3. Results

3.1. Subjective measures

Mean task accuracy in the three sessions was high in both experiments (Exp1M1right: SP mean accuracy ± S.D.: 90.7% ± 5.3; SICI: 89.5% ± 6.7 and ICF: 90.5% ± 5.3; Exp2M1left: SP mean accuracy ± S.D.: 92.7% ± 5.5; SICI: 91.7% ± 5.2 and ICF: 90.6% ± 4.9). The Experiment × Session ANOVA carried out on accuracy data showed no main effects or interactions (all $F < .95$; $p > .39$), suggesting similar accuracy across the two experiments and three TMS sessions.

The Experiment × Movement type ANOVAs carried out on valence ratings (Table 1) showed a main effect of Movement type ($F_{2,52} = 296.91$; $p < .001$; $eta^2 = .92$), but no main effect of Experiment or interaction (all $F < 2.82$, $p > .11$). Post-hoc analyses showed that valence ratings were lower for fearful movements relative to happy and neutral movements (all $p < .001$; $d > 3.05$); moreover, valence ratings were higher for happy relative to neutral movements (all $p < .001$; $d = 2.35$).

The Experiment × Movement type ANOVAs carried out on arousal ratings (Table 1) showed a main effect of Movement type ($F_{2,52} = 57.34$; $p < .001$, $eta^2 = .69$), but no main effect of Experiment or interaction (all $F < 1.63$, $p > .21$). Post-hoc analyses showed that arousal scores were greater for happy and fearful movements relative to neutral movements (all $p < .001$; $d > 1.67$). Moreover, arousal ratings were not significantly different between fearful and happy movements ($p = .33$).

The Experiment × Movement type ANOVAs carried out on implied motion ratings (Table 1) did not show any significant main effects or interactions (all $F < 2.87$; $p > .07$), suggesting that the three movement types contain similar amounts of implied motion.

	Arousal			Valence			Perceived motion		
	Happy	**Neutral**	**Fearful**	**Happy**	**Neutral**	**Fearful**	**Happy**	**Neutral**	**Fearful**
Exp1M1right	3.41 ± .78	2.21 ± .56	3.36 ± .93	4.18 ± .68	2.87 ± .58	1.39 ± .39	3.32 ± .66	3.41 ± .59	3.07 ± .67
Exp2M1left	3.57 ± .55	2.27 ± .55	3.90 ± .60	4.37 ± .33	3.15 ± .19	1.39 ± .19	3.44 ± .47	3.36 ± .55	3.17 ± .66

Table 1. Mean subjective evaluations ± standard deviation (arousal, valence and perceived implied motion) of stimuli used in the first (Exp1M1right) and the second experiment (Exp2M1left).

3.2. Neurophysiological data

MEPs recorded in the first block (mean raw MEP amplitude ± SD in Exp1M1right: 1.11 mV ± .26; in Exp2M1left: 1.02 mV ± .22) and last block of the baseline (Exp1M1right: 1.15 mV ± .43; Exp2M1left: 1.09 mV ± .38) were entered into an Experiment × Time ANOVA that showed no main effects or interactions (all F < 1, p > .45), confirming that the experiments did not alter participants' corticospinal excitability (Chen et al., 1997).

In a first analysis, MEPs collected in the various sessions and experimental conditions were expressed relative to the average of the two baseline blocks. The Experiment × Session × Time × Movement type ANOVA on MEP amplitudes (% of baseline) showed a main effect of Session ($F_{2,52}$ = 51.59; p < .0001; eta^2 = .66) accounted for by the lower MEP amplitudes recorded in the SICI (41% ± 23) relative to the SP (118% ± 37; p < .001; d = 1.99) and ICF sessions (195% ± 102; p < .001; d = 1.71) and the greater amplitudes recorded in the ICF relative to the SP session (p = .001; d = .75). Critically, a significant Session × Movement type interaction was found ($F_{4,104}$ = 3.51; p = .01; eta^2 = .12; Fig. 2). Post-hoc analyses showed that in the ICF session, MEPs were lower for fearful bodies (188% ± 90) than for happy (198% ± 116; p = .003; d = .30) and neutral bodies (200% ± 100, p = .002; d = .64) which in turn did not significantly differ from one another (p = .63). No significant modulations were found in either the SP or SICI sessions (all p > .44). The Session × Movement type interaction was not qualified by a triple or quadruple interaction involving the factor Time (all F < 1.01; p > .41), suggesting that, in the ICF session, MEPs recorded at 100 and 125 msec were similarly reduced in the fearful body condition. Similarly, no interaction with the factor Experiment was found to be significant (all F < 2.48; p > .094), suggesting that the reduction in ICF was similar in both motor cortices (see Table 2). No other significant effects were found in the ANOVA (all F < 3.03, p > .09).

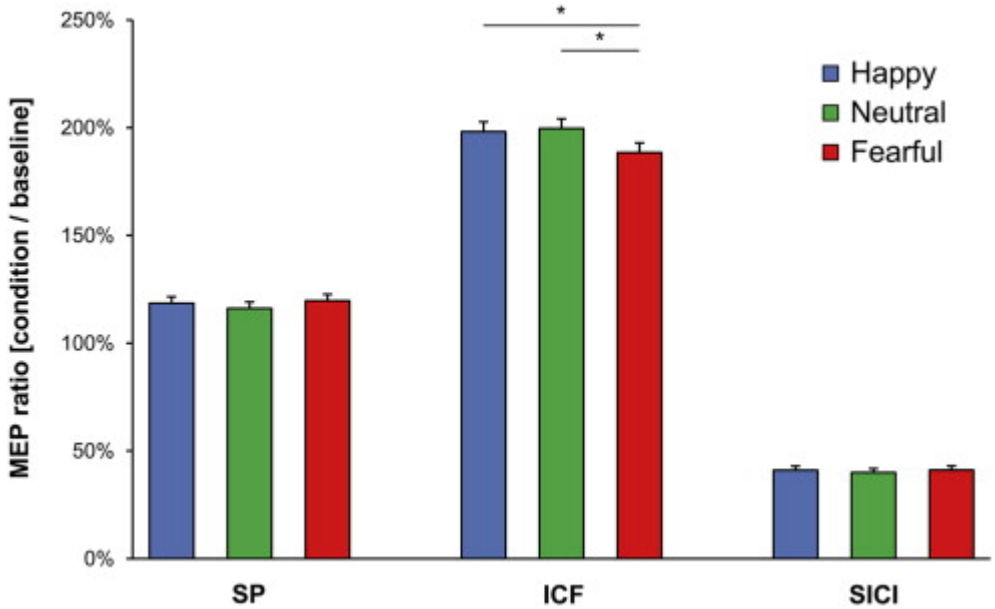

Fig. 2. Neurophysiological modulations during the emotion recognition task. MEP amplitude ratio (condition/baseline) during perception of happy, neutral and fearful body postures during single-pulse (SP), intracortical facilitation (ICF) and short intracortical inhibition (SICI) sessions. Data show the Session × Movement type interaction (average of the two experiments, Exp1M1right and Exp2M1left, and the two time points, 100 msec and 125 msec). Error bars indicate SEM. Asterisks (*) denote significant comparisons (p < .05).

	SP			ICF			SICI		
	Happy	**Neutral**	**Fearful**	**Happy**	**Neutral**	**Fearful**	**Happy**	**Neutral**	**Fearful**
Exp1M1right	133% ± 11	132% ± 11	133% ± 11	181% ± 17	185% ± 17	173% ± 17	42% ± 7	41% ± 7	41% ± 7
Exp2M1left	104% ± 7	100% ± 7	106% ± 7	215% ± 41	214% ± 34	204% ± 30	40% ± 7	42% ± 5	39% ± 5

Table 2. Mean MEP amplitude ratio (condition/baseline) ± SEM. in the first (Exp1M1right) and the second experiment (Exp2M1left).

Results from the first analysis on MEP amplitudes (% of baseline) confirm the robustness of the paired-pulse protocol observed in both experiments, with lower MEPs when the CS preceded the TS by 3 msec and larger MEPs when the CS preceded the TS by 12 msec (Kujirai et al., 1993, Ziemann et al., 1996b). Moreover, they show that emotional bodies significantly modulated MEP size in the ICF session but not in the SP or SICI sessions.

It should be noted that the index used in the first analysis (MEP amplitude relative to baseline) does not allow us to rule out a possible contribution of spinal excitability in the observed motor modulations. Therefore, to quantify SICI and ICF effects, a second Experiment × Session × Time × Movement type ANOVA was conducted on MEP ratios computed for each condition separately (mean conditioned MEP relative to mean unconditioned test MEP) (Kujirai et al., 1993, Ziemann et al., 1996b).

This second analysis revealed a main effect of Session ($F_{1,26}$ = 68.13; p < .0001; eta^2 = .72), with larger MEPs in the ICF relative to the SICI session: 182% ± 112 *vs* 38% ± 27), a non-significant main effect of Movement type ($F_{2,52}$ = 2.48, p = .09) and, importantly, a significant Session × Movement type interaction ($F_{2,52}$ = 4.70; p = .01; eta^2 = .15, Fig. 3). The interaction was due to lower ICF in the fearful body condition (173% ± 101) relative to the happy (182% ± 111; p = .03; d = .32) and neutral body conditions (191% ± 128; p < .001; d = .48); moreover, ICF was lower in the happy than in the neutral body condition (p = .03; d = .24). No significant modulation of the SICI index was found (p > .79). The ANOVA also showed non-significant trends for the main effect of Experiment and the Experiment × Session interaction (all F < 3.85, p > .06), suggesting that the gain in motor excitability in the ICF session tended to be larger in Exp2M1left than Exp1M1right. However, the factor Experiment did not interact with other factors (all F < .91, p > .41), suggesting that the reduction of ICF for fearful body expressions was similar in Exp1M1right and Exp2M1left (see Table 3). No other main effects or interactions were significant in the ANOVA (F < 1.28, p > .29).

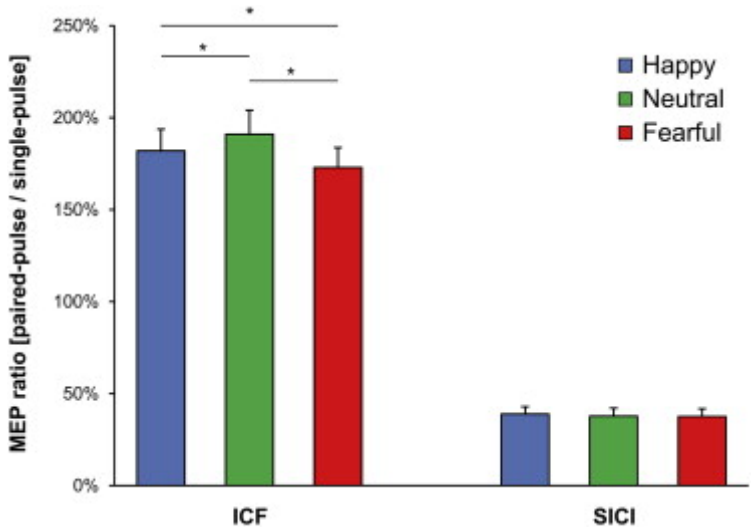

Fig. 3. Cortical motor modulations during the emotion recognition task. MEP amplitude ratio (paired-pulse/single-pulse) during perception of happy, neutral and fearful body postures during intracortical facilitation (ICF) and short intracortical inhibition (SICI) sessions. Data show the Session × Movement type interaction (average of the two experiments, Exp1M1right and Exp2M1left, and the two time points, 100 msec and 125 msec). Error bars indicate SEM. Asterisks (*) denote significant comparisons (p < .05).

	ICF			SICI		
	Happy	**Neutral**	**Fearful**	**Happy**	**Neutral**	**Fearful**
Exp1M1right	142% ± 12	147% ± 13	137% ± 11	32% ± 4	32% ± 4	31% ± 4
Exp2M1left	221% ± 38	235% ± 44	209% ± 35	46% ± 12	44% ± 8	44% ± 8

Table 3. Mean MEP amplitude ratio (paired-pulse/single-pulse) ± SEM. in the first (Exp1M1right) and the second experiment (Exp2M1left).

4. Discussion

Emotional body language represents a powerful vehicle for interpersonal communication (Darwin, 1872), and it is widely assumed that processing emotional language can prime the body for action (Ekman and Davidson, 1994, Frijda, 2009, Izard, 1994). However, little is known about how the sight of emotional bodies affects the observer's M1. Using the high temporal resolution of TMS, here, we tested the hypothesis that seeing emotional body expressions – and fearful expressions in particular – triggers a very early reduction of excitability in the observer's motor system. We used single-pulse TMS to characterize the functional state of the corticospinal system, and, for the first time in emotion perception research, the paired-pulse protocol to investigate the excitability of intracortical facilitatory (ICF) and inhibitory (SICI) circuits in the right and left M1. We tested M1 excitability in a time window (100–125 msec) corresponding to the latency of the P1, i.e., the earliest cortical ERP component that is modulated by emotional expressions (Pourtois et al., 2005, Righart and de Gelder, 2006, Van Heijnsbergen et al., 2007, Vuilleumier and Pourtois, 2007, Williams et al., 2006).

The results supported our initial prediction and allowed us to characterize a local neurophysiological mechanism in bilateral M1 involved in processing emotional bodies. In particular, we found that seeing fearful bodies reduced the magnitude of the ICF effect relative to seeing happy or neutral bodies. Moreover, happy bodies reduced ICF relative to neutral bodies. No similar modulations were found for SICI or corticospinal excitability in the 100–125 msec range. These findings show a surprisingly early cortical motor mechanism during processing of emotional body postures. We propose this decrease in ICF reflects the cortical motor counterpart of a fast orienting response toward emotionally salient body postures that would manifest as a quick and transient reduction in motor readiness, ultimately favoring perception of and subsequent motor reactions to the emotional cues.

The stronger motor suppression when viewing fearful relative to happy body postures may be accounted for by the greater biological salience of the former expression relative to the latter. Indeed, fearful expressions signal the presence of potential threats in the environment, which may require a strong and immediate mobilization of neural resources. More specifically, it is thought that because the source of danger is not clearly signaled, detecting fearful expressions increases sensory vigilance and prompts monitoring for 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, the suppression of excitatory activity in M1 may reflect a quick reduction in motor readiness that may favor such monitoring processes.

Our findings are in keeping with animal research showing a reduction in motor output when animals face novel or emotionally salient stimuli (and threatening stimuli in particular) (Fanselow, 1994, Frijda, 2010, Hagenaars et al., 2014, Lang and Bradley, 2010, Whalen et al., 1998). Moreover, they concur with studies in humans reporting that the observer's body freezes during passive observation of aversive and arousing stimuli (Azevedo et al., 2005, Eerland et al., 2012, Facchinetti et al., 2006, Hillman et al., 2004, Horslen and Carpenter, 2011, Lelard et al., 2013, Roelofs et al., 2010, Stins et al., 2011). Remarkably, our study significantly expands these observations by revealing a possible early cortical mechanism for implementing these motor reactions to emotional and, in particular, fear-related cues in humans. However, as we clarify below, our findings are suggestive of a transient reduction in motor readiness more than a complete and sustained body immobilization (Fanselow, 1994, Frijda, 2010, Hagenaars et al., 2014, Lang and Bradley, 2010, Whalen et al., 1998).

4.1. Local neurophysiological mechanisms supporting early motor suppression in response to emotional bodies

Our findings demonstrated a modulation of ICF but not of corticospinal excitability or SICI. Single-pulse MEPs, SICI and ICF reflect at least partially distinct neurophysiological mechanisms (Liepert et al., 1998, Ziemann et al., 1998). Modulations of corticospinal excitability as measured by single-pulse MEPs reflect the net effect of excitatory and inhibitory inputs to the descending corticospinal pathway, whereas SICI is thought to measure intracortical GABA-ergic inhibition in M1 through $GABA_A$ receptors. ICF is a more complex measure of intracortical excitation, as it is thought to be influenced by glutamatergic facilitation through N-methyl-D-aspartate (NMDA) receptors (Ziemann et al., 1998) but also GABA-ergic inhibition through $GABA_A$ receptors (Tandonnet, Garry, & Summers, 2010). Moreover, ICF results from the recruitment of local M1 circuits related to the activation of long-range connections originating from remote areas (Ziemann et al., 1998, Ziemann, 2004).

Hence, our data indicate that emotional bodies induce a fast modulation of cortical motor excitability in the two hemispheres, with a comparatively stronger reduction of intracortical excitatory activity when perceiving fearful bodies and a weaker reduction for happy bodies. The fact that fearful and happy postures modulated ICF but not SICI suggests that processing of emotional bodies is mainly associated with a reduction in the input to excitatory glutamatergic interneuronal networks in M1 originating from interconnected regions, while it does not conspicuously modulate GABAergic cortical circuits. Similar changes in ICF in the absence of SICI modulations have been reported immediately after the administration of painful stimuli and have been interpreted as reflecting a role of intracortical glutamatergic networks in limiting the execution of body movements in the acute phase of pain (Schabrun & Hodges, 2012). However, in contrast to what we have found here, painful stimulation induced sustained suppression of ICF that was accompanied by a reduction in corticospinal excitability and also affected SICI at a later time (Schabrun & Hodges, 2012), thus indicating a massive and prolonged reduction of motor output when processing pain. In contrast, the motor modulation we report here: i) is not associated with changes in SICI and corticospinal excitability; and ii) is likely transient. The fact that emotional bodies modulated ICF, but not corticospinal excitability, suggests that the suppressive motor response we detected in our study occurs at the cortical level and does not immediately influence descending pathways. These features support the idea that ICF modulation reflects a reduction in the propensity to move the body, i.e., a reduction in motor readiness while processing visual stimuli, more than a complete motor inhibition, which might be supported by additional modulation of GABAergic cortical circuits and corticospinal excitability (Reis et al., 2008, Stinear et al., 2009). Secondly, it should be considered that while the present study shows similar ICF suppression at both the time points tested (100 and 125 msec) and in both hemispheres, previous research suggests that these fast motor responses might be transient, as very different modulations are observed when motor excitability is tested at 150 msec and 300 msec after the presentation of emotional bodies (Borgomaneri et al., 2012, Borgomaneri et al., 2014bb; see below). The transient nature of the reduction in motor activity we detected in our present study suggests it may favor early perceptual processing (e.g., threat monitoring) without counteracting subsequent implementation of adaptive motor responses (e.g., fight/flight reactions).

4.2. Possible networks supporting early motor suppression in response to emotional bodies

While our study indicates that visual processing of emotional bodies transiently reduces the input to excitatory glutamatergic interneuronal networks in M1 originating from interconnected regions, we can only speculate about the specific pathway supporting this early motor suppression.

Studies have suggested that visual processing of affective stimuli could influence motor output via subcortical routes bypassing the cortex (de Gelder et al., 2011, Filmer and Monsell, 2013, Liddell et al., 2005, Morris et al., 1999, Tamietto and de Gelder, 2010, Tamietto et al., 2009). Imaging evidence indicates that the perception of emotional bodies activates subcortical structures (i.e., pulvinar, caudate nucleus and amygdala; de Gelder et al., 2010, Van de Riet et al., 2009) even in cortically blind patients with damage to the striate cortex (Van den Stock et al., 2011), suggesting that subcortical structures receive inputs from the retina that bypass the damaged visual cortex. Notably, these structures also possess upstream projections influencing not only the visual system (Pourtois, Schettino, & Vuilleumier, 2013) but also M1 (Grèzes et al.,

2014, Tamietto et al., 2012) and may thus have a role in influencing ICF when processing emotional body postures.
On the other hand, ICF modulation may occur through fast activation of a cortical route including regions involved in visual processing (e.g., occipito-temporal areas), lateral parieto-premotor circuits involved in action execution (de Gelder, 2006, de Gelder et al., 2004, de Gelder et al., 2010) and mesial regions of the frontal cortex that are involved in emotional processing and are densely connected to M1 via the SMA (Cavada et al., 2000, Morecraft et al., 1993, Oliveri et al., 2003). In particular, a possible key role in the suppressive response to fearful (and happy) bodies could be played by the inferior frontal cortex (IFC, which includes the inferior frontal gyrus and the ventral premotor cortex; Avenanti, Annella, et al., 2013a, Avenanti, Candidi, et al., 2013b, Urgesi et al., 2014). Monkey studies suggest this region implements fast flicking reactions to unpleasant stimuli (Cooke and Graziano, 2004, Gharbawie et al., 2011, Graziano et al., 2002). Moreover, the IFC is critically involved in inhibiting motor behavior (Aron et al., 2014, Chambers et al., 2007) and provides inhibitory input to M1 either directly or via SMA (Cattaneo and Barchiesi, 2011, Davare et al., 2009, Zandbelt et al., 2013). Moreover, IFC suppression appears to disrupt inhibitory responses to salient auditory stimuli presented close to the body (Avenanti et al., 2012), suggesting a possible role for the IFC not only in voluntary outright action stopping and inhibitory control (Aron et al., 2014), but also in driving automatic inhibitory reactions. Future studies are needed to directly test the role of the IFC in reacting to emotional body cues.

4.3. Motor dynamics during perception of emotional bodies

The early timing of the physiological modulation identified in our study is in keeping with the evidence that not only fearful facial expressions (Pourtois et al., 2005, Righart and de Gelder, 2006, Vuilleumier and Pourtois, 2007, Williams et al., 2006) but also fearful body expressions affect the ERP response in the earliest stages of visual perception, i.e., the P1 and N1 components (Jessen and Kotz, 2011, Van Heijnsbergen et al., 2007). However, these ERP studies did not include positive emotional expressions, and thus it was unclear whether the early ERP modulations produced by fearful bodies merely reflected an arousal response. Our data significantly expand on the ERP evidence by showing, in the very same time window as the P1 component, clear evidence of a 'negative bias' for fearful bodies in cortical motor areas, with a stronger reduction in ICF when viewing fearful bodies than when viewing happy bodies, relative to neutral body expressions. Notably, in our study, fearful and happy expressions were matched for arousal. Moreover, fearful, happy and neutral expressions did not differ in implied motion (i.e., the quantity of movement perceived in the body posture), suggesting that these factors did not influence our results. However, some limitations of our design should be considered. Our stimuli depicted only male actors and the relatively small sample size prevented reliable analysis of sex-dependent effects. Moreover, we used a limited number of emotional expressions and, therefore, it is unclear whether a reduction in ICF could be found with other expressions. Therefore, further studies are needed to test motor excitability using larger numbers of stimuli and participants.
Nevertheless, our study indicates a clear reduction in bilateral cortical motor activity when seeing particular emotional body postures. Together with our previous studies on emotional body perception (Borgomaneri et al., 2012, Borgomaneri et al., 2014bb), the present experiments suggest specific dynamics of neural activity in the motor system during perception of emotional bodies. A negative bias in the form of a cortical suppressive response is initially detected in bilateral M1 (but not in the corticospinal system) at about 100–125 msec post-stimulus onset, and may reflect a fast and transient reduction in motor readiness, with a stronger reduction for fearful than for happy body expressions relative to neutral body expressions. In a second stage (150 msec post-stimulus onset), the sight of emotional bodies starts to influence the corticospinal system, and it does so in different ways for the two hemispheres, with the left hemisphere being more involved in preparing a potential motor response when exposed to fearful expressions and the right hemisphere being critically involved in the perceptual recognition of all body postures (Borgomaneri et al., 2014b). Finally, at around 300 msec, the corticospinal motor system implements motor resonance processes which appear to reflect a mapping of the observed body movements that *follows* recognition of the body posture (Borgomaneri et al., 2012, Borgomaneri et al., 2014bb). Thus, our studies support a three-stage model of motor cortex engagement during processing of emotional body language. Overall, the specific dynamics we observed across these studies support the notions that emotional cues trigger motor-

related activity in the brain and that potential threats require particularly quick motor reactions to secure the survival of the organism (Carretié et al., 2009, Frijda, 2009, Lang et al., 2000, Öhman and Mineka, 2001).

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Authors have no conflicts of interest to declare.

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