

Special Lecture

Human empathy

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Abstract : The psychological construct of empathy refers to an emotional response that emanates from the emotional state of another individual without losing sight of whose feelings belong to whom. This response is contingent on cognitive as well as emotional factors. Empathy involves not only the affective experience of the other person's actual or inferred emotional state but also some minimal recognition and understanding of another's emotional state. Drawing on cognitive neuroscience and neuropsychological data, I propose that empathy involves parallel and distributed processing in a number of dissociable computational mechanisms. Shared neural representations, self-awareness, mental flexibility and emotion regulation constitute the basic macro-components of empathy, which are underpinned by specific and interacting neural systems. Furthermore, this model of empathy is consistent with the view that social cognition draws on both domain-general mechanisms and domain-specific embodied representations.

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The ability to perceive and process the information about the emotional states of others is considered a cornerstone of social sensibility and adaptation. Among the various forms of emotional connections with others, empathy has received lots of attention from philosophers and psychologists, and more recently from social neuroscientists. The construct of empathy denotes, at a phenomenological level of description, a sense of similarity between the feelings one experiences and those expressed by others. It can be conceived of as an interaction between any two individuals, with one experiencing and sharing the feeling of the other. This sharing of feelings does not necessarily imply that one will act or even feel impelled to act in a supportive or sympathetic way (empathy's paradox is that this

ability may be used for both helpful and hurtful purposes). Moreover, the social and emotional situations eliciting empathy can become quite complex depending on the feelings experienced by the observed and the relationship of the target to the observer (Feshbach, 1997). This capacity to understand others and experience their feelings in relation to oneself illustrates the social nature of the self, its inherent intersubjectivity.

The goal of this paper is to propose a new model of empathy that articulates data from social psychology and cognitive neuroscience (including neuropsychology). Bridging social psychology and cognitive neuroscience provides important guidelines for investigating the neural processes underlying empathy. On the other hand, cognitive neuroscience may help disam-

biguate competing social theories. To that end, instead of addressing each of these research domains separately, theoretical notions and findings from these different approaches will be marshaled with the guidance of an overarching conceptual framework. This framework considers that empathy involves parallel and distributed processing in a number of dissociable computational mechanisms. Shared neural circuits, self-awareness, mental flexibility and emotion regulation constitute the basic macro-components of empathy, which are mediated by specific neural systems, including aspects of the prefrontal cortex, the anterior insula and frontoparietal networks. Consequently, damage to each of these components may lead to an alteration of empathic behavior, and produce selective social disorders depending on which aspect is disrupted.

Evolutionary origins of empathy

Much of our social behavior is similar to that of other primates and other mammals. However, it seems evident from the descriptions of comparative psychologists and ethologists that some behaviors homologous to empathy can be observed in other species (e.g., Plutchik, 1987). For de Waal (1996) empathy is not an all-or-nothing phenomenon, and many forms of empathy exist between the extremes of mere agitation at the distress of another and full understanding of their predicament. Many other comparative psychologists, however, view empathy as a kind of induction process by which emotions, both positive and negative, are shared, and by which the probabilities of similar behavior are increased in the participants. In my view, this is not a sufficient mechanism to account for the full-blown ability of human empathy. This does not mean that some aspects of empathy are not present in other species, like motor mimicry and emotion

contagion (see de Waal & Thompson, 2005), which mediate emotional sharing between different conspecifics. But humans may be unique in their ability to intentionally “feel for” and act on behalf of other people whose experiences may differ greatly from their own (Batson, 1991; Decety & Hodges 2006; Davis, 1994). In addition, social neuroscience research has shown that empathic concern is often associated with prosocial behaviors such as helping a kin, and has been considered as a chief enabling process for altruism (Batson, 1991). Note that Wilson (1998) suggested that empathic helping behavior has evolved because of its contribution to genetic fitness (kin selection). In humans and other mammals, an impulse to care for offspring is almost certainly genetically hard-wired. It is however far less clear that an impulse to care for siblings, more remote kin, and similar non-kin is genetically hard-wired (Batson, 2006). The emergence of altruism, of empathizing with and caring for those who are not kin is thus not easily explained within the framework of neo-Darwinian theories of natural selection. Social learning explanations of kinship patterns in human helping behavior are thus highly plausible. However, one of the most striking aspects of human empathy is that it can be felt for virtually any target - even targets of a different species. In addition, as emphasized by Harris (2000), humans, unlike other primates, can put their emotions into words, allowing them not only to express emotion, but to report on current, as well as past emotions. These reports provide an opportunity to share, explain and regulate emotional experience with others to an extent that is not found in any other species. Notably, conversation helps to develop empathy, for it is often here that one learns of shared experiences and feelings. Importantly, this self-reflexive capability (which includes emotion regulation processes) may be an

important difference between humans and other animals (Povinelli, 2001).

Overall, this evolutionary conceptual view is compatible with the hypothesis that advanced levels of social cognition may have arisen as an emergent property of powerful executive functioning assisted by the representational properties of language (Barrett, Henzi & Dunbar, 2003). However, these higher levels operate upon previous levels of organization, and should not be seen as independent or conflicting with one another. Evolution has constructed layers of increasing complexity, from non-representational to representational and meta-representational mechanisms, which need to be taken into account for a full understanding of human empathy. This distributed nature of social processing poses a challenge to understanding the neurology of social cognition in general and empathy in particular. In addition, social psychological concepts, such as empathy, do not necessarily correspond to neurological processes. Relations between psychological and biological processes cannot be comprehended fully by investigations at a single level of organization. Therefore multi-level research is necessary to form bridges among disciplines, and ultimately achieve a truly interdisciplinary social neuroscience (Cacioppo, Tassinari & Berntson, 2000). Given the fact that empathy is a psychological construct, the first step is to break it down into its component neurocognitive functions.

Breaking down empathy into its constitutive components

For many psychologists, empathy implies at least three different processes : feeling what another person is feeling ; knowing what another person is feeling ; and having the intention to respond compassionately to another person's distress (Thompson, 2001). Yet, regardless of the

particular terminology that is used, there is broad agreement among scholars on three primary aspects : 1) an affective response to another person, which often, but not always, entails sharing that person's emotional state, 2) a cognitive capacity to take the perspective of the other person, and 3) some self-regulatory and monitoring mechanisms that modulate inner states (e.g., Batson, 1991 ; Davis, 1996 ; Decety & Hodges, 2006 ; Eisenberg, 2000 ; Hodges & Wegner, 1997 ; Preston & de Waal, 2002). According to Ickes (1997), empathy is a complex form of psychological inference in which observation, memory, knowledge, and reasoning are combined to yield insights into the thoughts and feelings of others. As such, empathy involves not only the affective experience of the other person's actual or inferred emotional state, but also some minimal recognition and understanding of another's emotional state (or most likely emotional state) . This definition captures the multidimensional nature of empathy and makes explicit reference to some minimal mentalizing capacity. This latter concept refers to the broad social-cognitive ability used by humans to explain and predict their own behavior and that of others by attributing to them independent mental states, such as beliefs, desires, emotions or intentions (Flavell, 1999).

Of all the sources from which one can draw insight as to the constituents of human empathy, psychotherapeutic schools provide the most interesting experience-related knowledge. Indeed, empathy is appreciated to play a central role in psychotherapies, since almost all of them involve intersubjective communication between individuals in order for the clinician to understand his/her client sufficiently to proceed along a treatment path (Bohart & Greenberg, 1997). Although not a major construct for psychoanalysis, Freud (1921) wrote that empathy was indispens-

able when it came to taking a position regarding another person's mental life, and considered it as the process that plays the largest part in our understanding of what is inherently foreign to our ego in other people. A number of analysts have pointed out that empathy involves resonating with the other's unconscious affect and experiencing his/her experience with him/her while the empathizer maintains the integrity of his/her self intact. For instance, Basch (1983) speculated that, because their respective autonomic nervous systems are genetically programmed to respond in like fashion, a given affective expression by a member of a particular species tends to recruit a similar response in other members of that species. "*This is done through the promotion of an unconscious autonomic imitation of the sender's bodily state and facial expression by the receiver. It generates in the receiver the autonomic response associated with that bodily state and facial expression, which is to say, the receiver experiences an affect identical with that of the sender (p. 108).*"

Such a view subsequently received empirical validation by a series of studies conducted by Levenson and Ruef (1992). They found evidence that a perceiver's accuracy in inferring a target's negative emotional states was related to the degree of physiological synchrony between the perceiver and the target. In other words, when two people feel similar emotions, they more accurately perceive each other's intentions and motivations.

The model proposed here suggests that four major functional components dynamically interact to produce the experience of empathy :

1. Affective sharing between the self and the other, based on the shared circuits between perception-action, mediated by fronto-parietal networks.
2. Self-awareness, mediated by the inferior

parietal lobule and the anterior insula, especially on the right side.

3. Mental flexibility to adopt the subjective perspective of the other. This aspect heavily draws on executive resources of the prefrontal cortex.
4. Regulatory processes including emotion reappraisal, which depend upon interaction between prefrontal and anterior cingulate systems and subcortical emotion-generation systems.

In this view, none of these components can account solely for the potential of human empathy. The four components are intertwined and dynamically interact with one another to produce the subjective experience of human empathy. For instance, sharing emotion without self-awareness corresponds to the phenomenon of emotional contagion, which takes the form of 'total identification without discrimination between one's feelings and those of the other' (de Waal, 1996).

Furthermore, this model of empathy involves both bottom-up and top-down information processing (see Fig. 1). Furthermore, it combines representational aspects, i.e., memories that are localized in distributed neural networks that encode information and, when temporarily activated, enable access to this stored information, as well as processes, i.e., computational procedures that are localized and are independent of the nature or modality of the stimulus that is being processed.

Like many emotion-related processes, some components involved in empathy occur implicitly, without awareness, in a bottom-up fashion. This is the case of the emotion-sharing and motor mimicry aspect. Other components require explicit top-down processing, such as perspective-taking, representing our own thoughts and feelings as well as those of others, and also

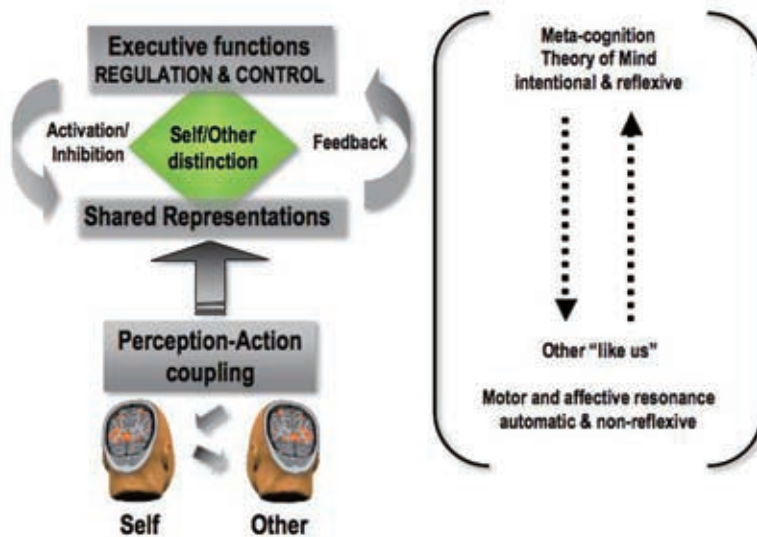


Fig. 1 Schematic representation of bottom-up (i.e., direct matching between perception and action), and top-down (i.e., regulation and control) information processing involved in human empathy. These two levels of processing are interrelated. The low level, which is automatically activated (unless inhibited) by perceptual input, accounts for the implicit recognition that others are like us. The metalevel is continuously updated by bottom-up information, and in return controls the lower level by providing top-down input. Thus metacognitive regulation, through executive functions modulates low levels and adds flexibility, making the individual less dependent on external cues.

some aspects of emotion regulation.

Affective sharing between self and other

In addition to their survival values for the organism, emotional expression and perception are an integral part of social interaction (Schulkin, 2004). Bodily expressions constitute an external, perceivable indication of people's intentions and emotions. At one level, emotional expressions are governed by rules and can be elicited by simple stimuli, as in the example of disgust in the presence of bitter taste. However, humans and other animals also use bodily expressions to communicate various type of information to members of their own species. Understanding other people's emotional signals has clear adaptive advantages and is especially important in the formation and

maintenance of social relationships.

Social psychological research shows that humans mimic unintentionally and unconsciously a wide range of behaviors, such as accents, tone of voice, rate of speech, posture and mannerisms, as well as moods (e.g., Chartrand & Bargh, 1999). This tendency to automatically mimic and synchronize one's own emotional behavior with others, also known as the phenomenon of emotion contagion, facilitate the smoothness of social interaction and may even foster empathy (Hatfield, Cacioppo & Rapson, 1994). For instance, a study demonstrated that participants who had been mimicked by the experimenter were more helpful and generous toward other people than non-mimicked participants (Van Baaren et al., 2004). They also found that these beneficial conse-

quences of mimicry were not restricted to behavior directed toward the mimicker, but included behavior directed toward people not directly involved in the mimicry situation.

This automatic mapping between self and other is supported by considerable empirical literature in the domain of perception and action, which has been marshaled under the common-coding theory (Prinz, 1997). Its core assumption is that actions are coded in terms of the perceivable effects (i.e., the distal perceptual events) they should generate. This theory also states that perception of an action activates action representations to the degree that the perceived and the represented action are similar (Wilson & Knoblich, 2005). Furthermore, these representations may be shared between individuals. Indeed, the meaning of a given object, action, or social situation may be common to several people and activate corresponding distributed patterns of neural activation in their respective brains (Decety & Sommerville, 2003 ; Jeannerod, 1999). This sharing explains how we come to understand each other, that is the isomorphism between action representations allows the individual to implicitly know the goal of others with the use of her/his own action representation system.

In neuroscience, evidence for this perception/action coupling ranges from electrophysiological recordings in monkeys in which mirror neurons in the ventral premotor and posterior parietal cortices fire both during goal-directed actions and observation of the same actions performed by another individual (Rizzolatti, Fogassi, & Gallese, 2001), to functional neuroimaging experiments in humans which indicate that the neural circuits involved in action execution overlap with those activated when actions are observed (Blakemore & Decety, 2001). This shared neural network for action production and observation includes the premotor cortex, the parietal

lobule, the supplementary motor area and the cerebellum. In addition, a number of neuroimaging studies have shown that similar brain areas, pertaining to the same network are reliably activated during imagining one's own action, imagining another's action, and imitating actions performed by a model (Decety & Chaminade, 2003a ; Decety & Grèzes, 2006). Such shared circuits reflect an automatic transformation of what another conspecifics do into the neural representation of one's own actions.

The perception-action mechanism accounts (at least partly) for emotion sharing and empathy, as suggested by Preston and de Waal (2002). This model posits that perception of emotion activates in the observer the neural mechanisms that are responsible for the generation of similar emotion. This mechanism was also proposed to account for emotion contagion. Indeed, Hatfield, Cacioppo and Rapson (1994) suggested 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. For example, while watching someone smile, the observer activates the same facial muscles involved in producing a smile at a sub-threshold level and this would create the corresponding feeling of happiness in the observer. Indeed, viewing facial expressions triggers expressions on one's own face, even in the absence of conscious recognition of the stimulus (e.g., Dimberg, Thunberg, & Elmehed, 2000 ; Wallbott, 1991). Interestingly, de Gelder and colleagues 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.

Making a facial expression generates changes in the autonomic nervous system and is associated with feeling the corresponding emotion. In a series of experiments, Levenson, Ekman and Friesen (1990) instructed participants to produce facial configurations for anger, disgust, fear, happiness, sadness, and surprise while heart rate, skin conductance, finger temperature, and somatic activity were monitored. They found that such a voluntary facial activity produce significant levels of subjective experience of the associated emotions as well as specific and reliable autonomic measures. Recently an fMRI experiment confirmed and extended these findings by showing that when participants are required to observe or to imitate facial expressions of various emotions, increased neurodynamic activity is detected in the superior temporal sulcus, the anterior insula and the amygdala, as well as areas of the premotor cortex corresponding to the facial representation (Carr et al., 2003).

The finding of paired deficits between emotion production and emotion recognition also provides strong arguments in favor of the perception-action matching model. A lesion study carried out with a large number of neurological patients by Adolphs and colleagues (2000) found that damage within the right somatosensory related cortices (including primary and secondary somatosensory cortices, insula and anterior supramarginal gyrus) impaired the judgment of other people's emotional states from viewing their face. Another study with brain-damaged patients indicated that recognizing emotions from prosody draws on the right fronto-parietal cortex (Adolphs, Damasio, & Tranel, 2002). These findings strongly support the hypothesis that the recognition of emotion in others requires the perceiver to reconstruct images of somatic and motoric components that would normally be associated with producing and experi-

encing the emotion signaled in the stimulus (Adolphs, 2002).

Moreover, there are several dramatic case studies that support the idea that the same neural systems are involved both in the recognition and in the expression of specific emotion. For instance, Adolphs and collaborators (1995) investigated S.M., a 30-year old patient, whose amygdala was bilaterally destructed 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 impairment of fear recognition from body postures and emotional sounds (Sprengelmeyer et al., 1999). The patient also reported reduced anger and fear in his everyday experience of emotion. There is also evidence for paired deficits for the emotion of disgust. Calder and colleagues (2000) described patient N.K., with left insula and putamen damage who was selectively impaired at recognizing social signals of disgust from multiple modalities (facial expressions, non-verbal sounds, and emotional prosody), and who was less disgusted than controls by disgust-provoking scenarios. Further and direct support for a specific role of the left insula in both the recognition and the experience of disgust was recently provided by an fMRI study in which participants inhaled odorants producing a strong feeling of disgust, and in another condition, watched video clips showing the facial expression of disgust. It was found that observing such facial expressions and feelings of disgust activated the same sites in the anterior insula and anterior cingulate cortex (Wicker et

al., 2003).

The expression of pain provides a crucial signal, which can motivate caring behaviors in others. It is thus an ecologically valid way to investigate the neural systems involved in empathy and evaluate to what extent there is an overlap between the response to self-experienced pain and pain perceived in others. It is already well known that a restricted number of neural regions are involved in the processing of painful stimuli, including the anterior cingulate cortex, the insula, the somatosensory cortex, the periaqueductal gray, the thalamus, and the ventral prefrontal cortex. Further, these regions are differentially involved in the sensory, and affective and motivational aspects of pain processing. Interestingly, a micro-electrode exploration in neurological patients has documented 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 (Hutchinson, Davis, & Lozano, 1999). In one of the first fMRI study of empathy for pain, it demonstrated that the ACC, the anterior insula, cerebellum, and brainstem were activated when healthy participants experienced a painful stimulus, as well as when they observed another person receiving a similar stimulus, but only the actual experience of pain resulted in activation in the somatosensory cortices and in subcallosal cingulate cortex (Singer et al., 2004). Similar results were also reported by Morrison et al. (2004) from a study in which participants were scanned during a condition of feeling a moderately painful pinprick stimulus to the fingertips and another condition in which they witnessed another person's hand undergo similar stimulation. Both conditions resulted in common hemodynamic activity in a pain-related area in the right dorsal ACC. Common activity in response to noxious tactile and to

visual stimulation was restricted to the right inferior Brodmann's area 24b. In contrast, the primary somatosensory cortex showed significant activations in response to noxious tactile, but not visual, stimuli. The different response patterns in the two areas are consistent with the ACC's role in coding the motivational-affective dimension of pain, which is associated with the preparation of behavioral responses to aversive events. These findings are supported by an fMRI study conducted by Jackson, Meltzoff and Decety (2005a) in which 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. Significant activation in regions involved in the affective aspect of pain processing, notably the ACC, the thalamus and the anterior insula was detected, but no activity in the somatosensory cortex (see Fig. 2). Moreover, the level of activity within the ACC was strongly correlated with subjects' mean ratings of pain attributed to the different situations.

In a follow up fMRI study, Jackson, Brunet, Meltzoff and Decety (2005b), again using pictures of hands and feet in painful scenarios, instructed the participants to imagine and rate the level of pain perceived from two different perspectives (self versus other). Results indicated that both the self and the other perspectives are associated with activation in the neural network involved in the processing of the affective aspect of pain, including the ACC and the insula. However, the self-perspective yielded higher pain ratings and recruited the pain matrix more extensively, including the secondary somatosensory cortex, the mid-insula, and the posterior part of the subcallosal ACC. Adopting the perspective of the other was associated with increase in the right temporo-parietal junction. In addition, distinct subregions were activated within the insu-

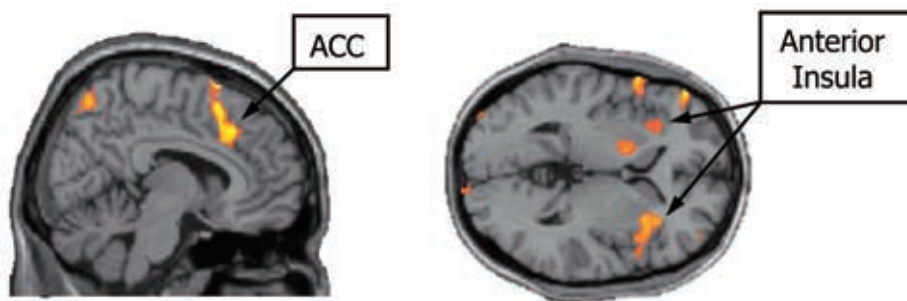


Fig. 2 Sagittal (on the left) and coronal (on the right) views of activated clusters in the anterior cingulate and insular cortex elicited by the perception of pain in others, superimposed on an averaged structural MR image. Physiological research in pain processing demonstrates that the ACC has a role in the affective dimension of pain, particularly those related to behavioral responses associated with avoiding or escaping the nociceptive stimulus. This region interrelates attentional and evaluative functions with that of establishing emotional valence and response priorities. The insular cortex is involved in monitoring the physiological state of the body. It receives direct input from the spinothalamic pathways via the medial thalamic nuclei (the major nociceptive pathway). Interestingly both the ACC and the anterior insula are found activated by the mere sight of pain in others (adapted from Jackson, Meltzoff and Decety, 2005).

lar cortex for the two perspectives (anterior aspect for others and more posterior for self). 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), consistent with the spino-thalamic nociceptive projections, while the perception of pain in others is represented in more rostral (and dorsal) regions (within area 32). 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).

Shared circuits between emotion generation and emotion perception in others have also been documented in a positron emission tomography study which compared the neural response to

externally (by watching emotional laden film clips) versus internally (by autobiographical scripts) generated emotions (Reiman et al., 1997). Both film-generated emotion and recall-generated emotion were associated with symmetrical increases in the medial prefrontal cortex and thalamus. The film condition also resulted in activation of the hypothalamus, the amygdala, the anterior temporal cortex and the occipito-temporo-parietal junction, while the recall condition was specifically associated with activation in the anterior insula and orbitofrontal cortex. Thus, there is an overlap between externally and internally produced emotions, but this overlap is partial. It should be noted that the films and recall scripts included three emotions (happiness, sadness, and disgust), which were not analyzed separately.

A more recent neuroimaging study demonstrated the involvement of shared representations (in both emotion-processing areas, and fronto-parietal networks) when subjects feel sympa-

thy for another individual (Decety & Chaminade, 2003b). In this study, participants were presented with a series of video-clips showing individuals telling sad and neutral stories, as if they had personally experienced them. At the end of each movie, subjects were asked to rate the mood of the actor and also how likable they found that person. Watching sad stories versus neutral stories was associated with increased activity in emotion processing-related structures (including the amygdala and parieto-frontal areas) predominantly in the right hemisphere.

Altogether, shared neural circuits between self and other at the cortical level have been documented for action understanding, emotion recognition, and pain processing. This mechanism offers an interesting foundation for intersubjectivity because it provides a functional bridge (i.e., shared representations) between first-person information and third-person information (Decety & Sommerville, 2003), which allows an implicit connection between the self and the other. There is no specific cortical site for shared representations: their neural underpinnings are widely distributed and the pattern of activation (and also presumably deactivation) varies according to the processing domain, the particular emotion, and the stored information.

The affective-sharing mechanism is necessary but not sufficient for empathic understanding. 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 likely induce emotional distress or empathic over arousal (a self-oriented aversive emotional response), which is not the goal of empathy. In fact, when experiencing empathy, individuals must be able to dis-

entangle themselves from others. Therefore, self-agency is a crucial aspect to successfully navigate shared representations between self and other (Decety & Sommerville, 2003; Decety, 2005).

Self-awareness and mentalizing

Individuals who are self-aware, as evidenced by being able to become the object of their own attention, experience a sense of psychological continuity over time and space (Gallup, 1998). It has been speculated that any organisms capable of self-recognition would have an introspective awareness of their own mental states and the ability to ascribe mental states to others (Humphrey, 1990). Having a clear sense of self may have evolved to solve at least two kinds of adaptive problems: 1) the self is the repository of the social feedback one receives from others and, 2) it allows to model and understand the internal, subjective worlds of others, making easier to infer intentions and causes that lay behind observed behaviors, thus improving interaction efficacy (Forgas & Williams, 2002). Interestingly, the development of self and other mental state understanding is functionally linked to that of executive functions, i.e., the processes that serve to monitor and control thought and actions, including self-regulation, planning, cognitive flexibility, response inhibition, and resistance to interference (Russell, 1996). There is increasingly clear evidence of a specific developmental link between the development of mentalizing and improved self-control at around the age of four (Carlson & Moses, 2001). The development of cognitive control is related to the maturation of the prefrontal cortex (Tamm, Menon & Reiss, 2002). In addition, there is hard evidence that a region around the paracingulate sulcus in the medial prefrontal cortex plays a specific role in mentalizing. This region contains spindle cells, a

class of large projection neurons found only in great apes and humans, which are thought to be involved in coordinating widely distributed neural activity involving emotion and cognition (Allman et al., 2001). This region has been found to be reliably activated by mentalizing tasks of various cognitive difficulty, ranging from judging the emotion in another person's gaze, detection of intention in simple dynamic animations, attribution of intention to cartoons characters, stories comprehension, detection of social transgression and appreciation of humor. It was proposed that activity in the medial prefrontal cortex occurs when cues are used in a particular way ; that is, to determine an agent's mental state, such as a belief, that is decoupled from reality, and to handle simultaneously these two perspectives on the world (Gallagher & Frith, 2003).

Self-awareness does not rely upon a specific brain region. Rather, it arises from the interaction between processes distributed in the brain, especially the medial prefrontal cortex and the inferior parietal lobule. Neuropsychological research supports a preeminent role of the right frontal lobe in self-related processing. For instance, Keenan, Nelson, O'Connor and Pascual-Leone (2001) demonstrated that patients undergoing a Wada test were temporarily desensitized with regards to the recognition of their own faces when the right hemisphere was anaesthetized. This was not the case when the left hemisphere was anaesthetized. Right hemisphere damage has also found to be linked with impairments in autobiographical memory and self-evaluation. Furthermore, clinical examination has shown that personal confabulation (akin to the creation of fictitious stories about the self) appears to be associated with damage to the right frontal lobe (Feinburg, 2001).

Based on these numerous studies (and many others not reviewed here) , it was argued that

the right hemisphere is a key player in self-awareness and mental state attribution (Keenan, Gallup & Falk, 2003). It is worth noting that their definition of consciousness includes awareness of one's own thoughts as well as awareness of others' thoughts. Similar (but not identical) neural processing for self and other raises the question of how we distinguish between representations activated by the self and those activated by other.

Neuroscience research indicates that the right inferior parietal cortex in conjunction with prefrontal areas and the insula may be critical in distinguishing the self from the other, and therefore navigating shared representations. The inferior parietal cortex is a heteromodal association area, which receives 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 (Eidelberg & Galaburda, 1984). 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 & Arzy, 2005). Its lesion can produce a variety of disorders associated with body knowledge and self-awareness such as anosognosia, asomatognosia, or somatoparaphrenia (Berlucchi and Aglioti, 1997). For instance, Blanke and colleagues (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 TPJ. 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 generat-

ed by others (Blakemore & Frith, 2003 ; Jackson & Decety, 2004 for reviews). In addition, some recent data suggest that this region is specifically involved in theory of mind (Apperly et al., 2004 ; Saxe & Wexler, 2005). Interestingly, the right inferior parietal cortex/right temporo-parietal junction is also involved when subjects mentally simulate the actions from a third-person perspective person in comparison to first-person perspective (Ruby & Decety, 2001). There are new findings suggesting that this mechanism is also at play during thinking about others. For instance, it has been demonstrated that when subjects are asked to adopt another person's perspective to evaluate their beliefs (Ruby & Decety, 2003), imagine their feelings (Ruby & Decety, 2004) and imaging their pain (Jackson et al., 2005b) as compared to their own perspective, the right inferior parietal cortex is strongly involved.

All the aforementioned evidence strongly suggests that the inferior parietal cortex at the junction with the posterior temporal lobe, in conjunction with the medial prefrontal cortex, plays a pivotal role in the sense of self by comparing the source of sensory signals (whether they originate from the self or from the environment) . 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. Such a function is crucial for empathy in order to maintain a minimal distinction between the self and other and to keep track of the origin of the feelings.

Mental flexibility and executive functions

Empathy may be initiated in a variety of situations. For instance when one sees another person in distress or in discomfort, when one imagines someone else's behavior, by the reading of a narrative in a fiction book or when one sees a moving TV-report. However, in these conditions,

empathy requires one to adopt more or less consciously the subjective point of view of the other.

Several social psychologists have suggested, and documented through empirical work, that our default mode to reasoning about others is biased towards self-perspective, and that this constitutes a general feature of human cognition (e.g., Hodges & Wegner, 1997 ; Keysar, 1994 ; Royzman, Cassidy & Baron, 2003). Stated in other words, people are fundamentally egocentric and have difficulty getting beyond their own perspective when anticipating what others are thinking or feeling. Usually people are unaware of this projective tendency, which also applies to goals. This view is coherent with the shared representations mechanism. One sees others through one's own embodied cognition and uses one's own knowledge (including beliefs, opinions, attitudes, feelings) as the primary basis for understanding others. Self-perspective may thus be considered as the default mode of the human mind. It is a very parsimonious and advantageous mechanism to understand and predict the behavior of others. Yet it is far from perfect, as individual differences in people's thoughts and emotions abound. Errors in taking the perspective of others stem from the inability to suppress the self-perspective, and many costly social misunderstandings are rooted in people's failure to recognize the degree to which their construals of a situation may differ from those of others (Decety & Hodges, 2006 ; Hodges & Wegner, 1997) . For successful social interaction, and empathic understanding in particular, an adjustment must operate on these shared representations. Hence, mental flexibility and self-regulation are important components of empathy. One needs to calibrate one's own perspective that has been activated by the interaction with the other or even its mere imagination. Such calibration requires prefrontal cortex executive resources as demon-

strated by neuroimaging studies in healthy participants as well as neuropsychological observations.

A series of three neuroimaging studies investigated in healthy volunteers the neural underpinning of perspective taking in three different modalities (i.e., motoric, conceptual, and emotional) of self-other representations. In a first study, participants were scanned while they were asked to either imagine themselves performing a variety of everyday actions (e.g., winding a watch up), or imagining another individual performing similar actions (Ruby & Decety, 2001). Both conditions were associated with common activation in the supplementary motor area (SMA), premotor cortex, and the occipito-temporal region. This neural network corresponds to the shared motor representations between the self and the other. Taking the perspective of the other to simulate his behavior resulted in selective activation of the frontopolar cortex and right inferior parietal lobule. In a second study, medical students were shown a series of affirmative health-related sentences (e.g., taking antibiotic drugs causes general fatigue) and were asked to judge their truthfulness either according to their own perspective (i.e., as experts in medical knowledge), or according to the perspective of a layperson (Ruby & Decety, 2003). The set of activated regions recruited when the participants put themselves in the shoes of a layperson included the medial prefrontal cortex, the frontopolar and right inferior parietal lobule. In a third study, the participants were presented with short written sentences that depicted real-life situations (e.g., someone opens the toilet door that you have forgotten to lock), which are likely to induce social emotions (e.g., shame, guilt, pride), or other situations that were emotionally neutral (Ruby & Decety, 2004). In one condition, they were asked to imagine how they would feel

if they were experiencing these situations. And in another condition, they were asked to imagine how their mother would feel in those situations. Reaction times were statistically greater when the subjects imagined emotional-laden situations as compared to neutral ones, both from their own perspective and from the perspective of their mothers. Neurodynamic changes were detected in the frontopolar cortex, the ventromedial prefrontal cortex, the medial prefrontal cortex, and the right inferior parietal lobule when the participants adopted the perspective of their mother, regardless of the affective content of the situations depicted. Cortical regions that are involved in emotional processing were found activated in the conditions that integrated emotional-laden situations, including the amygdala and the temporal poles. Consistent findings were reported from a functional MRI study in which participants were asked to make food preference judgments about themselves or about someone else (a person who they fairly knew). Self-judgments were associated with increases in the medial prefrontal cortex, the anterior insula and secondary somatosensory areas. Other-judgments resulted in activation of the medial prefrontal cortex, the frontopolar cortex and the posterior cingulate (Seger, Stone & Keenan, 2004).

One of the most striking findings of these studies that investigated self- versus other's perspective is the systematic involvement of the frontopolar cortex, medial prefrontal cortex and posterior cingulate when the participants adopt the perspective of another person. Converging evidence from clinical neuropsychology and neuroscience points to the frontopolar cortex as being chiefly involved in inhibitory and/or regulating processing. Patients studies have demonstrated that frontal damage may result in impaired perspective-taking ability and a lack of

cognitive flexibility (Eslinger, 1998). For instance, Anderson and colleagues (1999) reported the cases of two patients with early damage to the anterior prefrontal cortex (encompassing the frontopolar cortex) who, when tested on moral dilemmas, exhibited an excessively egocentric perspective. In one major study, frontal lobe patients with limited focal lesions were tested for visual perspective taking and detection of deception. Results revealed a dissociation of performance within the frontal lobes (Stuss, Gallup & Alexander, 2001). Right frontal lobe lesions were associated with impaired visual perspective taking, whereas medial frontal lesions, particularly right ventral, with impaired detection of deception.

These findings support the hypothesis that an inhibitory component is required to regulate and tone down the self-perspective tendency to allow cognitive and affective flexibility necessary in the evaluation of the other's perspective. Such a view is in agreement with the role of the prefrontal cortex in top-down control of behavior (Miller & Cohen, 2001). An alternative interpretation for the role of the frontopolar cortex in adopting the perspective of another individual is based on the distinction between different psychological operations mediated by distinct subregions of the prefrontal cortex. There is evidence that the frontopolar cortex is involved in the process of evaluation of self-generated responses, and is recruited when the task requires monitoring and manipulation of information that has been internally represented (Christoff & Gabrieli, 2000). One may suggest that adopting the subjective perspective of another individual to understand his/her feelings is a self-generated process that operates upon internally represented information fed by the internal activation of shared representations. Such process requires the participation of the frontopolar cortex.

Emotion regulation

Emotion regulation refers to the processes by which individuals influence which emotions they have, when they have them, and how they experience and express these emotions (Gross, 1998). It also applies to the modulation of the behavioral and the physiologic dimension of emotion. It is likely that in the experience of empathy the emotional state and affective consequences generated in the self from the perception or the imagination of the other's affective state benefit from some regulation and control. Indeed, without such control, the mere activation of the perception-action mechanism, including the associated autonomic and somatic responses, could lead to emotional contagion or emotional distress. Such a regulation is then important to modulate one's own vicarious emotion so that it is not experienced as aversive. Previous research indicates that emotion regulation is positively related to feelings of concern for others (Derryberry & Rothbart, 1988 ; Eisenberg et al., 1994). In contrast people who experience their emotions intensely, especially negative emotions are prone to personal distress, i.e., an aversive emotional reaction, such as anxiety or discomfort based on the recognition of another's emotional state or condition (Eisenberg, Shea, Carlo & Knight, 1991). It has also been shown that chronic incapacity to suppress negative emotion may be a key factor in anxiety, aggressive and violent behavior (Jackson et al., 2000).

A complex neural circuit that includes several interconnected regions of the prefrontal cortex, the amygdala, hippocampus, anterior cingulate cortex, insular cortex and ventral striatum is implicated in various aspects of emotion regulation (Davidson et al., 2000). In neurology, a "self-regulatory disorder" has been coined for the syndrome exhibited by patients with ventromedial

prefrontal cortex damage (particularly on the right). This syndrome is defined as the inability to regulate behavior according to internal goals and constraints (Levine et al., 1999). It arises from the inability to hold a mental representation of the self on-line and to use this self-related information to inhibit inappropriate responses. Interestingly, lesions of the orbitofrontal, ventromedial and dorsolateral cortices have been reported in the neurological literature to be associated with empathy deficits. Notably, damage of the orbitofrontal is associated with a wide range of social emotional disorders, including impaired social judgment and disinhibited behavior. For instance, Stone, Baron-Cohen and Knight (1998) found that patients with bilateral lesions of the orbitofrontal cortex are impaired in the "faux pas" task. This task requires both an understanding of false or mistaken belief, and an appreciation of the emotional impact of a statement on the listener. A study conducted by Stuss and colleagues (2001) extended this finding by showing that only lesions in the right orbitofrontal produce such a deficit. In addition, a number of clinical studies reported a relationship between the deficit in empathy and performance of cognitive flexibility tasks among patients with lesions in the dorsolateral lesions, while those with orbitofrontal cortex lesions were more impaired in empathy but not in cognitive flexibility (Grattan et al., 1994; Shamay-Tsoory et al., 2003). The ventromedial prefrontal cortex with its reciprocal connections with brain regions involved in emotional processing (amygdala), memory (hippocampus) and executive functions (dorsolateral prefrontal cortex) plays also a major role in emotion regulation. Damasio's (1994) somatic markers hypothesis, positing that memories of somatic states are associated with particular experiences or outcomes are stored in the ventromedial prefrontal cortex, is directly relevant in the process

of affective regulation. Recent work by Shamay-Tsoory and colleagues (2005) supports this hypothesis. They tested patients with lesions of the ventromedial prefrontal cortex or dorsolateral prefrontal cortex with three theory-of-mind tasks (second-order beliefs and faux pas) differing in the level of emotional processing involved. They found that patients with ventromedial lesions were most impaired in the faux pas task but presented normal performance in the second-order belief tasks. The authors further argued that in order to detect faux pas, one is required not only to understand the knowledge of the other but also to have empathic understanding of their feelings. Finally, the ACC is part of a circuit involved in a form of attention that serves to regulate both cognitive and emotional processing (Bush, Luu, & Posner, 2000). And its lesion produces a host of symptoms, which include apathy, inattention, dysregulation of autonomic functions and emotional instability.

Neuroimaging research has recently begun to investigate neural mechanisms involved in affective reappraisal, a cognitive strategy used to regulate emotion. For instance, an fMRI experiment of emotion reappraisal has detected co-activation of the lateral prefrontal and medial prefrontal cortices, and decreased activity in the medial orbitofrontal cortex and the amygdala (Ochsner et al., 2002). Another study identified a circuit composed of the right orbitofrontal, right dorsolateral prefrontal cortex and anterior cingulate for voluntary suppression of sadness (Lévesque et al., 2003). One recent functional MRI study investigated whether observation of distress in others leads to empathic concern and altruistic motivation, or to personal distress and egoistic motivation (Lamm, Batson & Decety, 2006). In this experiment behavioral measures and event-related functional MRI were used to explore the effect of perspective taking and emotion regulation on

empathy processing while participants watched video-clips of patients expressing pain resulting from medical treatment. Video-clips were presented either with the instruction to imagine the feelings of the patient (“imagine other”), or to imagine oneself to be in the patient’s situation (“imagine self”). Need for emotion regulation was manipulated by providing information that the medical treatment had or had not be successful. Behavioral measures clearly demonstrated that imagery and reappraisal instructions were effective. Neuroimaging data showed consistent activity in the insular cortex and anterior medial cingulate cortex (aMCC). Graded responses related to the imagery instructions were observed in dorsal insula, aMCC, and left and right parietal cortex. Emotion regulation resulted in hemodynamic changes in anterior paracingulate cortex, subgenual ACC, orbitofrontal and right temporal cortex. These findings support the view that humans’ responses to the pain of others can be modulated by cognitive and motivational processes, which influence whether observing a conspecific in need of help will result in empathic concern, an important instigator for helping behavior.

Empathy as an internal brain simulation of the subjectivity of the other

The way our nervous system is organized and tailored by evolution provides the basic biological mechanism for resonating with others. We have seen that research in social neuroscience indicates the activation of shared neural circuits when we perform an action, feel an emotion or sense a sensation and when we observe or listen to someone else perform the same actions, express the same emotions and experience the same sensations. Such shared circuits reflect an automatic transformation of what other conspecifics do and feel into the neural representa-

tion of our own actions, emotions and feelings. This mechanism provides the default mode to implicitly relate to others, and may be responsible for the projective tendency to ascribing one’s own characteristics and self-traits onto others (Decety & Sommerville, 2004 ; Decety & Jackson, 2004).

However, for successful social interaction, this tendency needs to be regulated (or calibrated) when sharing emotions or when adopting the perspective of others in order to understand their feelings and behave appropriately (Decety & Hodges, 2006). Indeed, the other is similar but never identical to the self. This requires additional computational mechanisms including monitoring and manipulation of internal information generated by the activation of the shared representations between the self and the other, as well as holding separate perspective and/or resisting interference from one’s own perspective. In addition, there are limits to the extent to which the experiences are isomorphic as demonstrated by the non-overlapping neural areas.

One of the core components of empathy relies on the unconscious neural emulation of the emotional state of others. This idea is far from new (e.g., Damasio, 1994 ; Goldman, 1993). For instance, Ax (1964) suggested that empathy might be thought of “ as an autonomic nervous system state which tends to simulate that of another person.” Such a view fits neatly with the notion of embodiment, which refers both to actual bodily states and to simulations of experience in the brain’s modality-specific systems for perception, action and the introspective systems that underlie conscious experiences of emotion, motivation and cognitive operations (Niedenthal et al., 2005). However, this simulation is not exclusively under automatic management and, at least in humans fall under conscious control. This makes empathy as described here, an intentional capac-

ity. I have suggested that without self-awareness and emotion regulation processing, there may be no true empathy. The automatic activation of shared representations would instead be associated to anxiety, discomfort, and would lead to responses oriented to the self (e.g., emotional distress). Such a formulation is also consistent with the observation that prosocial behaviors, which stem from empathy, emerge during child development in parallel with self-conscious emotions (Lewis, 1999). These emotions involve self-evaluation and comparison with other selves. Forming an explicit representation of another person's feeling, as an intentional agent, thus necessitates additional computational mechanisms, beyond the shared representation level. This requires that second-order representations of the other are available to consciousness (i.e., a decoupling mechanism between first-person information and second person information), for which the anterior paracingulate cortex seem to play a unique function (Frith & Frith, 2003). Thus, human empathy cannot only be described as a simple resonance of affect between the self and other. It also involves an explicit representation of the subjectivity of the other and a minimal self-other distinction (Fig. 3).

Recent neuroimaging investigations of the perception of pain in others support such a view (Jackson et al., 2005ab; Lamm et al., 2006; Morrison et al., 2004; Singer et al., 2004). Indeed, all these studies have shown part of the neural circuit (including the anterior cingulate cortex and the anterior insula) mediating self-experienced pain is shared when empathizing or observing the pain in others, but also that non-overlapping aspects within these regions are specifically activated for the self or the other. This supports the idea that personal and vicarious experiences at some level differ physiologically (Craig, 1968), and result in qualitatively distinct responses. Fi-

nally, empathy also necessitates emotion regulation for which the ventral prefrontal cortex, with its strong connections with the limbic system, dorsolateral, and medial prefrontal areas, plays an important role.

To conclude and sum up, empathy refers to an emotional response that emanates from the emotional state of another individual without losing sight of whose feelings belong to whom. This response is contingent on cognitive as well as emotional factors and involves parallel and distributed processing in a number of dissociable computational mechanisms operating at both bottom-up and top-down levels. Affective sharing, self-awareness, mental flexibility and emotion regulation constitute the basic macro-components of empathy, which are mediated by specific neural systems. These components may comprise more elementary components that future social neuroscience research will elucidate.

Moreover, because this model assumes that empathy relies on dissociable information processing components, it predicts a variety of structural or functional dysfunctions in psychiatric disorders depending on which aspect is disrupted (Decety & Jackson, 2004). For instance autistic individuals, who are profoundly impaired in social and emotional abilities, may lack of empathy because of an impairment of the automatic emotional mimicry mechanism. Interestingly, a study recently demonstrated that autistic participants do not show spontaneous facial mimicry, but can do voluntary mimicry just fine (McIntosh et al., in press). Such a core deficit in involuntary motor resonance would also account for their profound difficulties in perceiving and responding to the affective expressions of others. Psychopaths also lack of empathy, but for very different reasons. It has been suggested that their empathic dysfunction is relatively selective and may be linked with amygdala dysfunction,

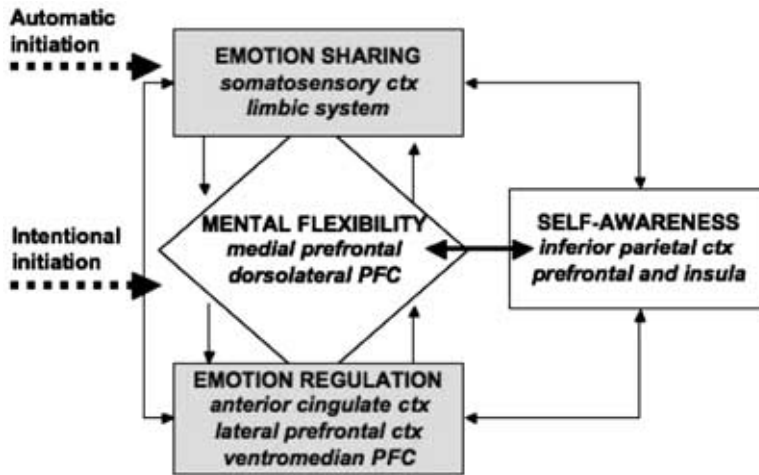


Fig. 3 The major neural components that subserve empathy. This model combines both representational aspects (i.e., memories that are localized in distributed neural networks that encode information and, when temporarily activated, enable access to this stored information, e.g., shared affective representations), and processes (i.e., computational procedure that are neurally localized and are independent of the nature or modality of the stimulus that is being processed (e.g., decoupling mechanism between self and other). Motor resonance that leads to emotion sharing is mediated by the perception-action mechanism (Preston & de Waal, 2002). The medial prefrontal cortex/paracingulate sulcus has a key role in decoupling between first-person and third-person information (Gallagher & Frith, 2003). The right inferior parietal cortex at the junction with temporo-parietal cortex plays a critical role in the distinction between self-produced actions and emotions and those generated by others (Decety & Grèzes, 2006). This heteromodal association cortex is a key neural locus for self-processing. It is involved in multisensory body-related information processing as well as in the processing of phenomenological and cognitive aspects of the self. The ventromedial prefrontal cortex has been described as a convergence zone in which information from amygdala, hippocampus and sensory regions interacts to influence social behavior (Damasio, 1994). The insular cortex is the main cortical target of interoceptive afferents and mediates interoceptive state of the body (Craig, 2002). The lateral prefrontal cortex and the anterior cingulate are part of a circuit that regulates emotion and cognition (Davidson et al., 2000). Note the bidirectional links between the (widely distributed) areas in which representation of emotions are temporarily activated (including autonomic and somatic responses) during empathic experience and the areas involved in emotion regulation. Each area has unique patterns of cortico-cortical connections, which determine its function, and differences in neural activity during the experience of empathy are produced by distributed subsystems of brain regions. Even though there is massive parallel processing, the dynamic of activation in these regions is also an important aspect to be investigated further.

especially in the processing of fearful and sad expressions (Blair, 2002). Lacking empathy is also a profound disturbance in a number of personality disorders, such as in antisocial personality and narcissistic personality disorders. It is worth noting for the latter disorder, that individuals are also hypersensitive to evaluation of others. Although there is no neuroscience work, one may speculate that the self-awareness component is immature and that emotion regulation processes do not function optimally.

Future social cognitive neuroscience research will continue to provide clues for an understanding of brain circuits (including their neurochemistry) and neural dynamics underlying empathy, especially if individual differences in personality styles are taken into account.

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