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Your emotion moves into my motor system

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Chapter 1

Temporal dynamics of motor cortex excitability during perception of natural emotional scenes*

Abstract

Although it is widely assumed that emotions prime the body for action, the effects of visual perception of natural emotional scenes on the temporal dynamics of the human motor system have scarcely been investigated. Here, we used single-pulse transcranial magnetic stimulation (TMS) to assess motor excitability during observation and categorization of positive, neutral and negative pictures from the International Affective Picture System (IAPS) database. Motor-evoked potentials (MEPs) to TMS of the left motor cortex were recorded from hand muscles, at 150 and 300 ms after picture onset. In the early temporal condition we found an increase in hand motor excitability that was specific for the perception of negative pictures. This early negative bias was predicted by interindividual differences in the disposition to experience aversive feelings (personal distress) in interpersonal emotional contexts. In the later temporal condition, we found that MEPs were similarly increased for both positive and negative pictures, suggesting an increased reactivity to emotionally arousing scenes. By highlighting the temporal course of motor excitability during perception of emotional pictures, our study provides direct neurophysiological support for the evolutionary notions that emotion perception is closely linked to action systems and that emotionally negative events require motor reactions to be more urgently mobilized.

Introduction

Perceiving and immediately reacting to potential threats are critical for survival (Darwin, 1872). Negative stimuli require perceptual processing and action resources to be more intensely and urgently mobilized to minimize negative consequences associated with unpleasant cues. In support of this view, behavioral and electrophysiological studies have found that unpleasant stimuli are detected more quickly (Hansen and Hansen, 1988; Fox et al., 2000; Öhman et al., 2001) and are associated with larger early (100-200 ms) occipito-temporal components of event-related potentials (ERPs) relative to pleasant or neutral stimuli (Schupp et al., 2003; Smith et al., 2003; Pourtois et al., 2004 for a review see Olofsson et al., 2008) suggesting a rapid bias in visual attention allocation with greater resources devoted to negative stimuli (Vuilleumier, 2002; Carretié et al., 2009). This "negative" bias may reflect interactions between cortical and subcortical structures as suggested for example by the rapid amygdala activation during processing of aversive stimuli (Oya et al., 2002; Tamietto and de Gelder, 2010) and the reduced amplitudes of occipito-temporal ERPs components for negative stimuli when the amygdala is lesioned (Rotshtein et al., 2010).

The impact of negative bias has also been explored at the motor level. For example, studies indicate that while both positive and negative stimuli can modulate motor behavior (e.g. by favoring approach and avoidance movements, respectively), negative stimuli are particularly adept at evoking rapid reactions in the observer (Cacioppo et al., 1993; Bradley et al., 2001; Coombes et al., 2005, 2009; Freina et al., 2009; Naugle et al., 2010) providing support to the evolutionary contention that increased motor readiness in the face of threat may best secure survival of the organism (Lang et al., 2000; Öhman and Mineka, 2001; Carretié et al., 2009; Frijda, 2009). These findings would also suggest that seeing emotionally negative stimuli while at rest should automatically trigger short-latency activation of the motor representation of the dominant hand.

Single-pulse TMS is a valuable method to non-invasively stimulate the human motor cortex in resting conditions and thus instantaneously assess changes in the excitability of distinct corticospinal

representations of the body (Hallett, 2007; Serino et al., 2009; Avenanti et al., 2012b). This approach has been classically used to probe motor excitability when imaging (Fadiga et al., 1999; Fourkas et al., 2006), observing (Fadiga et al., 2005; Urgesi et al., 2010; Avenanti et al., 2013a, 2013b), planning or performing an action (Hoshiyama et al., 1997; Hasbroucq et al., 1999; Michelet et al., 2010). The high temporal resolution of the technique and the possibility to distinguish between excitatory and inhibitory activity allows effectively exploration action-related dynamics and can provide direct information about how neural processing in the motor cortex unfolds over time (Prabhu et al., 2007; Michelet et al., 2010; Avenanti et al., 2012a; Barchiesi and Cattaneo, 2013).

Recently, studies have used TMS to investigate the excitability of the hand representation in the left motor cortex during observation of natural emotional scenes. These studies have typically reported comparable increase in motor excitability for both emotionally positive and negative stimuli (Baumgartner et al., 2007; Hajcak et al., 2007; Coombes et al., 2009; Borgomaneri et al., 2012). Notably, however, in such studies, motor excitability was tested in a relatively late time window, i.e. at >300ms after stimulus onset, when the amplitude of brain responses to emotional images is typically similar for positive and negative stimuli and likely reflects increased resource allocation to motivationally relevant cues as suggested by ERPs studies (Cuthbert et al., 2000; Keil et al., 2002; Codispoti et al., 2007; Olofsson et al., 2008).

Here we tested the hypothesis that a greater increase in excitability of the left motor cortex occurs for negative stimuli before increased motor reactivity for positive stimuli can be detected. We capitalized on ERPs studies showing that responses in the visual system are: i) larger for negative stimuli in an early temporal window (~100-200ms); and ii) similar for positive and negative stimuli at a later time (~300-600ms) (Vuilleumier, 2002; Olofsson et al., 2008). We reasoned that to ensure survival, action reactivity should be closely coupled with visual processing and thus we predicted greater facilitation of the hand motor representation for negative stimuli in an early time window (at 150 ms from stimulus onset) followed by a comparable motor facilitation for both negative and positive stimuli (at 300 ms as in Borgomaneri et al., 2012). To test these hypotheses we administered single-pulse TMS

over the hand region of the left motor cortex to induce motor-evoked potentials (MEPs) in right hand muscles while participants observed and actively categorized positive, neutral and emotionally negative visual scenes from the International Affective Picture System (IAPS) database. Emotional pictures in the IAPS typically depict humans in emotionally arousing scenarios (e.g. smiling or distressed individuals, or people in sexual or threatening contexts etc.) that may also induce empathy-related processing or personal distress (Lang et al., 1999, 2000; Lamm et al., 2007a, 2008; Morelli et al., 2012); notably, studies have shown that stable empathy or personal distress dispositions predict motor reactivity during social perception (Gazzola et al., 2006; Avenanti et al., 2009a, 2010; Minio-Paluello et al., 2009; Ferri et al., 2010; Lepage et al., 2010). Thus we investigated whether empathy and personal distress dispositions predicted the magnitude of motor reactivity to the different classes of pictures.

Materials and methods

Participants

Fourteen healthy participants (6 men, mean age ± S.D.: 24.1y ± 1.4) took part in the study. All the subjects were right-handed according to a standard handedness inventory (Briggs and Nebes, 1975), had normal or corrected-to-normal visual acuity in both eyes, and were naïve as to the purposes of the experiment. None of the participants had neurological, psychiatric, or other medical problems or any contraindication to TMS (Rossi et al., 2009). Participants provided written informed consent, and the procedures were approved by the ethics committee at the Psychology Department of Bologna University and were in accordance with the ethical standards of the 1964 Declaration of Helsinki. No discomfort or adverse effects during TMS were reported or noticed.

Visual stimuli

Color pictures from the IAPS database (Lang et al., 1999; Figure 1A) were presented on a 19-inch screen located 80 cm away from the participants. A total of 32 pleasant, 32 unpleasant and 32 neutral pictures (subtending a 21.2° by 16.2° region) were shown. The stimuli were already included in previous TMS studies (Hajcak et al., 2007; van Loon et al., 2010; Borgomaneri et al., 2012) and are listed in Supplementary Table 1.

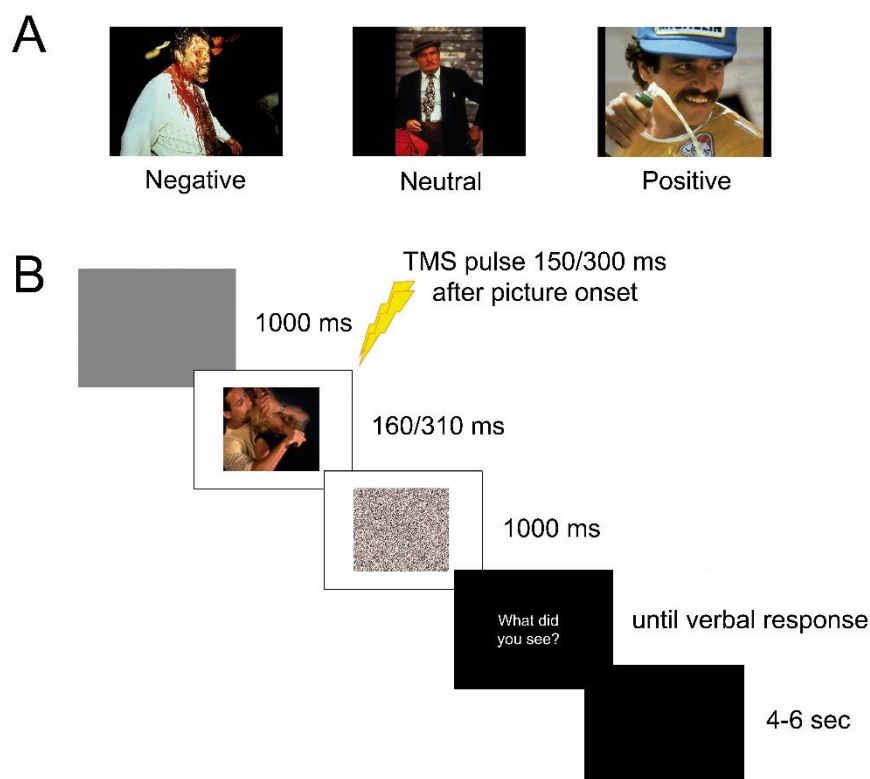**Figure 1**. Examples of visual stimuli and trial sequence.

Transcranial magnetic stimulation and electromyography recording

MEPs induced by TMS were recorded from the right first dorsal interosseus (FDI) and abductor pollicis brevis (APB) with a Biopac MP-35 (Biopac,U.S.A.) electromyograph. We selected these two muscles to compare our results with previous studies that explored the excitability of the FDI (Oliveri

et al., 2003), the APB (Hajcak et al., 2007; van Loon et al., 2010) or both FDI and APB motor representations (Borgomaneri et al., 2012) during the observation of emotional pictures. Electromyographic (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-8 coil connected to a Magstim Rapid2 stimulator (Magstim, Whitland, Dyfed, U.K.) was placed over the left 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. Using a slightly suprathreshold stimulus intensity, the coil was moved to determine the optimal position from which maximal amplitude MEPs were elicited in the controlateral FDI muscle. The optimal position was then marked on the scalp to ensure correct coil placement throughout the experiment. The intensity of magnetic pulses was set at 120% of the resting motor threshold (rMT), defined as the minimal intensity of the stimulator output that produces MEPs with amplitude of at least 50μV in the higher threshold muscle with 50% of probability (Rossini et al., 1994). This way a stable signal could be recorded from both muscles (Avenanti et al., 2007). The absence of voluntary contractions was continuously visually verified throughout the experiments. When muscles tension was detected the experiment was briefly interrupted and subjects were invited to relax.

Procedure

The experiment was programmed using Matlab software to control picture presentation and to trigger TMS. MEPs were collected in four blocks. The first and the last blocks (10 trials each) served as baseline: subjects kept their eyes closed with the instruction to imagine watching a sunset at the beach (Fourkas et al., 2008; Tidoni et al., 2013) while receiving TMS over M1 (inter-pulse interval ~10 s). In the other two blocks (48 trials each) subjects performed an emotion evaluation task, in which they were presented with a picture and were asked to categorize it as positive, negative or neutral. It is held that active categorization maximizes the chance of detecting emotion specific modulations in

different brain regions, including the motor system as suggested by previous imaging (Gur et al., 2002; Hariri et al., 2003; Habel et al., 2007), TMS (Oliveri et al., 2003) and ERPs studies (Mikhailova and Bogomolova, 2000; Hajcak et al., 2006). A grey screen (1000 ms duration) indicated the beginning of the trial. This was followed by a test picture lasting 160 or 310 ms projected at the centre of the screen (Figure 1B) and by a TMS pulse delivered at 150 or 300 ms after picture onset, respectively. The picture was followed by a random-dot mask (obtained by scrambling the corresponding sample stimulus by means of a custom-made image segmentation software) lasting 1000 ms. Then, the question "What did you see?" appeared on the screen, and participants answered verbally (forced choice: positive, neutral or negative). An experimenter recorded the answer by pressing a computer key.

To avoid changes in excitability due to verbal response (Tokimura et al., 1996; Meister et al., 2003), participants were invited to answer only during the question screen, a few seconds after the TMS pulse (Tidoni et al., 2013). After response, the screen appeared black for 4-6 sec. This way the inter-pulse interval was >10 s, 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 magnetic pulses were delivered over M1 (inter-pulse interval >10 s). Each baseline and experimental block lasted about 2 and 10 minutes, respectively. At the end of the TMS sessions, all stimuli (shown in a randomized order for 160 and 310 ms as in the TMS experiment) were presented to subjects, who were asked to rate arousal and valence of each picture using an electronic 5-points Likert scale. Arousal and valence ratings were collected in two separate blocks whose order was counterbalanced across subjects. Afterwards, to assess empathy and personal distress dispositions, subjects were asked to complete the Interpersonal Reactivity Index (IRI) (Davis, 1996), a 28-item self-report survey that consists of four subscales, namely Perspective Taking (PT, that assess the tendency to spontaneously imagine and assume the cognitive perspective of another person), Fantasy scale (FS, that assess the tendency to project oneself into the place of fictional characters in books and movies), Empathic Concern (EC, that assess the tendency to feel sympathy and compassion for others in need) and

Personal Distress (PD, that assess the extent to which an individual feels distress in emotionally distressing interpersonal contexts). PT and FS assess cognitive components of empathy, while EC and PD correspond to the notions of other-oriented empathy reaction and self-oriented emotional distress, respectively (Davis, 1996). The PD subscale reflects an anxiety-related interpersonal reactivity that may interfere with mature forms of empathy; thus it tends to drop as the other scales rise and is negatively related to measures of overall social functioning.

Data analysis

Neurophysiological data were processed off-line. Mean MEP amplitude values in each condition were measured peak-to-peak (in mV). Since background EMG is known to modulate the MEP amplitude, pre-TMS EMG was assessed by calculating the mean rectified signal across a 100ms interval prior to TMS. MEPs with preceding background EMG deviating from the mean by more than 2 S.D., were removed from further analysis (less than 5% and similarly distributed across conditions). It should be noted that pictures were presented for relatively short time and online TMS may potentially distract participants. To assure that motor excitability reflected effective perception of IAPS stimuli, MEPs associated to incorrect picture classification were discarded from the analysis (see Supplemental data for a discussion of the relation between classification accuracy and motor excitability). Mean accuracy in the emotion evaluation task was high (mean accuracy $\pm$ S.D: 92% $\pm$ 4). Accuracy and MEP data across subjects were normally distributed (as revealed by Shapiro-Wilk test) and were analyzed by means of repeated measure analysis of variance (ANOVA). Significant effects in the ANOVAs were followed by post-hoc analyses using Duncan tests corrected for multiple comparisons. To investigate the relationship between early motor reactivity, dispositional empathy and personal distress, MEP contrasts (negative minus mean of positive and neutral pictures; mean of the two muscles) recorded at 150 ms and the four subscales of the IRI were entered into a correlation analysis. Partial correlations were computed between MEP contrasts and each IRI subscale while controlling for the remaining subscales. A further partial correlation analysis was computed on MEP contrasts

(mean of positive and negative minus neutral pictures; mean of the two muscles) computed at 300 ms and the four IRI subscales. The two different MEP contrasts were chosen based on the results of the main ANOVA that showed a selective increase of motor excitability for negative pictures at 150 ms and a comparable increase of motor excitability for positive and negative pictures at 300 ms. MEP contrasts and IRI subscales were normally distributed as shown by Shapiro Wilk test. The significance level for the two correlation analyses was set at $p = 0.025$.

To confirm emotional features of the IAPS stimuli, we assessed mean scores of arousal and valence. These data were not normally distributed and thus were analyzed by means of nonparametric Friedman ANOVAs. Preliminary Wilcoxon test comparisons revealed that subjective ratings were statistically comparable for pictures presented for 150 ms and 300 ms (all $p > 0.27$) and thus data were collapsed across temporal conditions. Bonferroni-corrected planned Wilcoxon tests were used to analyze significant Friedman ANOVAs effects.

Results

Subjective judgements and classification accuracy of IAPS pictures

Subjective judgements confirmed emotional features of the IAPS stimuli (Table 1). Friedman ANOVAs carried out on mean valence and arousal scores were significant (all $\chi^2 > 26.14$ $p < 0.001$). Bonferroni-corrected planned Wilcoxon test confirmed that valence was lower for negative relative to positive and neutral IAPS stimuli (all $p < 0.001$); moreover, positive IAPS stimuli obtained higher valence scores than neutral IAPS stimuli ($p < 0.001$). Arousal scores were higher for positive and negative IAPS stimuli relative to neutral IAPS stimuli (all $p < 0.001$).

	Negative 150	Neutral 150	Positive 150	Negative 300	Neutral 300	Positive 300
Arousal	4.0 ± 0.8	1.3 ± 0.3	3.0 ± 0.6	4.0 ± 0.7	1.3 ± 0.2	3.0 ± 0.6
Valence	-1.4 ± 0.3	0.0 ± 0.05	1.1 ± 0.2	-1.3 ± 0.3	0.0 ± 0.1	1.1 ± 0.2

Table 1. Mean ± S.D. of arousal and valance ratings of stimuli in the different conditions.

Overall, classification accuracy during the TMS session was high. A Time (2 levels: 150 ms and 300ms) x Emotional scene (3 levels: positive, neutral and negative) repeated measure ANOVA on percentage of correct responses indicated a main effect of Emotional scene ($F_{2,26} = 4.24$, $p < 0.05$). Duncan tests indicated greater accuracy for negative (mean accuracy ± standard deviation; 97% ± 7) relative to positive images (87% ± 14, $p < 0.01$). Accuracy for neutral images (91% ± 11) was statistically comparable to negative and positive images (all $p > 0.10$). No main effect of or interaction with the factor Time (all $F < 1.98$, $p > 0.16$).

Temporal dynamics of motor excitability during perception of emotional scenes

Preliminary neurophysiological analyses assured that no change in excitability due to TMS *per se* was detected throughout the experiment and showed that motor excitability during the emotion evaluation task was greater relative to baseline levels (Figure 1; Supplementary Data).

To specifically investigate the effect of time and visual conditions on motor excitability a Muscle (2 levels: FDI and APB) x Time (2 levels: 150 ms and 300ms) x Emotional scene (3 levels: negative, neutral and positive) repeated measure ANOVA on MEP amplitudes recorded during observation of IAPS stimuli was carried out. The analysis showed a main effect of Emotional scene ($F_{2,26} = 6.77$, $p < 0.01$) and, most importantly, a significant Time x Emotional scene interaction ($F_{2,26} = 4.76$, $p < 0.05$; Figure 2).
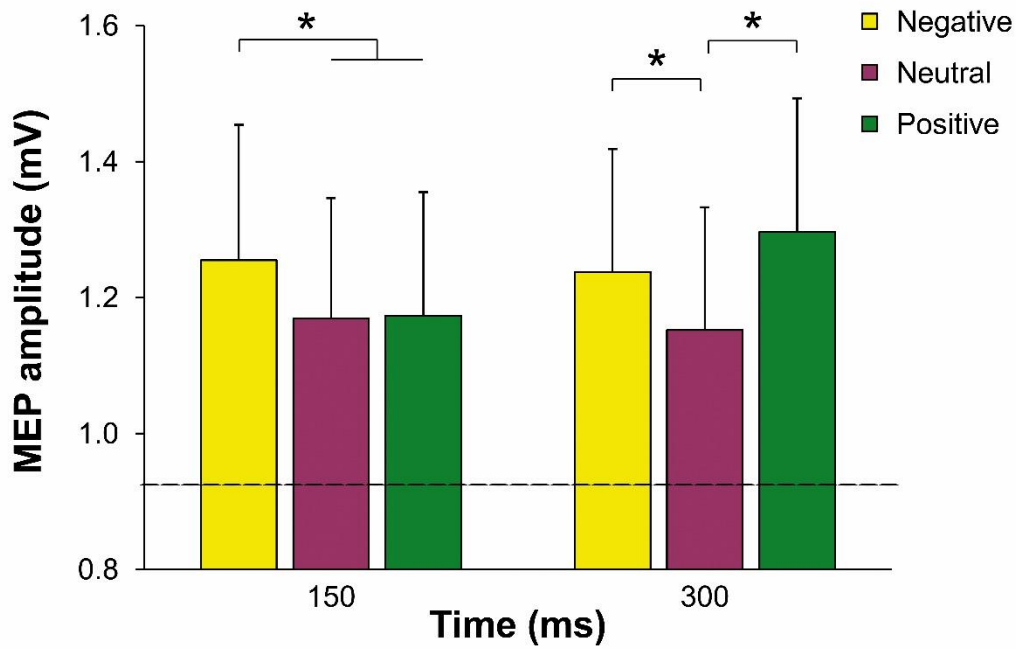
Figure 2. MEP amplitude (in mV) recorded at 150 ms and 300 ms after presentation of negative, neutral and positive pictures (average of the two muscles, FDI and APB). The dashed line represents mean MEP amplitude during baseline blocks. Error bars indicate s.e.m. Asterisks (*) denote significant post-hoc comparisons (p < 0.05).

	Negative 150	Neutral 150	Positive 150	Negative 300	Neutral 300	Positive 300
FDI	1.50 ± 0.99	1.38 ± 0.81	1.38 ± 0.90	1.46 ± 0.89	1.37 ± 0.89	1.55 ± 0.95
APB	1.01 ± 0.50	0.96 ± 0.51	0.97 ± 0.47	1.01 ± 0.46	0.94 ± 0.46	1.04 ± 0.52

Table 2. Raw MEP amplitude ± S.D. (in mV) from the two target muscles during the experimental conditions.

Post-hoc analysis (performed with the Duncan test to account for multiple comparisons) indicates that at 150 ms MEP amplitude was greater during the observation of emotionally negative relative to

both positive (p < 0.05) and neutral scenes (p < 0.05), which in turn did not differ from one another (p = 0.93). At 300 ms, MEP amplitude was greater during observation of both emotionally positive (p < 0.01) and negative (p < 0.05) relative to neutral scenes. No difference between positive and negative scenes was found (p = 0.15). No other main effects or interactions were significant, including those with the factor Muscle, indicating that similar changes in excitability were detected in the FDI and APB muscles (all F < 3.04, p > 0.10; Table 2).

Relation between personality and motor reactivity

The comparable motor facilitation for positive and negative IAPS images that we observed in the 300 ms condition, confirms previous TMS studies that tested motor excitability within the same temporal frame (Borgomaneri et al., 2012) or at a later time (Baumgartner et al., 2007; Hajcak et al., 2007; Coombes et al., 2009). Notably, our study reveals that at an earlier stage of processing (150 ms) a selective increase of excitability for negative images occurs within the motor system. We explored whether inter-individual differences in dispositional empathy and personal distress predicted the magnitude of these two neurophysiological effects.

An index of early motor reactivity for negative pictures (MEP contrast computed at 150) entered in a partial correlation analysis with the four IRI subscales. Partial correlations showed that the PD was marginally significantly related to MEP contrast at 150 ms (r = 0.66, p = 0.027; Table 3). This relation strongly increased after the removal of one outlier with standard residuals <-2σ (r = 0.90, p < 0.001; Figure 3).
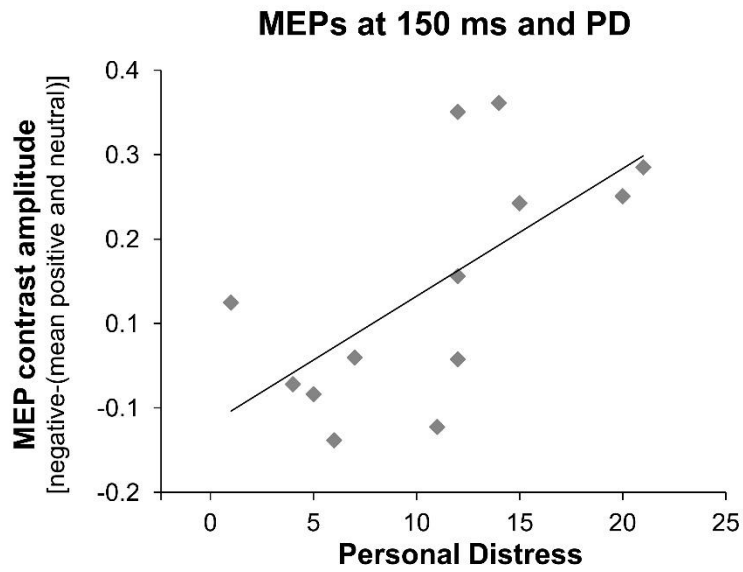
Figure 3. Simple correlation between MEPs contrasts at 150 ms (amplitude during negative pictures minus mean amplitude in the positive and neutral conditions) and Personal Distress subscale of the Interpersonal Reactivity Index.

IRI subscale	MEP contrast 150 ms		MEP contrast 300 ms	
	correlation coefficient	associated p-level	correlation coefficient	associated p-level
PD	0.66	0.03	0.57	0.06
EC	-0.25	0.46	-0.23	0.50
PT	-0.02	0.95	0.37	0.26
FS	-0.42	0.20	-0.17	0.61

Table 3. Partial correlations between MEP contrasts and IRI subscales.

An index of late motor reactivity for positive and negative pictures (MEP contrast computed at 300 ms) was entered in a further partial correlation analysis showing no significant relation with the IRI subscales (Table 3).

Discussion

Although it is widely assumed that emotions prime the body for action, the effects of visual perception of natural emotional scenes on the dynamics of the human motor system have rarely been investigated. In the present study we directly tested the hypothesis that perception of emotionally negative scenes triggers fast reactivity in the corticospinal system. We used single-pulse TMS to monitor changes in excitability of the dominant hand cortical motor representation while participants observed and actively categorized pictures from the IAPS database. We found that seeing negative pictures increased the amplitude of MEPs from the right FDI and APB muscles at 150 ms from stimulus onset. The magnitude of this early increase in hand motor reactivity was predicted by inter-individual differences in the disposition to experience personal distress. Moreover, the early motor excitability increase was followed by a comparable motor facilitation for both positive and negative pictures detected at 300 ms. These findings suggest that perception of natural emotional scenes dynamically modulates the functional state of the human corticospinal system with faster reactivity for potentially threatening scenarios. Moreover, they highlight a functional link between interpersonal anxiety-related personality traits and motor reactivity to complex negative emotional scenes.

The neural network involved in the perception of emotional scenes has been highlighted in a series of functional imaging studies (see Sabatinelli et al., 2011, for a recent meta-analysis of 57 studies). This network includes not only occipitotemporal visual regions but also medial frontal cortices (orbitofrontal and cingulate cortex) that are densely connected to the motor cortex either directly or via premotor and supplementary motor areas (Morecraft and van Hoesen, 1998; Cavada et al., 2000; Oliveri et al., 2003); and may thus provide a cortical pathway for emotional cues to modulate motor

excitability (Pessoa and Adolphs, 2010). Remarkably, motor reactions to aversive visual stimuli may also be implemented through predominantly subcortical routes as suggested by studies on brain damage patients with permanent cortical blindness (Tamietto et al., 2009). Moreover, imaging evidence indicates that subcortical structures (i.e. pulvinar, thalamus and amygdala) are active during perception of complex emotional scenes (Sabatinelli et al., 2011) and in principle these structures may provide additional signals to different segments of the motor pathway during processing of emotional stimuli (Tamietto and de Gelder, 2010; de Gelder et al., 2011).

ERPs studies have highlighted the cortical dynamics of emotional scene processing and, particularly relevant to the present findings, they have reported an initial greater reactivity for negative scenes in occipitotemporal regions (within 100-200 ms from stimulus onset; Olofsson et al., 2008) and, in some cases, also in frontal regions. For example, Carretié and colleagues (2001, 2006) have reported that seeing negative scenes increases the amplitude of frontal positive ERP components with latency in the 160-200 ms range which are thought to reflect the activation of medial prefrontal cortices (see also Northoff et al., 2000 and Kawasaki et al., 2001). Our data significantly expand these findings by demonstrating that this early "negative bias" is not limited to neural regions involved in sensory processing and affective evaluation but extends to the cortical motor representation of the dominant hand, supporting the notion that emotional cues drive action preparation in the brain and, that potential threats require particularly quick motor reactions to secure the survival of the organism (Lang et al., 2000; Öhman and Mineka, 2001; Carretié et al., 2009; Frijda, 2009).

The early motor facilitation for negative pictures appears strictly related to inter-individual differences in personal distress but not empathy dispositions. Personal distress is an aversive, self-focused emotional reaction to the negative state of another and the PD subscale of the IRI assesses this anxiety-related interpersonal disposition (Davis, 1996). While personal distress may counteract mature forms of empathy (Avenanti et al., 2009; Batson et al., 1997; Lamm et al., 2007), studies have reported that participants who score high on the PD scale show enhanced reactivity of the insula when seeing negative facial expressions (i.e. pain or disgust, Jabbi et al., 2007; Saarela et al., 2007). Seeing

stimuli depicting painful stimulation of the body of another reduces motor excitability, an effect that may be due to the 'resonant' activation of pain representations in the observer (Minio-Paluello et al., 2006; Avenanti et al., 2009b). Interestingly, participants with high PD scores tend to show increased motor excitability when seeing the pain of others (Avenanti et al., 2009), in line with the notion that anxiety-related traits are associated with greater motor excitability (Wassermann et al., 2001). Notably greater PD scores are also associated with heightened action readiness but weaker motor control when facing negative images, suggesting that increased motor reactivity may be non-functional (Ferri et al., 2010). Our study is consistent with such evidence and supports the view that anxiety-related traits influence the way in which social and emotional signals are processed in the brain (Azevedo et al., 2005; Lawrence et al., 2006; Moriguchi et al., 2006; Kret et al., 2011a).

The early motor facilitation for negative pictures may seem at odds with previous TMS studies testing the excitability of the left motor cortex during perception of emotional scenes. Most of these studies reported comparable motor facilitation of right hand muscles for positive and negative pictures, either during passive observation (Hajcak et al., 2007) or active categorization of the images (Borgomaneri et al., 2012), or when planning a movement during observation of task-irrelevant pictures (Coombes et al., 2009). Similar findings were also reported by Baumgartner and colleagues (2007) during passive presentation of emotional scenes and emotionally congruent auditory stimuli. Notably in all such studies, MEPs were collected at 300 ms from picture onset (Borgomaneri et al., 2012) or at a later time (Baumgartner et al., 2007; Hajcak et al., 2007; Coombes et al., 2009) and ERP studies suggest that electrophysiological responses to positive and negative pictures are similar in the 300-600 ms range (Olofsson et al., 2008). Thus, our study confirms these temporal dynamics and, on the other hand, indicates the presence of an earlier modulation of the motor cortex when facing emotionally negative scenes.

While MEPs were collected at two discrete time points, it is likely that during perception of emotional scenes the excitability of the observer's motor cortex gradually changes over time, in line with traditional models of continuous information processing (Miller et al., 1992; Massaro and Cohen,

1995). Future studies testing motor excitability at earlier time windows and with more intervals have the potential to disclose how neural responses to emotional scenes gradually build up (see Michelet et al., 2010; Barchiesi and Cattaneo, 2013) for recent examples in the domain of action execution and observation).

It is worth noting that the reported modulations of motor excitability occurred in the left hemisphere. Traditionally, two theories have linked emotion perception to the issue of hemispheric laterality. According to one view, the right hemisphere is specialized to process all emotions, whereas another view suggests that the right and the left hemispheres are relatively specialized in processing negative and positive emotions, respectively (Silberman and Weingartner, 1986; Davidson and Hugdahl, 1995; Borod, 2000). Since our results showed that negative scenes are able to modulate the left motor cortex, none of these laterality effects can be considered as confounds for the reported changes in motor excitability. Further studies are needed to directly investigate how perception of negative and positive emotional scenes may differentially influence neural motor dynamics in the two hemispheres.

That negative scenes could be particularly adept at facilitating action mechanisms was already suggested by behavioral studies exploring motor performance and action readiness (Coombes et al., 2005, 2009; Naugle et al., 2010). This notion has also been supported by studies reporting enhanced motor cortex plastic reactivity to repetitive TMS during presentation of negative pictures (Koganemaru et al., 2012) as well as increased behavioral imitation (Grecucci et al., 2011) and motor and premotor cortex response to the observation of other's actions (Enticott et al., 2012; Ferri et al., 2013) when action stimuli were primed by unpleasant cues. Moreover, increased EEG motor readiness potentials were found when planning to grasp unpleasant relative to pleasant or neutral objects (de Oliveira et al., 2012) or when moving a finger after negative relative to neutral pictures (Grecucci et al., 2009). Relevant to the present findings are TMS studies in which MEPs were recorded during action execution. In a first study participants pressed a button when seeing emotionally negative IAPS pictures (Oliveri et al., 2003). In such condition, hand motor excitability was greater than in neutral control conditions. However, only negative and neutral conditions were

tested and thus it was not clear whether motor facilitation was driven by unpleasant valence or emotional arousal. More recently, van Loon et al. (2010) asked participants to respond to symbolic targets during presentation of task-irrelevant IAPS pictures. MEPs were recorded at various delays from target onset. Overall, MEP amplitude was larger during positive and negative than during neutral pictures, similarly to previous studies in which MEPs were recorded at rest (Baumgartner et al., 2007; Hajcak et al., 2007; Coombes et al., 2009; Borgomaneri et al., 2012). However, when the TMS pulse was delivered during actual finger movement, MEPs were larger for negative relative to positive and neutral pictures.

In sum, despite the long-held view that negative stimuli require fast processing and reactions, to date, previous TMS studies on the perception of natural emotional scenes tested the excitability of the left motor cortex only in a relatively late temporal window. In these conditions a negative bias was detected only when the motor system was pre-activated (van Loon et al., 2010). Our study provides direct evidence that a negative bias can be detected also at rest when motor excitability is tested early. This negative bias is then followed by a comparable increase in motor excitability for both negative and positive stimuli. In conclusion, our study highlights the temporal dynamics of the human corticospinal system during perception of natural emotional scenes.

Supplementary Data

Supplementary Table 1 - List of IAPS stimuli

Positive pictures: 1601, 2000, 2070, 2080, 2091, 2092, 2165, 2311, 2340, 4002, 4220, 4290, 4572, 4608, 4658, 4659, 4660, 4664, 4800, 4810, 7325, 8032, 8080, 8200, 8280, 8320, 8330, 8370, 8400, 8465, 8490, 8540. Neutral pictures: 2480, 2570, 2840, 2880, 5390, 5500, 5510, 5532, 5731, 5740, 5800, 5900, 7000, 7002, 7004, 7006, 7009, 7025, 7034, 7035, 7040, 7060, 7090, 7100, 7140, 7175, 7190, 7205, 7217, 7233, 7235, 7491. Negative pictures: 2800, 3051, 3102, 3110, 3261, 3530, 3550, 6230, 6242, 6250, 6260, 6313, 6370, 6540, 6570, 6571, 6821, 9040, 9050, 9253, 9300, 9400, 9405, 9410, 9433, 9490, 9520, 9530, 9570, 9810, 9920, 9921.

Preliminary neurophysiological analyses

Before analyzing motor responses to emotional pictures we first tested whether TMS during the experimental blocks altered motor excitability *per se*, by comparing MEP amplitudes recorded in the first and the last baseline blocks using a Muscle (2 levels: FDI, APB) x Block (2 levels: first, last) repeated measure ANOVA. The analysis yielded no significant main effects or interaction (all $F < 1.63$, $p > 0.22$). Thus, motor excitability of the two muscles was comparable in the baseline and did not change from the first (mean MEP amplitude $\pm$ SD: FDI = 1.06 mV $\pm$ 0.87; APB = 0.81 mV $\pm$ 0.46) to the last block (FDI = 1.09 mV $\pm$ 0.84; APB = 0.75 mV $\pm$ 0.46), ruling out changes in motor excitability due to the prolonged magnetic stimulations (Chen et al., 1997). We then checked whether motor excitability during the emotion evaluation task differed from baseline levels. We compared MEPs collected during the six experimental conditions with those recorded during baseline (average of the two blocks) using a Muscle (2 levels: FDI, APB) x Condition (7 levels: baseline, negative-150, neutral-150, positive-150, negative-300, neutral-300 and positive-300) repeated measure ANOVA. The analysis revealed a significant main effect of Condition ($F_{6,78} = 8.95$, $p < 0.0001$). Dunnett tests showed that MEPs recorded in all the experimental conditions were greater than those recorded in the baseline control condition (all $p < 0.001$). No main effect of or interaction with the factor Muscle resulted significant (all $F < 2.90$, $p > 0.11$). Thus, during the emotion evaluation task there was an increase of motor excitability relative to baseline levels and this increase was similar in the FDI and APB muscles (151% $\pm$ 58 and 143% $\pm$ 84, respectively; Borgomaneri et al., 2012; Tidoni et al., 2013).

Relation between classification accuracy and neurophysiological data

The analysis of the emotion evaluation task accuracy indicates that overall negative pictures were recognized more frequently than positive pictures (~31 and ~28 correct classifications out of 32 pictures, respectively).

Thus, one may ask to what extent this difference may explain the greater MEP amplitude for negative relative to positive emotional scenes in the early time window.

We believe MEP changes reflect adaptive motor reactions to negative and positive emotional cues and do not reflect unspecific factors linked to the different recognizability of the two classes of pictures. Contrary to MEP data, the difference between negative and positive pictures in classification accuracy occurred independently of the factor time. Thus, were picture recognizability the key factor affecting motor excitability, we should have found greater response for negative relative to positive also in the late time window. Moreover, it should be noted that classification accuracy was comparable for negative and neutral pictures whereas motor excitability was greater for negative than for neutral pictures in both time windows. Thus, overall classification accuracy and MEPs data exhibited different patterns of results.

We nevertheless carried out a further analysis to provide direct evidence that motor excitability for positive and negative pictures remained the same after balancing classification accuracy. We ordered pictures based on participants' accuracy in the emotion evaluation task (independently of time of presentation, since this factor did not influence accuracy) and started removing positive pictures with the lowest accuracy values and negative pictures with the highest values until a match was reached in the remaining sample. This procedure yielded to a sample of 19 negative and 19 positive pictures with comparable classification accuracy ($94.4\% \pm 10$ and $94.3\% \pm 9$, respectively; $t_{13} = 0.04$, $p = 0.97$). The analysis of neurophysiological data associated to this subsample of stimuli confirmed that at 150 ms MEPs were larger for negative (1.28 mV ± 0.65; mean of the two muscles) than for positive pictures (1.15 mV ± 0.54; $p < 0.05$) while they remained similar in the 300 ms condition (1.25 mV ± 0.52 and 1.30 mV ± 0.56; $p = 0.37$). These data speak against the possibility that a different recognizability of the emotional scenes may have played a role in determining the observed pattern of motor excitability.

Supplementary References:

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