



Your Emotion Moves into my Motor System  
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## Summary

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 other's behavior and emotions and the ability 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.

In recent years, neuroscientists discovered a particular class of neurons called "mirror-neurons" that have the property of firing both during the execution of an action and while observing (or listening to) a similar action when performed by another agent. This has led to the idea that understanding the inner state of other individuals relies on implicit motor simulation, that is, the activation of motor programs that we would use to perform similar actions when witnessing another individual perform a motor act. For example, seeing a friend grasping a glass of water in order to drink it would activate in the observer the motor program necessary for the observer to perform the same action, namely grasping the glass. Because when thirsty, the observer will grasp a glass of water using the same neural representation activated whilst observing her friend's action.

More recently, it has been suggested that brain areas involved in emotion processing might also be involved in simulative processes: they might perform an 'emotional simulation' of other individuals' experiences, showing activity not only when we experience positive and negative emotions but also when we witness those of others. For example, observing another person smiling evokes a similar neural brain activity as well as the corresponding facial motor representation in the observer. This motor representation and its associated somatosensory consequences are supposed to be involved in understanding the meaning of the other person's facial expression. Thus, as observing hand actions activates the observer's motor representation of that action, observing an emotion activates the neural representation of that emotion.

Current models of social cognition, therefore, incorporate the notion that regions involved in processing our motor acts and emotions can contribute to the perception of others by simulating their actions and emotions (embodied simulation theory). Another line of research has instead suggested that during emotional processing the motor system is merely involved in reacting to emotional cues by preparing the most appropriate motor act.

In support of this second notion, different behavioral studies found, for example, that participants were faster to pull a lever towards themselves for positive words and to push for negative words, demonstrating the role of the motor system in preparing the most opportune motor reaction (approach in case of positive stimuli, avoid in case of negative, dangerous stimuli). As a consequence of this last theory, the motor system would not play a role in comprehension but it would be merely recruited in appropriately reacting to the observed stimuli.

Taking into account the fundamental importance that understanding and appropriately reacting to social signals may hold for the survival of the species, in this thesis we try to investigate whether the two above-mentioned theories are competing alternatives or whether they can be bridged. We do this by probing the motor system at different time windows while facing someone else's actions and emotions.

When we interact in a social environment, we can capture information about others' feelings and emotions mainly by observing their facial expressions and body postures. Nevertheless, to date, most investigations of emotion perception have focused on brain activity generated by the perception of facial expressions and neglected the body, in comparison. Face observation is seen as a more automatic and direct way to investigate another person's feelings and intentions. However, faces and bodies are not separate but closely linked entities, to the point that the recognition of emotions through facial expressions is impaired if the emotions expressed by the body are incongruent. This evidence supports the idea that, in everyday life, we collect information from both the face and the body. Observing bodies, for example, offers the possibility to capture signals and perceive emotions over a

longer distance than observing faces. This also shifts the attention away from the personal identity shown by the face, which may not always matter for rapid decoding of the expressions. One of the questions tackled in the thesis is therefore whether the emotional information carried out by body postures is sufficient to start the chain of brain activity involved in emotion processing. Unfortunately, only few imaging studies exist on emotional body observation and they suggest that perceiving emotional bodies recruits brain regions also involved in action execution. However, the nature of such a motor activation, i.e., whether the activation represents a contribution to the planning of a reaction to or the encoding of the observed emotion, remains unclear. In this thesis, we therefore investigate the role of the motor system while subjects are requested to actively categorize emotional (happy and fear), neutral (depicting the mimic of an action) or static (at rest) human body postures presented in isolation.

We tested the motor system using Transcranial Magnetic Stimulation (TMS), which is a noninvasive technique that allows researchers to stimulate discrete brain areas delivering brief magnetic pulses to the scalp through a coil. After a single pulse stimulation (spTMS) of the primary motor cortex, a motor twitch named the *motor-evoked potential* (MEP) can be recorded from the connected muscles: its amplitude (in millivolt) represents the main measure of the corticospinal excitability. One example in support of the aforementioned embodied simulation theory in the action domain comes from a TMS study during action observation. Authors found a very similar pattern of muscle contraction (similar MEPs amplitude) during the execution of the same action. These findings clearly indicate that there is a neural system matching action observation and execution. Therefore, Transcranial Magnetic Stimulation seems to be the ideal tool to directly address possible fast motor system modulations during emotional stimuli perception, with a high temporal resolution. To date, only a few TMS studies investigated the effect of emotional stimuli observation on an observer's motor system activity and these studies mainly tested the left motor cortex excitability relatively late in time ( $>300$  ms), specifically during emotional faces or complex scenes observation. By changing the temporal sequence and the duration of the pulses delivered to the scalp, TMS can also be used to

assess the causal role of the targeted brain area in a given process (such as emotion perception). For example, in a TMS study on action perception, authors have temporally interfered with activity in the extrastriate body area, driving impaired discrimination of bodily forms; in contrast, temporarily interfering with the activity in the ventral premotor cortex impaired the discrimination of bodily actions. These results demonstrate that, whereas the extrastriate body area mainly processes actors' body identity, premotor cortex is crucial for visual discrimination of actions.

Importantly for the relevance of my thesis, there are no existing studies that have tested the role of the motor system on visual recognition of emotional signs.

In the four chapters of this thesis, we aim to investigate the role of the motor system in the recognition of emotional body postures. In particular, we aim to test whether the motor system is implementing more simulative processes or preparing motor reactions to the stimuli, as suggested by the two mainstream theories proposed above. In order to investigate our questions we combined different TMS protocols to test the different role of the left and the right primary motor cortices in the observation of dynamic body stimuli. Importantly, to investigate whether different processes occur at different time points, TMS stimulation is applied from 100 to 300 ms after the stimulus onset. Due to the high temporal resolution of the TMS and its capacity to temporarily interfere with the activity of a specific area of the brain, we can get a clearer picture about the time course and the causal role of the motor system when faced with emotional and neutral stimuli.

**Fig 1A.** The man in front of the computer shows the general experimental set-up; **B.** Trial example; **C.** The two renderings show the location of the TMS stimulation through different experiments (left or right primary motor cortex); **D.** the hand shows an example of the location of the MEP recording (FDI muscle) and an example of what the EMG signal looks like.

Our findings outline a 3-stage model of the motor system's involvement in processing another person's bodily expression of emotions. In the very first stage, happening at a time window of 100-125 ms, we find that, regardless of the stimulated hemisphere, the facilitatory intracortical connections are inhibited when subjects observe fearful, potentially dangerous, stimuli. This result suggests the existence of fast motor reactions that we interpret as suppression of motor readiness when seeing fearful bodies in order to prevent possibly erroneous actions when we are observing something potentially harmful in the environment. This result additionally supports 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.

At 150 ms, immediately after the aforementioned fast fear-related motor reactions, we observe evidence for a second stage, in which the two hemispheres seem to play different roles: the

right motor cortex continues to show inhibitory modulation but, this time, it is independent of the emotional meaning of the stimuli (similar inhibitory motor reaction during fearful and happy body postures observation). We interpret the motor response we observe from the right M1 as the sign of a rapid orienting reaction toward emotionally relevant stimuli. The data further suggest a positive correlation between the orienting reaction and the recognition of the emotion carried out through the body posture: the more subjects exhibit the orienting reaction, the more they were able to accurately identify the observed body postures. This correlational result suggests that this orienting response implemented by the motor system supports perception-related processes. In support of this interpretation, we find that when we selectively interfere with the activity of the right M1, subjects show worse accuracy performance at 150 ms (no effect when stimulating either left M1 or in the Sham group). Altogether, these findings suggest that the orienting reaction we record from the right motor cortex appears to be, not only related to, but also necessary for the perception of the observed stimuli. At the same time (150 ms) the left motor cortex appears to be more activated, rather than inhibited, by the observation of fearful stimuli (bodies or complex scenes) compared to the observation of the corresponding happy or neutral stimuli. This effect is stronger when subjects are asked to observe violent, disgusting or fearful complex dynamic scenes relative to fearful human body postures, probably because these latter stimuli were less powerful than the selected scenes. We interpret this stronger facilitatory left hemisphere response to negative stimuli as a sign of a motor preparation of the dominant hand towards negative stimuli.

Finally, we report that both the orienting for emotional bodies and the facilitatory effect for negative stimuli are related to anxiety-related interpersonal traits: the more anxiety traits the subjects exhibit, the more they show the aforementioned motor effects. Taken together, these data suggest that anxiety-related traits influence the way in which social and emotional signals are processed in the brain.

In a third last stage (300 ms), we find the two motor cortices are equally involved (facilitation) in responding to the emotional pictures and that their activation is more likely to reflect the motor

simulation of the implied stimuli than the preparation of a motor reaction. As posited by the embodied simulationists, at 300 ms from the stimulus onset, when we observe the actions and emotions of others, we internally simulate them. However, our results indicate that motor resonance takes place *after* the emotional signals have already been perceived in the right motor cortex. Although our data suggest that motor resonance is not necessary for perception, at least not during simple emotion recognition tasks, it is important to entertain the possibility that resonance processes necessary for perception could occur earlier in time (e.g., before 150 ms) or in other anatomical locations (e.g., in premotor or parietal regions) without being immediately evident in the primary motor cortex activity as measured by TMS. Thus, further studies are needed to test the chronometry and causal involvement of motor resonance in the visual perception of emotional body language.

To conclude, data present 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 suggest that the motor system involvement in inferring the emotional states of others may be “imitative” in nature (i.e., motor resonance) and related to perceptual processes. On the other hand, based on the notion that emotions may prime the human body for action, other scholars propose that the perception of emotional bodies triggers the preparation of emotionally appropriate motor reactions, which is supposed to occur independent of perception-related processes. In this vein, changes in motor reactivity would not represent action simulation processes triggered by the sight of corresponding actions but rather potential motor reactions stemming from the fast processing of emotional features in visual and subcortical-cortical emotional circuits. Our data demonstrate that, as proposed by evolutionary theorists, fast reactions towards threat-related stimuli are detectable in the motor system (Chapter 4). However, such fast modulations are not merely involved in planning motor reactions, but seem to have a role in more cognitive processes, such as supporting visual recognition of the observed bodies (Chapter 3). On the other hand, as proposed by embodied simulation theorists, our data show motor resonance processes when subjects are asked to observed dynamic body stimuli (Chapter 1, 2 and 3). In contrast to what

is supposed by most radical “motoric-centric” versions of these theories, our data show that motor resonance processes are not necessary to extract the emotional meaning of such stimuli. The right M1 shows different modulations from emotional relative to neutral body observation well before (150 ms) the occurrence of motor resonance (300 ms). Furthermore, interfering with the motor activity of the right motor cortex at 150 ms was positively correlated to body posture recognition accuracy and recognition, whereas selectively interfering with motor resonance processes does not disrupt recognition performance.

**Fig 2.** Different phases of motor system involvement during human body posture observation. The top row represents the responses following right hemisphere stimulation, the bottom row following stimulation to the left hemisphere.