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Your emotion moves into my motor system

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General Discussion

Social animals have evolved a whole range of communicative abilities on which their well-being and survival in a society hinges. Foremost amongst the cognitive skills of social species is the ability to monitor each others' behavior and emotions and to adapt continuously to the social signals of others. Therefore, appropriately understanding and reacting to the emotions of others appear to be fundamental abilities for survival.

Our motor system has a fundamental role in these processes: it is involved in internally simulate others' behaviors (motor resonance), probably in order to better understand them and to prepare the most opportune motor reaction.

However, to date, only few Transcranial Magnetic Stimulation (TMS) studies have investigated the effect of emotional stimuli observation on the observers' motor system activity (Baumgartner et al., 2007; Hajcak et al., 2007; Schutter et al., 2008; Coombes et al., 2009). These studies mainly tested the left motor cortex excitability relatively late in time (> 300 ms) specifically during emotional faces or complex scenes observation. Moreover, very few studies have tested the role of sensorimotor system on visual recognition of emotional signs (Adolphs et al., 2000; Pitcher et al., 2007; Balconi and Bortolotti, 2013). Therefore, it remains unclear whether observers' motor system, and the motor cortex (M1) in particular, is specifically modulated by the observation of others' emotion. In particular, to date, there were no TMS studies on M1 modulation during emotion observation, conveyed by body postures (i.e., when processing body expressions presented in isolation, with no additional contextual or facial cues).

In the present thesis, we employed TMS in order to test possible cortico (using paired-pulse TMS, ppTMS) and corticospinal (using single-pulse TMS, spTMS) modulations while subjects were requested to actively categorize emotional (positive and negative) or neutral complex scenes, or

emotional (happy and fear), neutral (depicting the mimic of an action) or static (at rest) human body postures presented in isolation. We also tested the different role of the left and the right primary motor cortices in facing such stimuli, using different times of stimulation, namely from 100 to 300 ms after the stimulus onset. Due to the high temporal resolution of the TMS and its ability to temporarily interfere with the activity of a specific area of the brain, we get a clear picture about the time course and the causal role of the motor system when faced with emotional and neutral stimuli.

1. Fast fear-related freezing reaction: a cortical origin.

Data from Chapter 4 revealed that the motor system of an observer is recruited very fast (100-125 ms) when facing emotional potentially dangerous stimuli. We presented emotional (happy and fear), dynamic neutral (depicting the mimic of an action) or static (at rest) body postures to test the hypothesis that a negative bias can be detected for fearful bodies if motor excitability is assessed very early in time. We assessed motor excitability in both left and right M1 using 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) motor circuits. We found that, regardless of the stimulated hemisphere, seeing fearful bodies strongly reduced the magnitude of the ICF relative to watching happy or neutral bodies. Moreover, observing happy bodies reduce ICF relative to neutral bodies. Our data indicate that emotional bodies induce a fast modulation of cortical motor excitability, with a stronger reduction of intracortical excitatory activity when perceiving fearful bodies. The fact that emotional bodies modulated ICF but not SICI suggests that processing of fearful bodies was mainly associated to a reduction in the input to excitatory glutamatergic interneuronal networks in M1 originating from interconnected regions. Moreover, the fact that emotional bodies modulated ICF, but not corticospinal excitability (no effect in the single pulse session), suggests that the negative bias we detected has a predominantly cortical origin. We propose this decrease in ICF reflects the cortical

motor counterpart of an orienting response toward emotionally salient body postures that would manifest as strong suppression of motor readiness when seeing fearful bodies. From our data, we can conclude that, only after 100-125 ms, our motor cortex, together with the visual system (Smith et al., 2003; Williams et al., 2004; Pourtois et al., 2005; van Heijnsbergen et al., 2007; Jessen and Kotz, 2011), is recruited during fearful body stimuli observation, 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). Moreover, we observed that this effect has a cortical origin, which suggest that probably, at this time, our motor system is not already sending signals to the motor output in order to prepare an appropriate motor reaction but, probably, because what we found is an inhibition of facilitatory signals, M1 is planning to prevent potentially dangerous reaction toward harmful stimuli of the contralateral hand.

2. Different motor reactions toward emotionally salient stimuli in the two hemispheres: motor orienting *before* motor simulation.

Immediately after (at 150 ms) the aforementioned fear-related motor reaction, we observed (Chapter 3), using single-pulse TMS, that the right motor cortex continued to show an inhibitory modulation but, this time, the effect we record was related to corticospinal modulations and was independent of the emotional meaning of the stimuli (similar inhibitory reaction during observation of fearful and happy body postures).

We interpreted this inhibitory motor response as the sight of a rapid orienting reaction toward emotionally relevant stimuli. Additionally, since applying spTMS at variable times during task execution it is possible to investigate with a temporal resolution of a few tens of milliseconds (ms) at what exact time point neural activity at the stimulation site is critical for successful task performance

(chronometry of functional relevance), we also tested whether the TMS pulse interfered with recognition performance at any time or stimulation side. If early motor activity reflects neural processing necessary for perceiving body expressions, we might expect that right M1 stimulation at 150 ms would impair task performance. We found that, at 150 ms, TMS over right M1 interfered with accuracy in the emotion recognition task. No similar effects were found with sham or left M1 stimulation. Greater TMS interference on task accuracy correlated with reduced changes in motor excitability, suggesting a link between neural activity reflecting early orienting and visual recognition of body expressions. This effect provides a strong evidence of the fact that the corticospinal orienting reaction we found in the right motor cortex at 150 ms is necessary to the perception of the observed body stimuli.

In contrast, recording at the same time (150 ms) from the left motor cortex, we found a slightly activation of the corticospinal system (bigger MEPs) during fearful stimuli observation relative to happy and neutral body postures observation. This activation seems to reflect the preparation of a motor reaction specifically towards negative pictures (we found that it was stronger when facing negative complex scenes than isolated fearful body postures, Chapter 1). This effect was stronger when subjects were asked to observe violent, disgusting or fearful complex dynamic scenes relative to fearful human body postures, probably because these latter stimuli are not threatening enough to elicit such facilitatory motor reaction. This facilitatory effect seems to reflect the sign of motor preparation towards negative stimuli and it is independent of perceptual-related processes (no accuracy drop when TMS was applied over left M1).

Finally, we explored the relation between changes in motor excitability (found in Chapter 1 and 3) and individual scores of dispositional empathy using the Interpersonal Reactivity Index (IRI) (Davis 1996) and we observed that either the early right hemisphere reduction of motor excitability for emotional bodies (Chapter 3) and the facilitatory effect we found from the left M1 when facing threatening stimuli (Chapter 1) were related to inter-individual differences in personal distress (PD)

but not to the other IRI subscales (Davis 1996), which reflect empathic dispositions. Taken together, these data suggest that anxiety-related traits influence the way in which social and emotional signals are processed in the brain (Kret et al., 2011a; Azevedo et al., 2013; Borgomaneri et al., 2013). In particular, the more participants showed disposition to feel personal distress in interpersonal contexts the bigger were the effects we found at 150 ms in both hemispheres: on the right side, more orienting response to emotional cues, on the left side, more motor preparation when facing threatening complex scenes.

3. Bilateral motor simulation for complex scenes and dynamic body postures

As mentioned in the *incipit* of this discussion, most of the existing single pulse TMS studies have typically reported that the left motor cortex excitability is sensitive to emotional processing. In particular, they found larger motor evoked potentials (MEPs) when participants were asked to observe pleasant and unpleasant stimuli (Baumgartner et al., 2007; Hajcak et al., 2007; Coombes et al., 2009). Authors interpreted this facilitatory effect as the sign of the preparation of a motor reaction towards arousing stimuli. However, in all these studies, motor excitability was tested in a very late time window (after 3-7 sec of the stimulus onset). If the role of the motor system is to program the most adaptive reaction towards emotionally relevant stimuli, then 3-7 seconds after the stimulus appearance can be probably too late for implementing a motor reaction and secure the survival of an organism. In Chapter 2 we replicated previous findings, discovering that the same facilitatory effect facing emotionally complex scenes could be detected, from the left motor cortex, already after 300 ms. However, embodied simulation theorists posit that, during observation of emotional stimuli, our motor system is involved, not to react, but rather to internally simulate (motor resonance) the unobservable emotional states of others by embodying their observable motor behavior (Carr et al., 2003; Leslie et al., 2004; Gallese, 2007; Oberman et al., 2007; Jabbi and Keysers, 2008; Bastiaansen et al., 2009; Niedenthal et al., 2010; Gallese and Sinigaglia, 2011). Most radical “motoric-centric”

versions of these theories contend that motor resonance occurs prior to the activity in emotion-related regions (thus very early in time) and is necessary for assigning emotional meaning to visual signals (thus they would play a causal role in visual perception) (e.g., Carr et al., 2003; Iacoboni, 2009).

In order to test whether such facilitatory effect reflected the sign of a motor reaction towards arousing stimuli or motor resonance process (more implied motion conveyed by emotional complex scenes relative to the static ones) we used human body postures in isolation.

Using human bodies, we investigated motor system modulations observing emotional dynamic, static (no emotion and no implied movement) but also neutral body postures, which contain implied movement without conveying emotions. Indeed, it is important to notice that in the pool of stimuli we previously used (the same used in previous TMS studies, IAPS database) most of the positive and negative scenes depicted humans involved in dynamic complex situations while most of the neutral stimuli depicted static objects or landscapes with no humans. Therefore using our set of human dynamic body postures, we tested whether this facilitation was present, not only for fearful and happy body expressions, but also for also observing dynamic neutral body postures. Our data suggested that the facilitatory effect we found in Chapter 1 (and reported in the other TMS studies) is probably reflecting the internal simulation of the implied motion conveyed by the dynamic stimuli (i.e., the facilitatory modulation was present also observing neutral bodies, which convey no emotional meaning) rather than their emotional content.

Additionally, we observed the very same motion-related facilitatory effect recording MEPs from both hemispheres. Lastly, since studies suggest that participants with a greater tendency to take the psychological perspective of another may show stronger resonant activations (Gazzola et al., 2006; Cheng et al., 2008; Avenanti et al., 2009b; Minio-Paluello et al., 2009; Martínez-Jauand et al., 2012; Schaefer et al., 2012) and different empathy traits may modulate neural activity during social perception (Singer et al., 2004; Lamm et al., 2007a, 2010; Borgomaneri et al., 2013; Melloni et al., 2013), we explored the relation between changes in motor excitability and individual scores of

dispositional empathy using the Interpersonal Reactivity Index (IRI) (Davis, 1996). We found that this later motor facilitation marginally correlated with participants' tendency to assume the psychological perspectives of others (Perspective Taking subscale) and reflected simulation of the body movement implied in the emotional and neutral dynamic stimuli.

We can conclude that, at 300 ms, the motor system is bilaterally involved in responding to the emotional pictures and that its activation is reflecting the motor simulation of the implied stimuli rather than the preparation of a motor reaction (as posit by the embodied simulation theory; Carr et al., 2003; Iacoboni, 2009). However, our results demonstrated that motor resonance take place *after* the emotional signals have been already perceived in the right motor cortex and therefore our data suggested that motor resonance is not necessary, at least during simple emotion recognition tasks. However, in this context, it is important to entertain the possibility that resonance processes necessary for perception could occur earlier in time (e.g., after 150 ms and before 300 ms) or in other anatomical locations (e.g., in premotor or parietal regions) without being immediately evident in M1 activity as measured by TMS (Jabbi and Keysers, 2008; Avenanti and Urgesi, 2011; Cattaneo et al., 2011; Tidoni et al., 2013; Urgesi et al., 2014). Thus, further studies are needed to test the chronometry and causal involvement of motor resonance in visual perception of emotional body language. Moreover, we found a relation between cognitive empathy and motor resonance. This may suggest that this later neural phenomenon – reflecting the embodiment of the observed body expression in the observers' motor system – is involved in more sophisticated empathy-related understanding that occurs after visual recognition and may provide the observer with a reading of the body expressions 'from the inside' (Rizzolatti and Sinigaglia, 2010).

Conclusions

Data in this thesis shed new light on the temporal relation between the motor processes hypothesized by simulative and non-simulative theories of emotion processing. On the one hand, embodied simulation theories have suggested that the motor system's involvement in inferring the emotional states of others may be "imitative" in nature (i.e., motor resonance) (Carr et al., 2003; Leslie et al., 2004) and related to perceptual processes (Oberman et al., 2007). On the other hand, other scholars have proposed a different account based on the well established notion that emotions may prime the human body for action (Ekman and Davidson, 1994; Izard, 1994; Frijda, 2009). According to this view, the perception of emotional bodies would trigger the preparation of emotionally appropriate motor reactions, which is supposed to be independent of perception-related processes (Tamietto et al., 2009; de Gelder et al., 2010). In this vein, changes in motor reactivity are not action simulation processes triggered by the sight of corresponding actions but potential motor reactions stemming from the fast processing of emotional features in visual and subcortical-cortical emotional circuits (Tamietto et al., 2009; de Gelder et al., 2010). Our studies demonstrate that motor resonance occurs in M1 at 300 ms *after* the signals discriminating between emotional and non-emotional bodies have been already processed (at 150 ms in right M1). Moreover, we found that the orienting reaction we found at 150 ms in the right M1 was positively correlated to body postures recognition accuracy and that it was *necessary* for body postures recognition. We can conclude that, at this level, motor resonance is not a prerequisite for body posture's perception.

Therefore, the processes hypothesized by the two theories are not mutually exclusive. Our data demonstrated that, as supposed by evolutionary theorists, fast reactions towards threat-related stimuli, were detectable in the motor system (Chapter 4), however we found that such fast reactions are not merely involved in planning motor reactions but they have a role in more cognitive processes, such as supporting visual recognition of the observed bodies (Chapter 3). On the other side, as supposed by embodied simulation theorists, our data showed motor resonance processes when subjects were

asked to observed dynamic body stimuli (Chapter 1, 2 and 3), however, in contrast to what supposed by most radical “motoric-centric” versions of these theories, our data showed that motor resonance processes are not necessary to extract the emotional meaning of such stimuli: first, before the occurrence of motor resonance processes at 300 ms, we found that right M1 showed different modulations from emotional relative to neutral body observation then, importantly, we demonstrated that selectively interfering with motor resonance processes does not disrupt recognition performance. Anyway, this later neural phenomenon may be involved in more sophisticated empathy-related understanding that occurs after visual recognition and may provide the observer with a reading of the body expressions ‘from the inside’ (Rizzolatti and Sinigaglia, 2010).

Future directions

Our data suggest that very fast (100-150 ms) motor reactions take place in both motor cortices when observers have to actively categorize emotionally salient stimuli. First, future studies are necessary to deeper investigate these fast motor reactions, since it is possible to speculate that these fast inhibitory responses can be even more organized than what we interpreted as a general negative bias. It is possible to speculate that, even in this early time window, the functional meaning of this consistent inhibitory response we found in muscles normally involved in approaching action (grasping), is preventing non-adaptive actions. To test this hypothesis, future studies will test whether different hand-arm muscles, typically involved in opposite valence-related actions (i.e., approach or avoidance movements) show different modulations relatively to the valence of the observed body. Particularly, it is possible to speculate that muscles, which are typically recruited during avoidance reactions, will show an inhibitory reaction only when happy positive, approach-induced stimuli were presented. Opposite results will be expected in the muscles typically involved in approach reactions, namely inhibition of motor activity only when fearful, negative, avoidance-induced stimuli were

presented. These results will shed a new light over the functional meaning of this inhibitory effect suggesting that not only the emotional meaning is processed very fast (150 ms) in a sensorimotor or even cortico-subcortical network, but also that, at approximately the same time window (or even before, 100-125 ms), the primary motor cortices have already organized adaptive reactions toward arousing relevant stimuli in the environment.