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Motor mapping of implied actions during perception of emotional body language

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ABSTRACT

Background: Perceiving and understanding emotional cues is critical for survival. Using the International Affective Picture System (IAPS) previous TMS studies have found that watching humans in emotional pictures increases motor excitability relative to seeing landscapes or household objects, suggesting that emotional cues may prime the body for action.
Objective/Hypothesis: Here we tested whether motor facilitation to emotional pictures may reflect the simulation of the human motor behavior implied in the pictures occurring independently of its emotional valence.
Methods: Motor-evoked potentials (MEPs) to single-pulse TMS of the left motor cortex were recorded from hand muscles during observation and categorization of emotional and neutral pictures. In experiment 1 participants watched neutral, positive and negative IAPS stimuli, while in experiment 2, they watched pictures depicting human emotional (joyful, fearful), neutral body movements and neutral static postures.
Results: Experiment 1 confirms the increase in excitability for emotional IAPS stimuli found in previous research and shows, however, that more implied motion is perceived in emotional relative to neutral scenes. Experiment 2 shows that motor excitability and implied motion scores for emotional and neutral body actions were comparable and greater than for static body postures.
Conclusions: In keeping with embodied simulation theories, motor response to emotional pictures may reflect the simulation of the action implied in the emotional scenes. Action simulation may occur independently of whether the observed implied action carries emotional or neutral meanings. Our study suggests the need of controlling implied motion when exploring motor response to emotional pictures of humans.

Introduction

The ability to understand the emotions displayed by other individuals is critical to react adaptively in social environments. Nonverbal cues, such as body posture or hand gestures, convey important information about the emotional state of others [1,2]. Imaging studies suggest that reading the emotional language expressed in others' body postures and actions relies on the activity of a complex neural network which may include cortical–subcortical regions involved in emotional processing (e.g. the amygdala, anterior insula) and fronto-parietal sensorimotor regions involved in action planning and execution [3–6] (so-called putative mirror neuron system, pMNS). Embodied simulation theories suggest that, since covert emotional states (e.g. happiness) are often associated with overt motor behaviors (e.g. smiling, joyful body postures and gestures), observers can simulate and understand the unobservable emotional state of others by embodying their observable motor behavior [7–12]. Thus, according to this view, emotion perception is inherently linked to action simulation.

Strong evidence for action simulation in humans comes from single-pulse transcranial magnetic stimulation (TMS) studies showing that action observation selectively increases the amplitude of motor-evoked potentials (MEPs) recorded from those muscles involved in the observed actions [13–16]. Similar motor facilitation is also found when seeing pictures of humans depicted in the middle of a motor act (implied action stimuli) [17–19], indicating that the motor system can extract dynamic action information from static images that suggest an ongoing body movement.

These findings suggest that during observation of emotional expressions, even when displayed in a static snapshot, the motor

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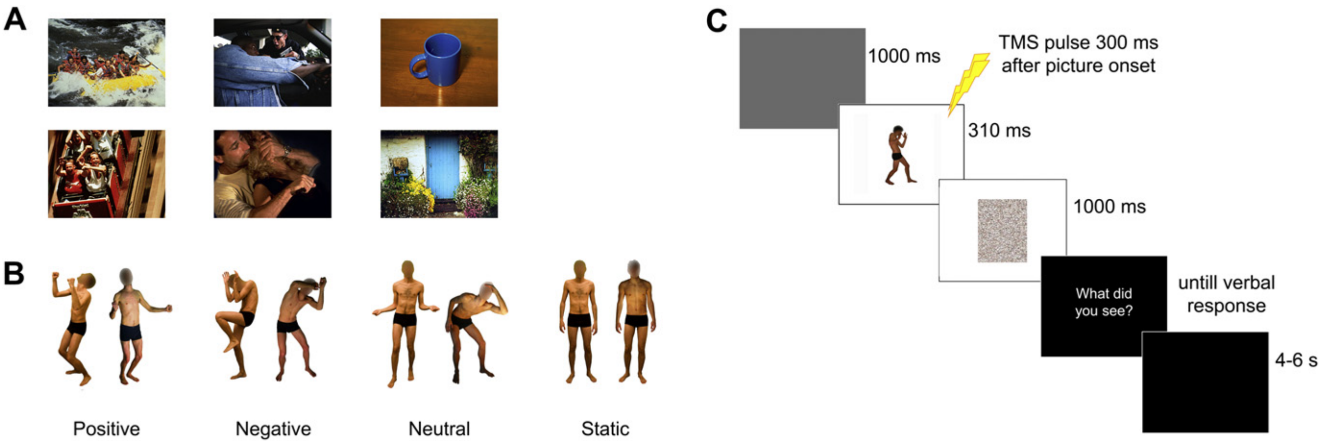

Figure 1. Examples of visual stimuli used in (A) experiment 1 (IAPS images) and (B) experiment 2 (body images). For each visual condition two representative images are shown. (C) Trial sequence.

system may be mainly involved in encoding motor features of the implied body movement, independently of its emotional meaning. Indeed, if the motor cortices are mainly involved in action simulation, as predicted by the embodied simulation account, then motor resonance should occur independently of the emotional content of the observed body movement.

However, another line of research has suggested that during emotional processing the motor system is mainly involved in reacting to emotional cues and preparing a potential motor act [20–23]. In keeping with this notion, behavioral studies have found that unpleasant and pleasant emotional cues facilitate defensive and approaching movements, respectively [24,25]. Moreover, relevant to the present research, TMS studies have shown that perception of emotional pictures from the International Affective Picture System [26] (IAPS) increases motor excitability [27–31]: in particular, seeing snapshots depicting humans in pleasant (e.g. sport, erotic scenes) or unpleasant situations (e.g. being assaulted, injured) increased the amplitude of MEPs from hand muscles relative to neutral control stimuli. However, in these studies, most of the neutral stimuli depicted landscapes or static objects but no humans. Therefore, it is unclear whether increased motor excitability for emotional IAPS stimuli reflected i) a reaction to emotionally arousing stimuli, possibly linked to the activation of approaching/avoidance motor programs; ii) the simulation of human actions implied in the emotional scenarios only.

Here we sought to clarify the involvement of the motor system in processing emotional and action cues embedded in scenes depicting human body movements. MEPs to single-pulse TMS of the left primary motor cortex (M1) were recorded during presentation of emotional and neutral stimuli during an active categorization task. In the experiment 1, we presented positive, neutral and emotionally negative complex scenes from the IAPS database (as in previous TMS research [28,29]) while in experiment 2, we compared positive and negative emotional body movements with neutral movements (i.e. with comparable perceived implied motion but no emotional meaning), and neutral static body postures (no implied motion). This way we tested whether motor facilitation for emotional pictures may reflect motor simulation independently of the emotional valence carried by the action implied in the observed scene.

Materials and methods

Participants

A total of 85 right-handed healthy participants took part in the study. Fourteen and fifteen subjects with no contraindication to TMS [32] were tested in experiment 1 (6 men, mean age ± S.D.: 24.1 y ± 1.4) and experiment 2 (6 men, age: 22.4 y ± 2.6), respectively. Moreover 50 subjects (21 men) were tested in one of three pilot studies and 16 subjects (8 men) were tested in one of two control behavioral experiments (see Supplementary material). The study was approved by the University of Bologna, Department of Psychology ethics committee and carried out according to the Declaration of Helsinki. All subjects gave their written informed consent. No discomfort or adverse effects during TMS were reported or noticed.

Visual stimuli

Different types of pictures were presented on a 19-inch screen located 80 cm away from the participants. In experiment 1, 108 stimuli from the IAPS database [26] were selected (Fig. 1A). All the stimuli (listed in the Supplementary material) were already used in previous TMS experiments [28,29] and included: 36 unpleasant (e.g. scenes of violence, threat, and injuries), 36 pleasant (e.g. sporting events, erotic scenes), and 36 neutral scenes (e.g. household objects, landscapes). Several of these emotional IAPS stimuli depicted humans performing actions. In contrast, IAPS database did not include a sufficient number of emotionally neutral scenes depicting humans performing neutral actions. Hence, the influence of action-related information was further tested using a set of novel emotional and non-emotional stimuli. In experiment 2, 104 pictures depicting four different actors in emotional or neutral postures were used (Fig. 1B). To focus specifically on body-related information, the faces were blanked out in all pictures. Images included 26 static neutral postures (static), 26 emotionally neutral actions (neutral), 26 emotionally negative (fear) and 26 positive body movements (joy). During the recording of neutral actions, actors' instructions specified the action to be performed. For emotional actions, 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).

The 104 stimuli used in experiment 2 were selected from an initial sample of about 1000 stimuli based on two pilot studies (Supplementary material) in which emotional ratings (pilot 1) and recognition performance (pilot 2) tasks were used to select 13 static, 13 neutral, 13 fearful and 13 joyful body expressions that were well recognized. For each category, the final set contained 13 original stimuli and 13 mirror-reflected copies of such stimuli. In a third pilot study (8 participants, 4 men, age: 26.9 y ± 4.8), we assessed the perceived implied motion sensation evoked by actors' hands in each of the 104 pictures using an electronic 5-points Likert scale. Mean ratings for each category were analyzed by means of one-way repeated measures ANOVA. The analysis was significant ($F_{3,21} = 4.68$, $P < 0.05$): implied motion was lower for static stimuli (mean implied motion score ± S.D.: 1.73 ± 0.90), than for neutral (3.19 ± 0.79), joyful (2.73 ± 1.00) and fearful stimuli (2.87 ± 0.62; all $P < 0.05$) which in turn did not differ from one another (all $P > 0.44$). Thus in the selected sample of body stimuli, emotional and neutral actions contained the same amount of implied hand motion.

Transcranial magnetic stimulation and electromyography recording

In both experiments, 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 based on previous TMS studies that explored motor excitability during observation of emotional pictures [27–30]. 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. By using a slightly suprathreshold stimulus intensity, the coil was moved to determine the optimal position from which maximal amplitude MEPs were elicited in the contralateral 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 50 μV in the higher threshold muscle with 50% probability [33]. This way a stable signal could be recorded from both muscles. The absence of voluntary contraction was continuously verified visually throughout the experiment. When muscle tension was detected the experiment was briefly interrupted and subjects were invited to relax.

Procedure and experimental design

The experiments were programmed using Matlab software to control picture presentation and to trigger TMS pulses. In both experiments MEPs were collected in four blocks. The first and the last blocks served as baseline: subjects held their eyes closed with the instruction to imagine watching a sunset at the beach [34] while receiving TMS over M1 (inter-pulse interval ∼10 s). Ten trials were recorded for each of the baseline blocks. In the other two blocks 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 picture (experiment 1) or as a joyful, fearful, neutral or static posture (experiment 2). Two control behavioral experiments ruled out that baseline procedures biases emotion categorization in experiments 1 and 2 (Supplementary material).

Emotional evaluation blocks included 54 (experiment 1) or 52 trials (experiment 2) each (108 and 104 trials in total). In the emotion evaluation blocks, trial sequence was the following: a grey screen (1 s duration) indicated the beginning of the trial and it was followed by the test picture (310 ms) projected at the centre of the screen (Fig. 1C). The TMS pulse was delivered 300 ms after the onset of the stimulus. The picture was followed by a random-dot mask (obtained by scrambling sample stimuli by means of a custom-made image segmentation software) lasting 1 s and then, subject had to verbally answer to the question “What did you see?” that appeared on the screen (forced choice). An experimenter collected the answer by pressing a corresponding computer key. To avoid changes in excitability due to verbal response [35,36], participants were invited to answer only during the question screen, few seconds after the TMS pulse. After response, the screen appeared black for 4–6 s. This way the inter-pulse interval was >10 s, thereby avoiding changes in motor excitability due to TMS *per se* [37]. This was directly confirmed by the lack of changes in FDI or APB MEP amplitudes between the first and the last baseline blocks in both experiments (all $P > 0.40$). 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 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 an electronic 5-points 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.

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 MEP amplitudes [38] pre-TMS EMG was assessed by calculating the mean rectified signal across a 100-ms 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%). Moreover, MEPs associated to incorrect answers were discarded from the analysis. Mean accuracy was high (experiment 1: mean accuracy ± S.D.: 91% ± 8; experiment 2: 92% ± 4) and comparable across the experiments ($t_{27} = 0.42$; $P = 0.68$).

Mean MEP amplitude in each condition was normalized by using the average of two baseline blocks (condition − baseline)/(condition + baseline). This MEP ratio index proved adept to normalize data distribution (as revealed by Shapiro–Wilk test) and was analyzed by means of two repeated measures two-way ANOVAs (one for each experiment) with factors: Muscle (2 levels: FDI, APB) and Stimulus (3 levels for experiment 1: positive, negative and neutral; 4 levels for experiment 2: positive, negative, neutral and static). In all ANOVAs, *post-hoc* comparisons were carried out by means of the Newman–Keuls test.

In the TMS experiments, mean ratings for arousal, valence and perceived movement induced by the different images were not normally distributed and thus were analyzed by means of nonparametric Friedman ANOVAs and Bonferroni-corrected planned nonparametric comparisons. Specifically, in experiment 1 we tested whether emotional IAPS stimuli had not only greater arousal but also greater implied motion than neutral IAPS stimuli. Moreover, in experiment 2 we tested whether emotional (positive, negative) body stimuli had greater arousal than non-emotional neutral action stimuli, but comparable implied motion. We also assured that emotional and neutral action stimuli had greater implied motion than static stimuli. Furthermore, in both experiments we tested whether valence of positive stimuli was greater than neutral and negative stimuli and valence of negative stimuli was lower than that of neutral stimuli.

Results

Experiment 1

The Muscle × Stimulus ANOVA on normalized MEP amplitudes recorded during observation of IAPS stimuli showed a main effect of

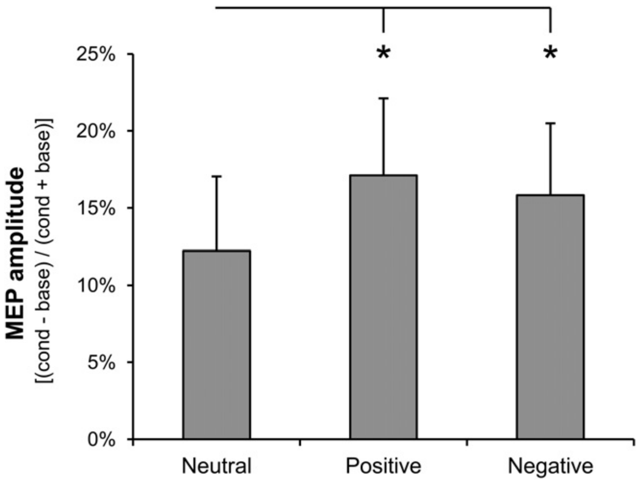

Figure 2. MEP amplitude [(condition − baseline)/(condition + baseline)] during perception of neutral, positive and negative IAPS images in experiment 1 (average of the two muscles, FDI and APB). Error bars indicate s.e.m. Asterisks (*) denote significant *post-hoc* comparisons ($P < 0.05$).

Stimulus ($F_{2,26} = 6.50$, $P < 0.01$; Fig. 2) accounted for by the greater MEP amplitude during observation of emotionally positive ($P < 0.01$) and negative ($P < 0.05$) relative to neutral scenes. No difference between positive and negative scenes was found ($P = 0.37$). No Muscle main effect or Muscle x Stimulus interaction was found indicating that similar changes in excitability were detected in the FDI and APB muscles (all $F < 2.19$, $P > 0.13$; raw MEP amplitudes in Table 1).

Table 2 illustrates subjective evaluations of IAPS stimuli. Friedman ANOVAs carried out on arousal, valence and implied motion scores of IAPS stimuli were all significant (all $\chi^2_2 > 26.14$, $P < 0.001$). Follow-up comparisons 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 ($P < 0.001$). Critically, not only arousal but also implied motion scores were higher for positive and negative IAPS stimuli relative to neutral IAPS stimuli (all $P < 0.001$). Thus, greater motor excitability for emotional scenes may be due to arousal (as hypothesized in previous studies [28,29]), but also to the greater (implied) motion perceived in emotional relative to neutral scenes of IAPS database. Experiment 2 was designed to directly test whether implied motion *per se* may explain changes in motor excitability during observation of emotional and neutral body movements.

Experiment 2

The Muscle × Stimulus ANOVA performed on normalized MEPs recorded during observation of body stimuli showed a main effect of the Stimulus ($F_{3,42} = 4.24$, $P < 0.01$; Fig. 3) accounted for by the greater amplitude for positive (joy), negative (fear) and neutral body movements relative to static body postures (all $P < 0.05$). MEP amplitude during observation of positive, negative and neutral movements did not differ from one another (all $P > 0.46$). No Muscle main effect or Muscle × Stimulus interaction was found indicating that similar changes in excitability were detected in the FDI and APB muscles (all $F < 0.86$, $P > 0.37$; see also Table 1).

Table 1

Raw mean MEP amplitudes (in mV) ± S.D. recorded in the two muscles (FDI and APB) during the conditions of experiment 1 (top) and experiment 2 (bottom).

	Baseline	Neutral	Positive	Negative
FDI	1.08 ± 0.85	1.40 ± 0.92	1.55 ± 0.96	1.47 ± 0.89
APB	0.78 ± 0.44	0.96 ± 0.46	1.04 ± 0.51	1.01 ± 0.47

	Baseline	Static	Neutral	Positive	Negative
FDI	1.00 ± 0.40	1.22 ± 0.47	1.31 ± 0.48	1.32 ± 0.51	1.35 ± 0.50
APB	0.86 ± 0.59	1.21 ± 0.69	1.29 ± 0.78	1.33 ± 0.80	1.27 ± 0.71

Table 2

Mean ± S.D. of subjective evaluations (arousal, valance and perceived implied motion) of stimuli used in experiment 1 (top) and experiment 2 (bottom).

	Neutral	Positive	Negative
Arousal	1.24 ± 0.23	2.98 ± 0.60	3.98 ± 0.70
Valence	0.01 ± 0.06	1.10 ± 0.20	−1.31 ± 0.31
Perceived motion	1.28 ± 0.50	3.60 ± 0.50	2.40 ± 0.41

	Static	Neutral	Positive	Negative
Arousal	1.13 ± 0.20	2.25 ± 0.55	3.05 ± 0.84	3.53 ± 0.76
Valence	0.01 ± 0.03	0.16 ± 0.18	1.21 ± 0.31	−1.25 ± 0.38
Perceived motion	1.06 ± 0.12	2.94 ± 0.49	3.28 ± 0.58	2.94 ± 0.51

Table 2 illustrates subjective evaluations of body stimuli. Friedman ANOVAs carried out on arousal, valence and implied motion scores of body stimuli in experiment 2 were all significant (all $\chi^2_2 > 42.79$, $P < 0.001$). Follow-up comparisons confirmed that valence was lower for negative relative to positive, neutral and static body stimuli (all $P < 0.0001$); moreover, positive body stimuli obtained higher valence scores than neutral and static body stimuli (all $P < 0.0001$); and neutral action were considered more positive than static postures ($P < 0.008$).

On average, greater arousal was associated to emotional relative to neutral and static body stimuli ($P < 0.001$); moreover, greater arousal was found for neutral actions relative to static postures ($P < 0.001$). Critically, implied motion was greater for positive and negative relative to static body stimuli (all $P < 0.0001$) and for neutral actions relative to static body stimuli ($P < 0.0001$); moreover, implied motion was comparable for emotional relative to neutral action stimuli ($P > 0.07$). These data indicate that emotional and neutral body movements differed for arousal and valence, but contained the same amount of implied motion. Since MEPs were greater when seeing emotional and neutral movements than for static postures, implied motion but not arousal or valence can explain the pattern of changes in motor excitability.

Discussion

In the first experiment, we used single-pulse TMS to stimulate the left M1 and thus explore motor excitability during perception

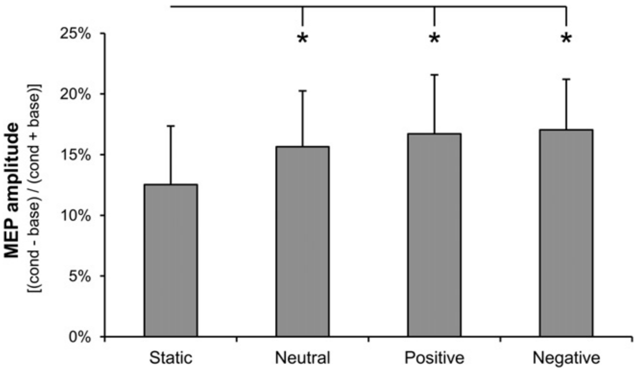

Figure 3. MEP amplitude [(condition − baseline)/(condition + baseline)] during perception of static, neutral, positive (joy) and negative (fear) body images in experiment 2 (average of the two muscles, FDI and APB). Error bars indicate s.e.m. Asterisks (*) denote significant *post-hoc* comparisons ($P < 0.05$).

and active categorization of complex scenes from the IAPS database [26]. We found greater MEP amplitudes from two hand muscles (FDI and APB) when seeing emotionally positive and negative scenes relative to emotionally neutral scenes. These findings confirm results obtained in a previous study [28] during passive observation of the same IAPS stimuli and suggest that perception of emotional scenes is associated to an increase of hand motor excitability, in keeping with the view that emotions may prime the body for action [20–23]. In experiment 1 (and in the study using the same stimuli [28]), positive and negative stimuli elicited comparable motor facilitation, suggesting that arousal but not valence may in principle account for by the pattern of changes in motor excitability (see also [30,31]). However, pleasant and unpleasant IAPS pictures mostly showed humans involved in dynamic situations – that is, engaged in some motor activity or operating an object such as a gun or a knife – while most of the neutral scenes depicted still objects and landscapes. Notably, our data also indicate that participants perceived more implied motion in the emotional than in the neutral scenes. Thus, it is unclear whether the pattern of motor excitability found in experiment 1 (and likely in previous TMS studies using the same IAPS stimuli) may be due to the arousing content of the emotional scenes or the human actions implied in such scenes.

In the second experiment, we directly addressed the issue of action-related changes in motor excitability during perception of a novel set of emotional body stimuli. Similar to experiment 1, MEPs to left M1 stimulation were recorded from the APB and FDI muscles during presentation of pictures that had to be actively categorized. To eliminate any possible confounding present in experiment 1, only scenes depicting humans were presented. Moreover, to directly test the influence of action-related information on motor excitability, snapshots of humans in dynamic situations (i.e. during emotionally positive, negative or neutral movements involving the two target hand muscles) and static postures were shown, and faces and contextual information were blanked out. This way, we specifically tested how perception of emotional body language would affect motor excitability.

A major point of novelty of our study is the demonstration that seeing positive (happy) and emotionally negative (fearful) body movements increased motor excitability relative to observation of static neutral postures. Critically, motor facilitation was also detected during observation of neutral body movements, and did not significantly differ from that found with emotional stimuli. Notably, pictures of neutral actions received lower emotional but comparable implied motion ratings relative to pictures of emotional body movement. Thus, after controlling for the amount of the perceived motion in static snapshots of body expressions, we found no evidence of emotional-specific motor facilitation.

Previous research has investigated whether activation in the motor system is influenced by the emotional meaning of body movements or postures [5,6]. One of the first imaging studies on the topic found increased M1 activation during the perception of negative (fearful) but not positive (joyful) body postures compared to neutral ones [39]; however another study found the opposite effect, with M1 activations during perception of positive but not negative postures [40]. Moreover, a number of additional imaging studies have found very little or no evidence of M1 activation when contrasting emotional expressions *versus* neutral actions with comparable real or implied motion [5,6,41–43]. To date no direct neurophysiological assessment of motor system excitability during processing of emotional and neutral actions was provided. Here, we found motor facilitation to depend more on the perceived motion implied in the observed scene/action than on the evoked arousal or emotional valence. Jointly, these results seem more compatible with activity in the motor system reflecting a “cold” motor simulation of the observed actions than a specific response to emotional cues [8–19].

The idea that motor system activation may reflect the internal simulation of others’ motor behavior comes from TMS studies showing that seeing or imaging others’ actions modulate the excitability of the motor representations of those muscles involved in the observed/imagined body movements [13–19,44–50]. These motor modulations are temporarily coupled with the observed action phase [17,51] and are mediated by neural activity in the premotor cortex [15,19,52] which may suggest that motor modulations reflect action simulation activity of the anterior node of the human pMNS [3,4,53,54].

Evidence for similar embodied simulation mechanisms comes from studies exploring motor excitability during observation of somatosensory stimulations in others: watching painful [55–57] or touching [58] stimuli shown on the body of other people induces modulations of motor excitability that are specific to the muscles involved in the observed stimulation. These motor modulations are inhibitory as those observed during first-hand experience of touch or pain and correlate with sensorimotor (e.g. intensity, localization) but not emotional (e.g. unpleasantness) features of the somatic experience [59,60]. Thus, seeing others’ actions or somatic feelings activates fine-grained sensorimotor representations of the observed state in the observer [3,4,7–13,61–63], and this notion is supported by imaging and neurophysiological evidence that motor and somatosensory networks involved in action execution, touch and pain perception are also activated during observation of similar actions [64–69] and similar somatic feelings in others [70–77]. Our study supports this view and suggests that the motor system encodes motor features of the observed movement, independently of its emotional content.

It should be noted that in both experiment 1 and 2, MEPs were recorded during active categorization of emotional pictures. We used an emotional categorization task because previous imaging [78–81], TMS [27] and event-related potentials [82] (ERPs) studies have shown that active categorization maximizes the chance of detecting emotion-specific modulations in different brain regions, including the motor system. Nevertheless, our study fails to reveal any emotion-specific modulation of motor excitability.

It is unlikely that the pattern of results may be accounted for by the semantic meaning of the verbal responses, as the very same response (“neutral”) was associated to reduced excitability in experiment 1 (neutral IAPS stimuli) and motor facilitation in experiment 2 (neutral actions with implied motion).

Our findings suggest that motor response to emotional stimuli found in previous TMS research [27–31] may reflect, at least in part, action simulation activity triggered by the processing of the action cues depicted in the observed emotional scene. However, the lack of emotion-specific motor facilitation in experiment 2 requires two final considerations. First, similarly to previous TMS research [27–31] we focused on the excitability of the hand motor representations in the left hemisphere. Thus, we do not exclude that a different reactivity (i.e. emotion-specific modulation) may be found in the right hemisphere which is specialized for emotional processing [83] or outside the hand region. Future studies will assess whether whole-body emotional actions may induce emotion-specific facilitation in other sector of the motor system. Second, it should be noted that in the present study we specifically explored motor cortex reactivity at 300 ms after stimulus onset. Thus we do not exclude that emotion specific signals may specifically modulate motor excitability at different time points. Moreover, since observed (neutral) actions are known to modulate the motor system at 200–400 ms [84–86], one may even wonder whether the present paradigm was optimized to assess the activity of the pMNS rather than the tendency of the motor system to react to emotional cues. However, ERPs studies suggest that emotionally arousing stimuli induce activity in the same temporal window at various electrodes, including fronto-central electrodes [87]. Moreover, a previous TMS study found increased motor excitability for facial emotional expressions (i.e. expressions with implied motion) relative to neutral (static) expressions at 300 ms after stimulus onset [88]. Such evidence indicates that the explored temporal window is potentially adept to reveal motor reactivity to emotional body language.

In conclusion, our study suggests that seeing others' emotional expressions and neutral actions in static pictures induces comparable action simulation activity in the observer's motor system. In keeping with embodied simulation accounts [7–19], we found that motor resonance occurred independently of the emotional meaning of the observed behavior. Our data also suggest that caution should be paid when selecting emotional stimuli (e.g. in the IAPS or in other databases) and the motion implied in such stimuli should be controlled when investigating neural activity within the motor system.

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Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.brs.2012.03.011.

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