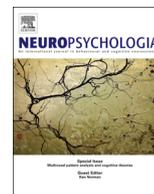




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# How do shared-representations and emotional processes cooperate in response to social threat signals?



Julie Grèzes<sup>a,b,\*</sup>, Guillaume Dezeache<sup>a,c</sup>

<sup>a</sup> Cognitive Neurosciences Lab., INSERM U960 & IEC—Ecole Normale Supérieure, Paris 75005, France

<sup>b</sup> Centre de Neuroimagerie de Recherche (CENIR), Paris, France

<sup>c</sup> Institut Jean Nicod, UMR 8129 & IEC—Ecole Normale Supérieure, Paris, France

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## ABSTRACT

Research in social cognition has mainly focused on the detection and comprehension of others' mental and emotional states. Doing so, past studies have adopted a "contemplative" view of the role of the observer engaged in a social interaction. However, the adaptive problem posed by the social environment is first and foremost that of coordination, which demands more of social cognition beyond mere detection and comprehension of others' hidden states. Offering a theoretical framework that takes into account the dynamical aspect of social interaction – notably by accounting for constant interplay between emotional appraisal and motor processes in socially engaged human brain – thus constitutes an important challenge for the field of social cognition. Here, we propose that our social environment can be seen as presenting opportunities for actions regarding others. Within such a framework, non-verbal social signals such as emotional displays are considered to have evolved to influence the observer in consistent ways. Consequently, social signals can modulate motor responses in observers. In line with this theoretical framework we provide evidence that emotional and motor processes are actually tightly linked during the perception of threat signals. This is ultimately reflected in the human brain by constant interplay between limbic and motor areas.

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## 1. Introduction

"Actions are critical steps in the interaction between the self and external milieu" (Jeannerod, 2006).

We are continuously confronted with a great number of opportunities for actions in our environment, and we are constantly collecting information in order to select the most relevant set of motor commands from among numerous potential action plans so as to respond to environmental challenges (Cisek, 2007; Cisek & Kalaska, 2010). This ability to form multiple motor plans in parallel and to flexibly switch between them brings survival advantage by dramatically reducing the time one takes to respond to environmental challenges (Cisek & Kalaska, 2010; Cui & Andersen, 2011). These action possibilities emerge from the relationship between species and their milieu, as well as from the interaction between individuals and their more immediate environment. They thus depend both on long-term attunement (at the evolutionary time-scale, through cognitive adaptations and natural selection), and on short-term attunement (at the

proximal level, through developmental patterns as well as through local accommodation) (Kaufmann & Clément, 2007). Note that contextual assumptions (through observer/actor's preferences and skills, as well as objects' characteristics) also play an important role in the interactions between individuals and their milieu and ultimately shape action opportunities.

Although the concept of action opportunities has mostly been used to account for interactions between animals and non-social physical objects in the world, it may equally apply to our interactions with the social world. We would therefore perceive our physical and social environments as maps of relevant action opportunities in a space which can also include potential actions of another present in one's own space (Sebanz, Knoblich, & Prinz, 2003; Sartori, Becchio, Bulgheroni, & Castiello, 2009; Bach, Bayliss, & Tipper, 2011; Ferri, Campione, Dalla Volta, Gianelli, & Gentilucci, 2011). Again, contextual assumptions do play a role within such a framework: observers' skills and the characteristics of the social objects (the individual[s] with whom one interacts) shape opportunities for action regarding others; they are function of one's own needs (Rietveld, De Haans, & Denys, 2012) and attitudes towards others (Van Bavel & Cunningham, 2012).

Opportunities for action may also well emerge from emotional signals (Grèzes, 2011; Dezeache, Mercier, & Scott-Phillips, 2013). A fearful display, for instance, invites observers to act upon it, whereby observers select among numerous potential actions

\* Corresponding author at: Laboratoire de Neurosciences Cognitives, INSERM U960 and IEC Ecole Normale Supérieure, 29 Rue d'Ulm, 75005 Paris, France.

Tel.: +33 1 44 32 26 76; fax: +33 1 44 32 26 86.

E-mail address: [julie.grezes@ens.fr](mailto:julie.grezes@ens.fr) (J. Grèzes).

<sup>1</sup> <http://www.grezes.ens.fr>.

(fleeing from the threatening element, fighting against it or rescuing potential endangered congeners, among other numerous potential actions) according to their preferences and appraisal of the situation. The concept of opportunities for action thus constitutes a fruitful framework within which we can better understand social and emotional perception and its modulation in different individuals.

One critical consequence of the view that our social world features opportunities for action in response to others' emotions is the necessity to propose an adequate cognitive and neural model of social interaction: behaviour and brain activity should reflect the processing of multiple representations of potential actions in response to others' behaviour, and their selection through the use of external, as well as internal sensory information. It also requires that socio-emotional understanding be tightly linked with social interactive skills (McGann & De Jaegher, 2009). The building of such a view, we shall argue, supposes the integration of two separate systems in the brain, i.e., the motor and the emotional systems that have been mainly studied independently in the literature. We believe the synthesis of these two lines of research will help generate a novel framework to better understand the cognitive and neural mechanisms which ensure the initiation of adaptive responses during social and emotional interactions. Since much of our work has been dedicated to the perception of threat signals, we will exclusively focus on the perception of fear and anger in others' face and body. The possibility that limbic and motor processes similarly interact during the perception of other emotional signals (such as joy and disgust) will be briefly discussed.

## 2. Shared motor representations: A key mechanism for the understanding of others' actions and emotions.

### 2.1. Perception of actions

The neural basis underpinning our ability to represent and understand the actions of others has been the object of considerable research in both monkeys and humans. It is now acknowledged that perceived actions are mapped onto the motor system of the observer, activating corresponding motor representations (henceforth "shared motor representations"). The motor system of the observer simulates the observed action by issuing corresponding motor commands that account for predictions of immediate outcomes of the perceived action (e.g. Jeannerod, 2001; Wilson & Knoblich, 2005). Shared motor representations were shown to be more selectively tuned to process actions that (1) conform to biomechanical and joint constraints of normal human movement (Reid, Belsky, & Johnson, 2013; Saygin, 2007; Dayan, Casile, Levit-Binnun, Giese, & Flash, 2007; Elsner, Falck-Ytter, & Gredebäck, 2012), and (2) are simple, and familiar within the observer's motor repertoire (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Kanakogi & Itakura, 2011) or for which the observer has acquired visual experience (Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009; Jola, bedian-Amiri, Kuppaswamy, Pollick, & Grosbras, 2012). Shared motor representations sustained by premotor, motor, somatosensory and parietal cortices (Grèzes & Decety, 2001; Morin & Grèzes, 2008; Caspers, Zilles, Laird, & Eickhoff, 2010; Van Overwalle, 2008; Shaw, Grosbras, Leonard, Pike, & Paus, 2012; Molenberghs, Hayward, Mattingley, & Cunnington, 2012) allow us to identify "what" the action is and "how" it is or will be performed (Thioux, Gazzola, & Keysers, 2008; Hesse, Sparing, & Fink, 2008).

### 2.2. Limits

If shared motor representations play a key role in deciphering and predicting other's actions, they are, per se, not sufficient to

allow for interpersonal coordination. What is involved in the perception of opportunities for actions during social interaction is, cognitively speaking, very different from what shared motor representations are known to do, that is, to allow for the simulation of an observed motor pattern (Rizzolatti, Fogassi, & Gallese, 2001). We assume those action opportunities to be emergent properties of the observer-environment interactions, such that interaction with the social world triggers a wide range of opportunities for actions in the engaged observer. It was shown that in an interactive context, the perception of another individual's gestures can override pre-planned actions towards physical objects: the opening of an empty hand or the mouth induces, in observers, changes in the trajectory of their grasping gesture toward an object (Sartori et al., 2009; Ferri et al., 2011). Importantly, these gestures here were perceived as a request to be given the object or to be fed, and not to reproduce the perceived action. These experiments strongly support the hypothesis that our brain processes both physical and social information as currently available potential actions, and that the context strongly impacts the selection between these action opportunities.

This perspective about social interaction calls for re-examination of previous findings on the neural bases suggested to sustain the shared representations. Activity in parietal cortex and connected premotor and motor regions (dorsal visuomotor stream) may also reflect the implementation of multiple representations of potential actions that one can perform (Cisek, 2007; Cisek & Kalaska, 2010). Within the dorsal visuomotor stream of the macaque brain, 20% of motor neurons showed object-related visual properties (canonical neurons) related to specification of the potential action triggered by the perceived object (Rizzolatti & Fadiga, 1998; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Raos, Umiltà, Murata, Fogassi, & Gallese, 2006). In parallel, 17% of motor neurons of dorsal visuomotor stream showed action-related visual properties (mirror neurons—(Gallese, Fadiga, Fogassi, & Rizzolatti, 1996)) associated with the understanding of other individuals' behaviour (Rizzolatti & Sinigaglia, 2010). Among these 17%, only 5.5% code for a strictly congruent action in the motor and the visual domain, whereas 8.6% code for two or more actions in the visual domain, and 1.3% for non-congruent actions. Similar proportions were revealed in the human supplementary motor cortex (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010): 14% of the recorded neurons in area responded to congruent observed actions, but 10% responded to non-congruent observed actions.

Before viewing all action-related visual activities in dorsal visuomotor stream as shared motor representations processes, one may first suggest that motor neurons that responded to non-congruent observed actions should not be considered mirror neurons, but should be categorized as "social" canonical neurons, that is, neurons that are active when foreseeing a possible social interaction (vs. interaction with an object as for canonical neurons) and preparing oneself accordingly (Dezecheche, Conty, & Grèzes, 2012). Also, one may suggest that, in parallel to shared motor representations activity, there is neural activity that is involved in the processing of the observer's potential opportunities for action in response to other individuals' behaviour.

### 2.3. Perception of emotions

The concept of shared motor representation is also influential in the emotional domain. The perception of others' emotional expressions is taken to trigger an automatic and non-affective motor matching (termed 'mimicry') of the perceived expressions (Hatfield, Cacioppo, & Rapson, 1993; Hatfield, Cacioppo, & Rapson, 1994; Chartrand & Bargh, 1999; Williams, Whiten, Suddendorf, & Perrett, 2001; Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Niedenthal, Barsalou, Winkielman, Krauth-Gruber, & Ric, 2005;

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