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Research Report
**The power of simulation: Imagining one's own
and other's behavior**
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ABSTRACT

A large number of cognitive neuroscience studies point to the similarities in the neural circuits activated during the generation, imagination, as well as observation of one's own and other's behavior. Such findings support the shared representations account of social cognition, which is suggested to provide the basic mechanism for social interaction. Mental simulation may also be a representational tool to understand the self and others. However, successfully navigating these shared representations – both within oneself and between individuals – constitutes an essential functional property of any autonomous agent. It will be argued that self-awareness and agency, mediated by the temporoparietal (TPJ) area and the prefrontal cortex, are critical aspects of the social mind. Thus, differences as well as similarities between self and other representations at the neural level may be related to the degrees of self-awareness and agency. Overall, these data support the view that social cognition draws on both domain-general mechanisms and domain-specific embodied representations.

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1. Introduction

One fascinating characteristic of human nature is our ability to consciously use our imagination to simulate reality as well as fictional worlds (think about a writer or a reader of a fiction novel). Deliberate generation of internal representations fosters creativity as well as lessens dependence on the physical and social environments. The social functions, such as planning one's own behavior, anticipating one's own and others' behaviors, and empathizing with others, suggest an evolutionary advantageous role of imagination. For instance, while we read fiction, we may identify with characters and become absorbed in the experience on a deep, emotional level.

We feel real emotion even though we know the characters themselves are not real.

One interesting aspect of imagination is that, under normal circumstances, reality and imagination are not confused. For instance, Taylor demonstrated that children and adults who entertain imaginary companionship understand the fictional nature of the characters and their relationship to them (Taylor, 1999). Writers often speak about their characters stepping out of the novel and telling them what to write. They say it can be spooky, particularly when they feel that the character is wittier or more clever than themselves. Nevertheless, there is no confusion between the self and the other, even when the other is

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produced by the imagination of the self. In terms of agency, the imaginer is an active organism, one who desires, creates fantasies, one who makes plans, carries out actions, and compares actions to their desires.

In this article, we will focus on one aspect of imagination, simulation of one's own and other's behavior. After a brief discussion regarding the different views of the notion of simulation, we will review recent cognitive neuroscience evidence indicating that actions are represented in the central nervous system, and that these representations may be emulated covertly or overtly in a number of ways, including by the observation of the behavior of others. These representations can also be activated by imagining one's own actions as well as those of others. Similarly, emotions and pain can be simulated for oneself and for others. Such representations may thus be shared both intrasubjectively (i.e., within oneself) and intersubjectively (i.e., between self and other). Therefore, self- and other's representations must be distinguished at some level, otherwise, confusion between one's own mind and the knowledge of other minds would occur. We will also discuss the central functions of self-awareness and agency (i.e., the awareness of oneself as an agent who is the initiator of actions, desires, thoughts, and feelings), arguing that these aspects play a pivotal role in navigating these shared representations. Importantly, this view is in agreement with the notion that social cognition depends on the interaction of domain-specific mechanisms with domain-general abilities.

2. Different accounts of the concept of simulation

The notion of simulation is used in cognitive and social neuroscience to account for different processes. Generally speaking, the simulation process can be conceived as a conscious reactivation of previously executed actions stored in memory (Decety and Ingvar, 1990). An individual who is engaging in simulation may replay her own past experience in order to extract from it pleasurable, motivational or strictly informational properties (Dokic and Proust, 2002). Such a view was clearly described by the Swedish physiologist Hesslow (2002). For this author, the simulation hypothesis states that thinking consists of simulated interaction with the environment and rests on the following three core assumptions: (1) simulation of actions: we can activate motor structures of the brain in a way that resembles activity during a normal action but does not cause any overt movement; (2) simulation of perception: imagining perceiving something is essentially the same as actually perceiving it, only the perceptual activity is generated by the brain itself rather than by external stimuli; (3) anticipation: there exist associative mechanisms that enable both behavioral and perceptual activity to elicit other perceptual activity in the sensory areas of the brain. Most importantly, a simulated action can elicit perceptual activity that resembles the activity that would have occurred if the action had actually been performed. There is a large body of neurophysiological evidence in support of this notion of simulation (Decety, 2002; Grèzes and Decety, 2001). For

instance, one recent functional MRI study demonstrated that similar fronto-parietal network is activated in pianist participants when they played music on a silent keyboard and when they imagined playing the same music (Meister et al., 2004).

Jeannerod put forward another account of simulation in the context of motor cognition. This theory states that an action involves a covert stage, corresponding to its pragmatic representation, which includes its goal, the means to achieve it, and its consequences (Jeannerod, 1999). Further, such pragmatic representation may be activated under a variety of conditions in relation to action, either self-intended or perceived from other individuals. Even though this process may have a conscious counterpart (one can consciously generate a mental image), most of its generation occurs at the covert level. One persuasive source of evidence in support of such a view comes from studies using transcranial magnetic stimulation that show that the mere observation of grasping movements results in the specific modulation of motor evoked potentials (e.g., Fadiga et al., 1995; Watkins et al., 2003).

Philosophy of mind and developmental science also draw on simulation to explain our capacity to mentalize, i.e., to understand mental states (intentions, desires, feelings, and beliefs) of others. In this context, the basic idea of simulation is that the attributor attempts to mimic the mental activity of the target by using her own psychological resources (Goldman, 2002). In order to understand the mental state of another when observing the other acting, the individual imagines herself/himself performing the same action, a covert simulation that does not lead to an overt behavior. One critical aspect of the simulation theory of mind is the idea that in trying to impute mental states to others, an attributor has to set aside her own current mental states and substitute those of the target (Goldman, 2005).

These different accounts of the concept of simulation mainly differ in two aspects. One aspect concerns the extent of automaticity and control that one may exert upon the simulation process. It is clear that most of the simulation processing occurs at the subpersonal level. However, such a process may be triggered automatically, when for instance, one individual watches another individual performing an action (e.g., Grèzes et al., 2004), or deliberately when one imagines how another person would feel in a given situation (e.g., Ruby and Decety, 2004). The second aspect deals with the scope of the simulation process. Whereas the simulation theory of mind includes the understanding of others mental states, i.e., emotions, desires, expectations, that are not necessarily related to motor action per se, the motor simulation theory proposed by Jeannerod (1999) accounts for the broad phenomenon of action representation, including one's own actions and is thus not limited to understanding actions performed or intended by others. In our view, the difference across these three notions of simulation is more of degree than of nature, and the same basic computational process is shared, i.e., aspects of actions (including emotions) that are represented (i.e., stored in a distributed network). The automatic level and the conscious level are not independent from each other; rather they represent different aspects of a common process. Finally, these accounts of simulation are in

agreement with theories of embodied cognition, which contend that cognitive representations and operations are fundamentally grounded in bodily states and in the brain's modality-specific systems (Niedenthal et al., 2005).

3. The direct link between perception and action

Over the last decade, an impressive number of findings from both psychophysics and cognitive neuroscience approaches strongly support a direct connection between the neural and cognitive systems involved in producing one's own action and the systems involved in perceiving the actions of others. This direct link between perception and action has several consequences (and adaptive values), including social mimicry, stereotypes activation that may influence the subsequent behavior of the perceiver (e.g., Chartrand et al., 2005). One influential theory, known as the common coding hypothesis, suggests that, somewhere in the chain of operation that lead from perception to action, the system generates certain derivatives of stimulation and certain antecedents of action that are commensurate in the sense that they share the same system of representational dimensions (Prinz, 2003). The core assumption of the common coding theory is that actions are coded in terms of the perceivable effects (i.e., the distal perceptual events) they should generate. Performing a movement leaves behind a bidirectional association between the motor pattern it was generated by and the sensory effects that it produces. Such an association can then be used backwards to retrieve a movement by anticipating its effects (Hommel, 2004). These perception/action codes are also accessible during action observation, and perception activates action representations to the degree that the perceived and the represented actions are similar (Wilson and Knoblich, 2005).

A variety of electrophysiological research has demonstrated that two primary areas of the primate brain (ventral premotor cortex and superior temporal sulcus) are selectively activated during the observation of actions executed by conspecifics. Some of these cells (mirror neurons), in area F5 of the ventral premotor cortex, are sensorimotor neurons that fire both when the monkey executes certain kinds of actions and when the monkey perceives the same actions being performed by another (Rizzolatti et al., 1996). It was also found that a subset of these mirror neurons also respond when the final part of an action, crucial in triggering the response when the action is seen entirely, is hidden, and can only be inferred (Ulmirà et al., 2001). Therefore, specific neurons in this region code the inferred goal of the action rather than the action itself. By automatically matching the agent's observed action onto its own motor repertoire without executing it, the firing of mirror neurons in the observer brain simulates the agent's observed action and thereby contributes to the understanding of the perceived action (Rizzolatti et al., 2004).

The Parma laboratory extended this conception of simulatory brain processes by showing that some neurons display mirror properties between motor and other modalities such as audition (Kohler et al., 2002). The researches thus argue that single neurons are concerned with some actions regardless of

the modality through which a given action is inferred (i.e., it is the consequence of the action that is represented). Such neurons are not restricted to the premotor cortex but have also been recorded in other areas of the brain, notably in the posterior parietal cortex (area PF) in relation to actions performed with objects (Gallese et al., 2002). In a new single cell electrophysiological study with monkeys, Fogassi et al. (2005) reported that inferior parietal mirror neurons, in addition to recognizing the goal of the observed motor acts, discriminate identical motor acts according to the action in which these acts are embedded. They further argued that because the discriminated motor act is part of a chain leading to the final goal of the action, this neuronal property allows the monkey to predict the goal of the observed action and, thus, to "read" the intention of the acting individual. It was suggested by Gallese and Goldman (1998) that this mirror neuron mechanism may be part of, or be a precursor to a more general mind-reading ability.

Another cortical region, the superior temporal sulcus (STS), responds to the observation of actions done by others. In the macaque monkey, Perrett et al. (1989) have found that there are neurons in the superior part of the STS that are sensitive to the sight of static and dynamic information about the body. The majority of these cells is selective for one perspective view and are thought to provide viewer-centered descriptions that can be used in guiding behavior. For some cells in the lower bank of STS, the responses to body movements were related to the object or to the goal of the movements. Movements effective in eliciting neuron responses in this region include walking, turning the head, bending the torso, and moving the arms. A small set of STS neurons discharge also during the observation of goal-directed hand movements (Perrett et al., 1989). Moreover, a population of cells, located in the anterior part of the STS, respond selectively to the sight of reaching but only when the agent performing the action is seen attending to the target position of the reaching (Jellema et al., 2000). In addition, the responses of a subset of these cells are modulated by the direction of attention (indicated by head and body posture of the agent performing the action). This combined analysis of direction of attention and body movements suggests a role for neural activation in the STS during the detection of intentional actions. These two regions (i.e., posterior STS and premotor cortex) are reciprocally connected via the posterior parietal cortex.

In human subjects, a number of functional imaging studies demonstrated the involvement of motor representation during the perception of action performed by others (e.g., Hamzei et al., 2003). Notably, one fMRI study showed that the activation pattern in the premotor cortex elicited by the observation of actions performed by another individual follows somatotopic organization related to the observed action. Watching mouth, foot, and hand actions elicits different sites in the premotor and superior parietal cortices, which are normally involved in the actual execution of the observed actions (Buccino et al., 2001).

Studies related to the phenomenon of apparent motion offer compelling evidence of the involvement of motor representation in the perception of bodily movements in humans (Shiffrar and Pinto, 2002). Stevens et al. (2000) adapted the apparent biological motion paradigm to present subjects

in the scanner with a human model in different postures. Depending on the activation conditions, the subjects were shown either possible or impossible biomechanical paths of apparent motion. The left primary motor cortex and parietal lobule in both hemispheres were found to be selectively activated when the subjects perceived possible paths of right limb human movement. No activation in these areas was detected during conditions of impossible biomechanical movement paths. Thus, only the perception of actions that conform to the motor capabilities evokes motor representations in the observer.

A recent fMRI study demonstrated that expert ballet dancers show stronger activation of premotor and parietal cortices when watching other ballet dancers than do novices. The extent of premotor and parietal activation in these areas is greatest when dancers observe their own style of dance versus another kinematically similar dance style (Calvo-Merino et al., 2005). Interestingly, this result (less activation in novices than in experts) cannot be interpreted in terms of neural efficiency because this latter interpretation would predict exactly the opposite pattern of results. Indeed, neural efficiency assumes that higher ability in a cognitive task is associated with more efficient neuronal processing of this task. Such efficiency is reflected in decrease in neural work (e.g., glucose metabolic rate). For instance, Lamm et al. (1999) documented significant event-related potential differences between good and poor performers in a visuo-spatial task. The poor performers showed higher activity in the posterior parietal region, and their topography was more extended into the fronto-central regions. Thus, the greater activation of the fronto-parietal circuit during the perception of dancing movements by experts fits neatly with the involvement of motor representations during observation of action when there is congruence between subjects' own motor repertoire and perceived actions performed by others.

The effect of similarity between the observer's motor repertoire and the perceived action was also demonstrated in one functional MRI study during which participants were shown video-clips of themselves and of others lifting a box and had to judge the beliefs of the actors about the weight of the box. Results showed activity in a number of cortical regions involved in motor control, namely the dorsal premotor cortex, left parietal cortex, and right cerebellum, when participants made judgments about their own actions as well as those of others (Grèzes et al., 2004). In addition, this study reported that the onset of the neurodynamic response starts earlier for the self than for others. This earlier activity in action-related areas can be explained by the fact that when one observes one's own actions, there is a closer match between the simulated and perceived action than there is when one observes the actions of others. This finding may be an important aspect to distinguish one's own actions from the actions of others.

4. Imagining actions

Numerous behavioral and functional imaging studies demonstrated that the actual production of actions and motor

imagery share a number of mental operations and rely upon common neural structures.

Functional imaging exploration in healthy individuals requested to imagine grasping objects with their right hand relative to the visual inspection of the same objects results in the activation of the prefrontal cortex, the anterior cingulate, the premotor cortex, the inferior parietal lobule, the cerebellum, the ventrolateral thalamus, and the caudate nucleus in the left hemisphere (Decety et al., 1994). The neural network implicated in motor imagery overlaps with that involved in performing similar actions (Grafton et al., 1996; Schubotz and von Cramon, 2004; Stephan et al., 1995). A study demonstrated that imagery of voluntary movement activates body-part-specific motor representations (Ehrsson et al., 2003). The authors asked subjects to imagine themselves performing finger and toe flexion and extension along with horizontal movements of the tongue. Activation maps were compared to functional images acquired when the subjects were actually executing these movements. The authors found that activation during motor imagery was specific to somatosensory and motor areas activated during actual motor execution. In one recent study, Michelon et al. (2005) tested whether motor imagery or motor preparation activates neural representations that are specific to the body part whose movement is imagined or prepared. Participants were required to perform, imagine, and prepare hand movements while undergoing functional MRI scanning. Actual hand movements activated components of the motor system including primary motor and somatosensory cortex, the supplementary motor area (SMA), the thalamus, and the cerebellum. All of these areas showed strong lateral organization, such that moving a given hand activated the contralateral cortex and ipsilateral cerebellum most strongly. During motor imagery and motor preparation, significant lateral organization was observed in primary motor cortex, the supplementary motor area, and the thalamus.

Imagining being the agent of an action or imagining another person being the agent of that action elicits partial similar neural response as demonstrated by Ruby and Decety (2001). The authors trained individuals to imagine a series of action as being performed either by themselves (first-person perspective) or by another individual (third-person perspective). Both subjective perspectives were associated with common activated clusters in the SMA, the precentral gyrus, and the precuneus. First-person perspective taking was specifically associated with increased activity in the left inferior parietal lobule and the left somatosensory cortex, whereas the third-person perspective recruited the right inferior parietal lobule, the posterior cingulate, and the fronto-polar cortex. These latter regions are hypothesized to play a role in holding separate perspectives or in resisting interference from one's own perspective (Ruby and Decety, 2003; Decety, 2005).

Altogether these findings can be interpreted in terms of a functional equivalence between the imagination and the production of action to the extent that they share the same motor representations underpinned by the same neural substrate (Decety and Grèzes, 1999; Jeannerod, 1999). These representations may be triggered during mental simulation, as they would be during action preparation, execution, and observation.

5. Imagining emotions

The perception–action coupling mechanism accounts (at least partly) for emotion processing and empathy, as suggested by [Preston and de Waal \(2002\)](#). Such a view receives empirical support from a variety of behavioral and neuroimaging studies. It was proposed that people may catch the emotions of others as a result of afferent feedback generated by elementary motor mimicry of others' expressive behavior, which produces a simultaneous matching emotional experience ([Hatfield et al., 1994](#)). For instance, viewing facial expressions triggers expressions on one's own face, even in the absence of conscious recognition of the stimulus (e.g., [Dimberg et al., 2000](#)). Interestingly, [De Gelder et al. \(2004\)](#) demonstrated that observing fearful body expressions not only produces increased activity in brain areas associated with emotional processes but also in areas linked with representation of action and movement. These results demonstrate that the mechanism of fear contagion automatically prepares the brain for action.

Furthermore, research documented that a perceiver's accuracy in inferring a target's negative emotional states is related to the degree of physiological synchrony between the perceiver and the target ([Levenson and Ruef, 1992](#)). In other words, when two people feel similar emotions, they more accurately perceive each other's intentions and motivations. Recently, an fMRI experiment confirmed these results by showing that when participants are required to observe or to imitate facial expressions of various emotions, increased neurodynamic activity is detected in the regions that are implicated in the facial expression of these emotion, including the superior temporal sulcus, the anterior insula and the amygdala, as well as areas of the premotor cortex corresponding to the facial expression ([Carr et al., 2003](#)). The similarity between the expression of an emotion and the perception of that emotion has been demonstrated for disgust. Lesion of the insula, an associative region crucial in monitoring body state, can impair both the experience of disgust and the recognition of social signal (e.g., facial expression, emotional prosody) that convey disgust ([Calder et al., 2000](#)). Functional neuroimaging studies have later shown that observing facial expressions of disgust and feelings of disgust activated very similar sites in the anterior insula and anterior cingulate cortex (e.g., [Wicker et al., 2003](#)). It should be noted, however, that some studies have reported only a partial overlap between observation and production of emotion. For instance, a neuroimaging study indicated a dissociation between the neural systems involved in face imitation and those involved in the response to a viewed expression ([Leslie et al., 2004](#)).

Moreover, there are several dramatic case studies that support the idea that similar neural systems are involved both in the recognition and in the expression of specific emotion. Notably, [Adolphs et al. \(1995\)](#) investigated S.M., a 30-year old patient, whose amygdala was bilaterally destroyed by a metabolic disorder. Consistent with the prominent role of the amygdala in mediating certain negatively valenced emotions such as fear, S.M. was found to be impaired at both the recognition of fear from facial

expressions as well as in the phenomenological experience of fear. Another case, N.M, who suffered from bilateral amygdala damage and left thalamic lesion, was found to be impaired in at recognizing fear from facial expressions and exhibited an equivalent deficit affecting fear recognition from body postures and emotional sounds ([Sprenelmeyer et al., 1999](#)). The patient reported reduced anger and fear in his everyday experience of emotion as well.

Altogether these results are consistent with the direct link between perception and action. Such a system prompts the observer to resonate with the emotional state of another individual, with the observer activating the motor representations and associated autonomic and somatic responses that stem from the observed target, i.e., by a sort of inverse mapping ([Preston and de Waal, 2002](#)).

6. Imagining pain

The experience of pain by the self and its perception in others provides an interesting avenue to investigate the shared representation mechanism and its contribution to empathy. An early single-neuron recording study in neurological patients had shown that there are pain-related neurons in the anterior cingulate cortex (ACC) that respond both to actual stimulation (thermal stimuli) and also to the observation of the same stimuli delivered to another individual ([Hutchison et al., 1999](#)). Recently, a handful of functional MRI studies indicated that the observation of pain in others is mediated by a restricted neural network known to process the affective aspect of pain perception. In one fMRI study, [Morrison et al. \(2004\)](#) compared the activation pattern during the actual experience of pain and its observation in others. In the scanner, participants underwent stimulation of one hand by a needle-like sharp probe, and in another condition, they watched videos of someone else's hand being pricked by a hypodermic needle. Results revealed common activated foci in the ACC and anterior insula. In another study, participants received painful stimuli and observed a signal indicating that their partner who was present in the same room had received the same stimuli ([Singer et al., 2004](#)). The rostral ACC, the insula, and cerebellum were activated during both conditions. In another functional MRI study, participants were shown still photographs depicting right hands and feet in painful or neutral everyday-life situations and asked to imagine the level of pain that these situations would produce ([Jackson et al., 2005a](#)). Significant activation in regions involved in the affective aspects of pain processing network, including the ACC and the anterior insula, was detected. Moreover, the level of activity within the ACC was strongly correlated with subjects' mean ratings of pain attributed to the different situations. Similarly, facial expressions of pain were found to engage cortical areas also engaged by the first-hand experience of pain, including the ACC and the insula ([Botvinick et al., 2005](#)). Recently, a transcranial magnetic stimulation study reported changes in corticospinal motor representations of hand muscles in individuals observing needles penetrating hands or feet of a human model ([Avenanti et al., 2005](#)). These results corroborate the idea that common neural circuits that can involve somatosensory–motor representations are

activated in representing one's own and others' affective pain-related states.

In a recent functional MRI study, participants were shown pictures of people with their hands or feet in painful or non-painful situations and instructed to imagine themselves or imagine another individual in the pictured situation and rate the level of pain perceived from these different perspectives (Jackson et al., 2005b). Both the self's and the other's perspectives were associated with activation in the neural network involved in pain processing, including the parietal operculum, ACC, and anterior insula. However, the self-perspective yielded higher pain ratings and involved the pain matrix more extensively in the secondary somatosensory cortex, the posterior part of the anterior cingulate cortex, and the insula proper.

Furthermore, while the insula was activated when participants imagine self and imagine other's pain, different non-overlapping clusters were identified within that region (the anterior part for the other and a posterior part for self). Likewise, both self- and other perspectives are associated with a common subarea in the ACC, but self-perspective selectively activated another subdivision of this region mediating visceral responses. A similar dissociation within the insula and the ACC between self-experience of pain and its perception in others was also reported by Singer et al. (2004).

These neuroimaging data highlight both the similarities and self-other distinctiveness as important aspects of human empathy. The experience of pain in self is associated with more caudal activations (within area 24 of the ACC), consistent with spino-thalamic nociceptive projections, while the perception of pain in others is represented in more rostral (and dorsal) regions (within area 32 of the ACC). A similar rostro-caudal organization is observed in the insula, which is coherent with its anatomical connectivity and electrophysiological properties. For instance, painful sensations are evoked in the posterior part of the insula (and not in the anterior part) by direct electrical stimulation of the insular cortex in neurological patients (Ostrowsky et al., 2002). Altogether, these findings are in agreement with the fact that first-person experience and third-person experience of pain share common circuitry, but also that indirect pain representations (as elicited by the observation of pain in others) are qualitatively different from the actual experiences of pain. It may be what allows us to distinguish empathic responses to others versus our own personal distress.

7. Self-awareness and agency

Given commensurability between self- and other action representations, a number of key additional processes are necessary for successful social interactions including the capacity to imagine others' behavior. However, in the case of emotion sharing, a complete overlap between self and other representations would induce emotional distress or empathic over arousal (a self-oriented aversive emotional response), which is not the goal of empathy (Batson et al., 1997). In fact, in the experience of empathy, individuals must be able to disentangle themselves from others. Therefore, agency is a crucial aspect to successfully navigate shared representations

between self and other (Decety and Sommerville, 2003; Decety, 2005). Further, it is acknowledged that agency plays a pivotal role in cognitive development, including the first stage of self-awareness (or pre-theoretical experience of one's own mentality), which scaffolds theory of mind capacities (Rochat, 1999). Indeed, the ability to recognize oneself as the agent of a behavior is the way the self builds as an entity independent from the external world (Jeannerod, 2003). In the case of empathy, affective sharing must be modulated and monitored by the sense of whose feelings belong to whom (Decety and Jackson, 2004), and thus, agency is a crucial aspect in promoting a selfless regard for the other rather than a selfish desire to escape aversive arousal.

It has been proposed that non-overlapping part of the neural circuit mediating shared representations (i.e., the areas that are activated for self-processing and not for other-processing) generates a specific signal for each form of representation (Jeannerod, 1999). This set of signals involved in the comparison between self-generated actions and actions observed from others ultimately allow the attribution of agency.¹ It has also been suggested that the dynamics of neural activation within the shared cortical network is an important aspect to distinguish one's own actions from the actions of others (see Figs. 1 and 2 for such findings). And that the latency difference between the changes in activity elicited by the perception of self versus others' actions reflects the calibration process of shared representations (Decety and Jackson, 2004). Furthermore, the fact that the onset of the hemodynamic signal is earlier for the self than for the others can be considered as a neural signature of the privileged (and readily) access of self-perspective.

Accumulating evidence from neuroimaging studies, as well as lesion studies in neurological patients, indicates that the right inferior parietal cortex, at the junction with the posterior temporal cortex (TPJ), plays a critical role in the distinction between self-produced actions and actions generated by others (Blakemore and Frith, 2003; Jackson and Decety, 2004). In addition, some recent data suggest that this region is specifically involved in theory of mind (Apperly et al., 2004; Saxe and Wexler, 2005). The TPJ is a heteromodal association cortex, which integrates input from the lateral and posterior thalamus, as well as visual, auditory, somesthetic, and limbic areas. It has reciprocal connections to the prefrontal cortex and to the temporal lobes. Because of these anatomical characteristics, this region is a key neural locus for self-processing that is involved in multisensory body-related information processing, as well as in the processing of phenomenological and cognitive aspects of the self (Blanke and Arzy, 2005). Its lesion can produce a variety of disorders

¹ This mechanism has been described as Forward models, i.e., hierarchically organized sets of motor representations, with representations at the higher level encoding relatively global specifications of the action, and representations at lower levels encoding subactions in a more detailed way (Jeannerod, 1997). Forward models also comprise comparison mechanisms testing the degree of match between the desired and the current state of the system and operating in parallel at all levels of processing (see Blakemore and Decety, 2001). Such a process may account not only for actions but also in the distinction between one's own emotions, feelings, and thoughts and those of other people.

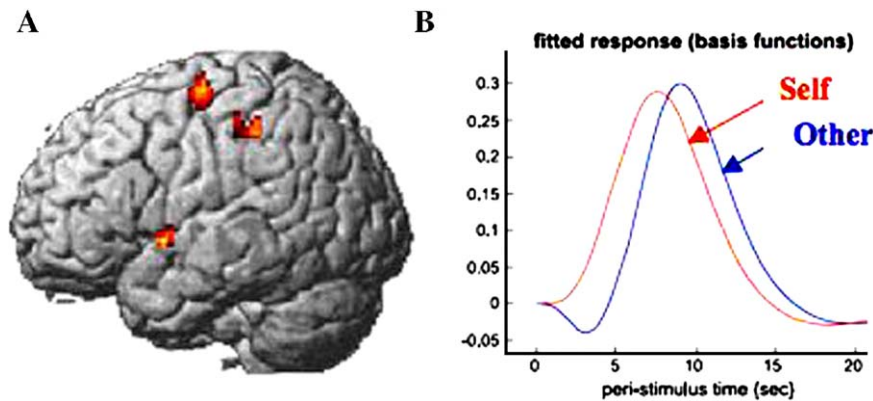


Fig. 1 – Brain responses associated with the perception of self and others actions. (A) Both the perception of one's own actions and of others are associated with activations in the dorsal premotor cortex bilaterally, the left frontal operculum, the left intraparietal sulcus, and the right cerebellum. These findings were based on an *F* test for the canonical HRF and its temporal derivative. (B) The fitted responses at the local maxima in the left dorsal premotor cortex ($x = -30, y = -12, z = 64$) showed that those regions show earlier responses for the perception of one's own actions as compared to the perception of the actions of others, in the absence of significant difference in the amplitude. Adapted from Grèzes et al. (2004).

associated with body knowledge and self-awareness such as anosognosia, asomatognosia, or somatoparaphrenia (Berlucchi and Aglioti, 1997). For instance, Blanke et al. (2002) demonstrated that out-of-body experiences (i.e., the experience of dissociation of self from the body) can be induced by electrical stimulation of the right TPJ.

In addition, a number of functional imaging studies have pointed out the involvement of the right inferior parietal lobule in the process of agency. Attribution of action to another agent has been associated with specific increased activity in the right inferior parietal lobe. In one fMRI study, participants were instructed to open and close their hand

slowly and continuously (0.5 Hz), while this movement was filmed and projected to them online onto a screen (Leube et al., 2003). They found a positive correlation between the extent of the temporal delay and activation in the right TPJ. In another fMRI study, Farrer and Frith (2002) instructed participants to use a joystick to drive a circle along a T-shaped path. They were told that the circle would be driven either by themselves or by the experimenter. In the former case, subjects were requested to drive the circle, to be aware that they drove the circle, and thus to mentally attribute the action seen on the screen to themselves. In the latter case, they were also requested to perform the task, but they were

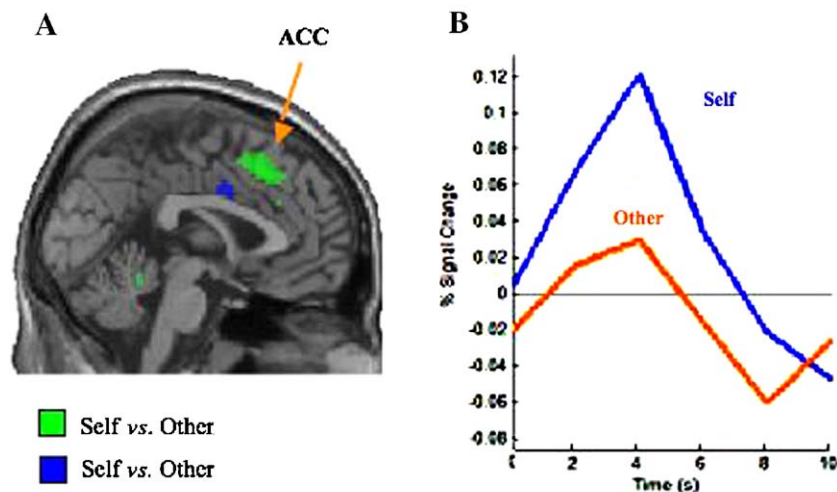


Fig. 2 – Hemodynamic response in the anterior cingulate cortex (ACC) during the imagination of painful experiences. In that functional MRI study, participants were shown pictures of painful familiar situations involving the hands and feet and were asked to either imagine how they would themselves feel (Self) or how another person (Other) would feel in those situations. The ACC plays a pivotal role in the integration of painful experiences with attention, arousal, and subjective emotional states. (A) Both imagining self and imagining other in painful situations were associated with signal increase in the ACC (green). However, imagining self also activated a specific subcallosal area of the cingulate cortex (blue). This latter region is implicated in the control of visceral functions. (B) Time courses in the ACC were extracted from the corresponding clusters found in SPM contrast. Adapted from Jackson et al. (2005b).

aware that the experimenter drove action seen on the screen. The results showed that being aware of causing an action was associated with activation in the anterior insula, whereas being aware of not causing the action and attributing it to another person was associated with activation in the right inferior parietal cortex.

Another study used a device that allowed modifying the participant's degree of control of the movements of a virtual hand presented on a screen. Experimental conditions varied the degree of distortion of the visual feedback provided to the participants about their own movements. Results demonstrated a graded hemodynamic activity of the right inferior parietal

lobule that parallels the degree of mismatch between the executed movements and the visual reafference (Farrer et al., 2003). In addition, studies on imitation have documented the involvement of right inferior parietal cortex/TPJ during reciprocal imitation, in which it may be difficult to keep track of agency (Chaminade and Decety, 2002; Decety et al., 2002). These results provide the strongest argument for the implication of the right TPJ in the process of agency by demonstrating a clear dissociation between the left and the right TPJ. When participants imitated the other, the left TPJ was strongly engaged, whereas greater activation was detected in the right TPJ when they were being imitated. Only this later condition

Box 1

The inferior parietal lobule: its role in the sense of agency and mentalizing

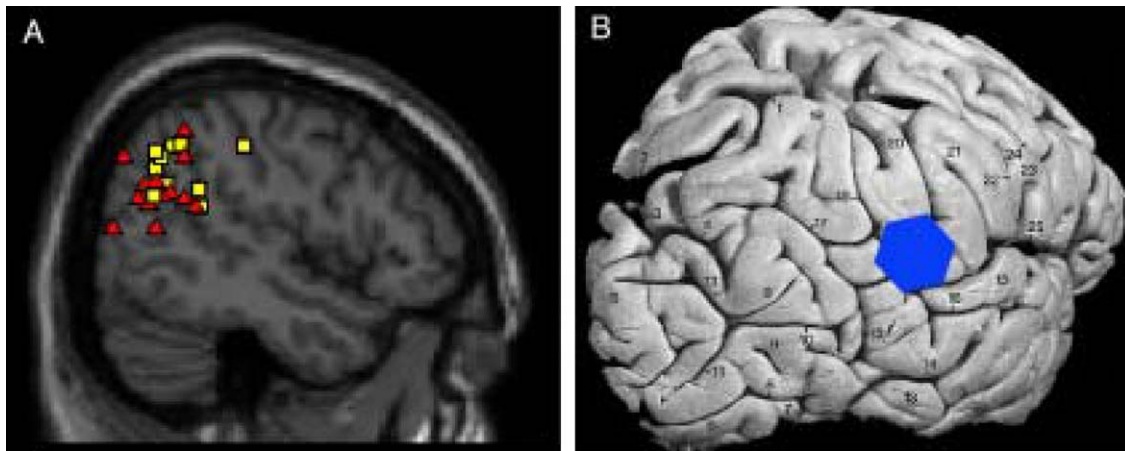


Figure A illustrates the distribution of clusters of activation around the right temporo-parietal junction (TPJ) reported in 14 functional neuroimaging studies of theory-of-mind tasks (▲) and 11 studies of agency (■). The coordinates from the Montreal Neurological Institute were used to superimpose the clusters onto a sagittal magnetic resonance imaging section ($x = 50$) using the SPM software. Some of these studies consider the clusters to fall into the posterior part of the superior temporal sulcus at the junction with the inferior parietal lobule (TPJ), while others report almost identical coordinates to be in the inferior parietal lobule (IPL). It must be emphasized that all these studies report group (i.e., averaged) data, often superimposed on a standard brain, which makes difficult to assess whether the activated region belongs to the TPJ or to the IPL.

Figure B shows an external view of the right hemisphere occipital pole from the Atlas of Duvernoy (1991) demonstrating the difficulty to visually distinguish the TPJ from the rostral part of the IPL (also labeled the supramarginal gyrus or area PF). Only observer-independent measurements of the cytoarchitecture can delineate these areas (Zilles and Palomero-Gallagher, 2001). In addition, there is no sharp border between this portion of the supramarginal gyrus and adjacent areas. 12: Anterior occipital sulcus; 15: Superior temporal gyrus; 18: Parallel sulcus, ascending posterior segment; 21: Supramarginal gyrus. Individual neuroanatomical and functional data are therefore needed for an accurate anatomical localization and decide whether mentalizing and agency share the same underlying computational mechanism implemented in the same cortical region. The blue polygon represents the center of gravity of the clusters from both theory-of-mind and agency studies.

Importantly, the posterior STS/TPJ is directly connected with the medial prefrontal cortex. There is some debate about whether the TPJ is involved in mental state reasoning per se (Apperly et al., 2004; Saxe and Wexler, 2005), or just in lower level processing of socially relevant stimuli. It is worth noting that this region is activated not only during mentalizing tasks, but also during the perception of actions made by others. It has been proposed that this area is involved in detecting the behavior of agents, and analyzing the goals and outcomes of this behavior (Frith and Frith, 2003). Furthermore, a number of neuroimaging studies have shown that the right TPJ/IPL is recruited in conjunction with the prefrontal cortex in distinguishing the perspectives of the self from those of others (Decety and Sommerville, 2003), an ability that is relevant to knowing the contents of other people's minds can be different from our own.

involved discrepancies between predicted outcomes of the action performed by the participants and those perceived.

The right inferior parietal cortex was also found to be activated when participants mentally simulated actions from someone else's perspective but not from their own (Ruby and Decety, 2001). Similarly, this region was specifically involved when participants imagined how another person would feel in everyday life situations that elicit social emotions (Ruby and Decety, 2004) or painful experiences but not when they imagined these situations for themselves (Jackson et al., 2005a). Such findings point to the similarity of the neural mechanisms that account for the correct attribution of actions, emotions, and thoughts to their respective agents when one mentally simulates actions for oneself or for another individual (see Box 1). Further, they support a role for the right TPJ, not only in mental state processing, but also in lower level processing of socially relevant stimuli.

8. Conclusions

The combined results of functional neuroimaging studies demonstrate that when individuals perceive the actions and the emotions produced by others, they use the same neural mechanisms as when they produce the actions and the emotions themselves. Moreover, a number of neuroimaging studies have shown that similar brain areas including the premotor and posterior parietal cortex are activated while imagining one's own action and imagining another's action. Likewise, similar neural networks mediate the simulation of pain for self and other. Such a perception–action coupling mechanism offers an interesting foundation for intersubjectivity because it provides a functional bridge between first-person information and third-person information, grounded on self-other equivalence (Decety and Sommerville, 2003), which allows analogical reasoning, and offers a possible route to understanding others (Gallagher, 2001).

However, under normal circumstances, there is no complete overlap between self- and others representations. This would lead to confusion and chaotic social interaction, as it is the case in schizophrenia, which may include the overextension of agency to the action of others (delusion of control) and the attenuation of agency (thought insertion and delusions of alien control; see Kircher and David, 2003). We have argued that self-awareness and agency play crucial functions both at the intrasubjective and intersubjective levels. Neuroscience research indicates that the right TPJ/inferior parietal cortex seems to mediate the mechanism underpinning the discrimination between self-agency and other agency. This process is likely to be an important component in higher level social cognition such as empathy and theory of mind.

Furthermore, although the process of motor representation is largely non-conscious, the content of higher level representations can be accessed consciously in certain conditions. This is important because by becoming aware of their intentions, actions, emotions, and desires, psychological agents are capable of action monitoring and self-regulation. And they may also consciously reflect on these shared representations and form explicit metarepresentation. These aspects heavily

rely on executive resources such as switch attention, working memory, and response inhibition, which are not limited to social cognition. Future social neuroscience research will clarify the functional relations between the temporo-parietal regions subserving self-agency and other areas that are involved in executive functions and mentalizing (especially the medial prefrontal and anterior cingulate cortices).

Let us acknowledge that such analogical reasoning provided by simulation cannot fully account for attribution psychological states to other people because at best it would only allow for an understanding of actions and mental events already experienced by the attributor (Proust, 2003). Simulation may be adequate to identify behaviors that are sufficiently transparent so that the perceiver who uncovers their meaning gets by without any mental state inferences, such as in the case of perception of pain in others where the meaning can initially be purely functional in that it can be associated with previous experience (see Malle, 2005). One interesting question is to what extent the former process (i.e., simulation) is necessary for the development and maturation of the full capacity of inferring other people's mental states. Finally, the work discussed here suggests that our capacity to imagine one's own and others' behavior including associated subjective states requires both domain-general mechanisms and embodied domain-specific representations.

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