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The Functional Architecture of Human Empathy

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Empathy accounts for the naturally occurring subjective experience of similarity between the feelings expressed by self and others without loosing sight of whose feelings belong to whom. 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. In light of multiple levels of analysis ranging from developmental psychology, social psychology, cognitive neuroscience, and clinical neuropsychology, this article proposes a model of empathy that 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 macrocomponents of empathy, which are underpinned by specific neural systems. This functional model may be used to make specific predictions about the various empathy deficits that can be encountered in different forms of social and neurological disorders.

Key Words: self-awareness, intersubjectivity, affective sharing, perspective taking, executive inhibition, shared representations, emotion regulation

You are peacefully reading your favorite newspaper while your child is playing with others in a playpen nearby, when suddenly, she cries. It does not take long to orient your attention toward her, perceive her distressed state, and understand what she feels. Not only do you perceive her plight, but you also actively want to comfort her. This natural ability to understand the emotions and feelings of others, whether one actually witnessed his or her situation, perceived it from a photograph, read about it in fiction book, or merely imagined it, refers to the phenomenological experience of empathy. This "every-day mind reading," to borrow Ickes's (2003) metaphor, is not something one needs to learn. Rather, the basic building blocks are hardwired in the brain and await development through interaction with others. Such a capacity to understand others and experience their feelings in relation to oneself illustrates the social

nature of the self, inherently intersubjective. Humans are indeed social animals, and virtually all of their actions (including their thoughts and desires) are directed toward or are produced in response to others (Batson, 1990).

Empathy denotes, at a phenomenological level of description, a sense of similarity between the feelings one experiences and those expressed by others. This sharing of the feelings of another person does not necessarily imply that one will act or even feel impelled to act in a supportive or sympathetic way. Given the complexity of this construct, we believe that only a multidisciplinary approach can help to better understand the information-processing mechanisms that give rise to this subjective psychological phenomenon. Our ambition in this article is to articulate different domains of research, including developmental science, cognitive and social psychology, and neuroscience. In addition, instead of addressing each of these research domains separately, we integrate data from these different approaches with the guidance of a putative model. This model should be considered as a heuristic tool for future research, especially to foster new investigations of social behavior disorders (e.g., anti-social personality disorders), whether they are clinical observations or empirical studies, as well as to cast some light into empathy deficits observed in brain damaged patients. We also hope that this endeavor adequately illustrates the emerging field of social-cognitive neuroscience (Ochsner & Lieberman, 2001).

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It is unlikely that empathy is the product of random mutation and just happened in humans without any evolutionary history. During the evolution of the mammal and primate brain, the organization of the neural activity has been shaped by the need for rapid evaluation of the motivations of others (Brothers, 1989). Indeed, affective communication is widely distributed in the animal kingdom (e.g., Buck & Ginsburg, 1997; Preston & de Waal, 2002). It has a survival value and contributes to inclusive fitness because it assists individuals in gathering and hunting for food, detecting predators, courtship, and ensuring reproductive success (Plutchik, 1987).

It is not, however, evident how selective pressures tailor such superordinate categories as empathy or social cognition. Selection operates at the level of function, not at the level of physical structures or behaviors that subserve the function. Evolution does not create specific behaviors; it creates mental organizations and inference systems that make people behave in particular ways (Boyer, 2001). Tooby and Cosmides (1996) proposed that humans have a specialized computational device—an implicit theory of human nature—that models what motivations and mental representations others would develop when placed in various evolutionarily recurrent situations. But this does not mean there is a single module in the brain for such a device. Rather, there is a collection of separate systems whose combination produces typically human "mind reading" and the hypertrophied social intelligence (Boyer & Barrett, 2004). Another interesting argument considers that social complexity (often indexed by group size) has been a driving force in brain evolution and that the demands of navigating more complex social landscapes constitutes a unique selection pressure among the ancestral apes for increased brain size and cognitive abilities (Dunbar, 1998). 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). In addition, the balance of cost and benefits for the individual who expresses feelings and the observer who interacts with this individual has implications for survival in social groups. Empathic concern is often associated with prosocial behaviors, such as helping a kin, and has been considered by Batson (1991a) as a chief enabling process to altruism. Evolutionary biologists such as Hamilton (1964) and Wilson (1988) 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 hardwired. It is far less clear that an impulse to care for siblings, more remote kin, and similar nonkin is genetically hardwired (Batson, in press). 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 (Eisler & Levine, 2002). Social learning explanations of kinship patterns in human helping behavior are 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. We favor the view championed by Cummins and Cummins (1999) that a viable evolutionary cognitive psychology requires neither extreme nativism nor modularity. There are, however, evolved biological predispositions (e.g., the capacity to distinguish agents from other objects and to engage in reciprocal interactions with the former but not the latter) that are necessary for the full maturation of empathy. But without social interaction and emotional bonds with others, it is unlikely that empathy develops.

It seems evident from the descriptions of comparative psychologists and ethologists that some behaviors homologous to empathy can be found in animals (Buck & Ginsburg, 1997; Plutchik, 1987). For de Waal (1996), empathy is not an all-or-nothing phenomenon, and many forms of empathy exist intermediate between the extremes of mere agitation at the distress of another and full understanding of their predicament. However, many other comparative psychologists 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 our view, this is not a sufficient mechanism to account for human empathy. Feelings may be shared, but humans are able to intentionally "feel for" and act on behalf of other people whose experiences differ greatly from their own (Batson, 1991a, in press; Decety & Hodges, 2004).

We believe that self-other awareness and self-regulation of emotions are vital components of human empathy (see sections titled Self-Other Awareness and Mental Flexibility and Self-Regulation). These components may well steer us toward a clear distinction between humans and other mammals when referring to empathy. 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 and explain emotional experience with others that is not found in other species. Conversation helps to develop empathy, for it is often here that one learns of shared experiences and feelings. Moreover, this self-reflexive capability (including emo-

tion reappraisal) may be a crucial difference between humans and other animals (Povinelli, 2001).

Batson (1991a) has put forward an attractive empathy-altruism hypothesis. This hypothesis claims that the pro-social motivation evoked by empathy is directed toward the ultimate goal of increasing the welfare of the person in need. This hypothesis seems necessary to explain why some people hold helping intentions that are not explained by egoistic motivations, such as relief of personal distress, the relief of sadness, and the desire to make oneself happy (Batson, 1991b). An egoistic explanation of the empathy-altruism hypothesis was proposed by Smith, Keating, and Stotland (1989). They suggested that empathically aroused individuals help to gain the good feeling of sharing vicariously in the needy person's joy at improvement (or, in other words, the empathically concerned witness to the distress of others helps to be happy). However, other authors have suggested that rather than empathy, it is the sense of self-other overlap between the helper and the person in need that motivates helping (e.g., Cialdini, Brown, Lewis, Luce, & Neuberg, 1997). Helping others with whom one feels some level of commonality would not be selfless because it leads to a more favorable mental state. Thus, as demonstrated by recent research from Kruger (2003), psychologically altruistic and egoistic pathways seem to operate simultaneously in empathic concern.

Even though empathy provides obvious benefits at both the individual and societal level by allowing people to coordinate their behavior and care for the other, it also has its cost in terms of maintaining an expanded self—that is, a self that is linked to others (Hodges & Klein, 2001). One example of such cost is the tendency to assume that others will feel the same way the self does, which is referred to as the false consensus effects (Marks & Miller, 1987). Another example is the anxiety that can result from watching an unpleasant situation happening to another person. It has also been argued that some aspects of psychopathology may be in part regarded as the evolutionary cost of humankind for the development of our advanced capacity to empathize (Brüne, 2001). How this cost-benefit equation is solved within each individual depends on regulatory mechanisms as well as several personality and situational characteristics.

EMPATHY AND ITS CONSTITUTIVE COMPONENTS

It is not an easy task to bridge our intuitive folk conception of empathy with the explanations offered by social psychology, developmental science, and neuroscience (the three domains we want to articulate). The real challenge, as insightfully expressed by Adolphs (2003), is that research in social cognition faces both theoretical and methodological problems. For instance, how do we unite the vocabularies of social psychology and cognitive psychology, the latter being easier to link with neuroscience data? Is social cognition domain specific or domain general? How are social-cognitive processes related to non-social-cognitive processes? These difficulties hold particularly true for the concept of empathy, for it is a psychological construct, which accounts for a superordinate category of behaviors. This construct has been the main focus so far of extensive research in social and developmental psychology (see, e.g., Batson, 1987; Eisenberg & Strayer, 1987; Ickes, 1997) and much less in cognitive neuroscience. Moreover, we think it is useless to seek "the" neural substrate of empathy in the same way that it appears futile to identify one specific empathy deficit in neurological or psychiatric patients. Rather, we suggest that a more successful approach would come from breaking down this concept into its constitutive components or processes and examining their respective neural instantiations. Thus, a clear definition of empathy is needed (for a history of the concept of empathy, see Wispé, 1987).

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 (Ickes, 1997). As such, empathy involves not only some minimal recognition and understanding of another's emotional state (or most likely emotional state) but also the affective experience of the other person's actual or inferred emotional state. There are many other definitions of empathy, almost as many as there are researchers in this field. 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. But regardless of the particular terminology that is used, there is broad agreement on three primary components: (a) an affective response to another person, which often, but not always, entails sharing that person's emotional state; (b) a cognitive capacity to take the perspective of the other person; and (c) some regulatory mechanisms that keep track of the origins of self- and other-feelings (e.g., Batson, 1991a, 1991b; Davis, 1996; Decety, 2002b; Decety & Hodges, 2004; Eisenberg, 2000; Hodges & Wegner, 1997; Ickes, 2003). Thus, empathy requires both the ability to share the emotional experience of the other person (affective component) and an understanding of the other person's experience (cognitive component). Some scholars favor in their definition

one aspect or the other. For instance, Hoffman (1981) views empathy as a largely involuntary vicarious response to affective cues from another person or her situation, whereas Davis (1996) or Batson (1991b, in press) stress the conscious role-taking ability, which taps mainly into cognitive resources.

We favor Ickes's definition presented above because it best 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 belief, desires, emotions, or intentions (Gallagher & Frith, 2003). This mentalizing ability is considered to set us apart from other primates (Povinelli, Bering, & Giambrone, 2000), with perhaps the exception of apes. Whether or not the concepts of empathy and mentalizing overlap remains an unsolved theoretical issue. Although emotions and feelings are generally included in the definition of mentalizing (also dubbed "theory of mind"), it is often considered that the recognition of the emotional state of others is a sort of direct, automatic process that does not require psychological inference and metarepresentation. Although this may be true for the recognition of basic emotions, more complex ones, such as self-conscious emotions, are likely to require cognitive processing. In addition, the extent to which attribution of desires, intentions, and emotions rely on distinct or common functional or anatomical substrates remains open. The neurophysiological evidence is scarce. For instance, most neuroimaging studies on these types of processes have used mentalizing tasks that did not include any affective components.

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 as almost all psychotherapy involves intersubjective communication between at least two individuals for the clinician to understand the client sufficiently to proceed along a treatment path (Bohart & Greenberg, 1997). For instance, Freud (1921) wrote that empathy was indispensable 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. In *Jokes and Their Relation to the Unconscious* (Freud, 1905), Freud used the concept of empathy (influenced by the work of Lipps, which he profoundly admired) to designate the process of putting oneself into another's position, either consciously or unconsciously. A number of analysts have pointed out that empathy involves resonating with the other's unconscious affect and experiencing the experience with this person while the empathizer maintains the integrity of his self intact (see Basch, 1983). According to Beres and Arlow (1974), a therapist can empathize with how the patient would feel if and when he or she could become consciously aware of the unconscious wishes, conflicts, fantasies, and other mental contents that are being warded off.

The psychoanalyst Theodor Reik (1949) offered a definition of the processes involved in empathy that is especially relevant to our view. He described the four following aspects:

- *Identification:* focusing one's own attention to another and allowing oneself to become absorbed in contemplation of that person.
- *Incorporation:* making the other's experience one's own via internalizing the other.
- *Reverberation:* experiencing the other's experience while attending to one's own cognitive and affective associations to that experience.
- *Detachment:* moving back from the merged inner relationship to a position of separate identity, which permits a response to be made that reflects both understanding of others as well as separateness from them.

More than to anyone else, the concept of empathy was an important part of the counseling technique developed by Carl Rogers. For him, empathy was one of the central conditions for therapeutic change. The therapist experiences an empathic understanding of the client's internal frame of reference and endeavors to communicate this experience to the client. By empathy, Rogers (1959) meant "to perceive the internal frame of reference of another person with accuracy and with the emotional components and meanings which pertain thereto as if one were the person, but without losing the as if condition." This last component reflects an active and controlled mechanism during which the person remains aware of the merging between the self and the other.

The model we propose here, as a heuristic framework, considers that the basic mechanism for empathy rests on the innate ability to recognize that the self and the other can be the same but also can be teased apart. Moreover, empathic understanding requires a minimal mental flexibility for the subjective viewpoint of the other to be adopted. Our model is strongly influenced by theories of psychotherapy and is compatible with both the humanistic and psychodynamic theories, as well as the behavioral approach. The former views empathy as an innate ability to experience the inner life of another while retaining objectivity, whereas the latter views empathy as a communication skill (Carlozzi, Bull, Stein, Ray, & Barnes, 2002).

We propose that three major functional components dynamically interact to produce the experience of empathy in humans:

- affective sharing between the self and the other, based on perception-action coupling that lead to shared representations;
- self-other awareness. Even when there is some temporary identification, there is no confusion between self and other;
- mental flexibility to adopt the subjective perspective of the other and also regulatory processes.

In our view, empathy entails these components, and none of them can account solely for the potential of human empathy. The three are intertwined and must interact with one another to produce the subjective experience of 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). Models or theories based only on the affect-sharing component of empathy may well reflect the continuity observed across species (in particular, emotion communication, see Preston & de Waal, 2002). We argue that there are unique features of empathy (e.g., perspective-taking, self-awareness, and emotion reappraisal) emerging in the course of evolution that distinguish human and non-human species. This model of empathy 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) and 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 and sometimes without awareness. This is the case of the emotion-sharing aspect. Other components require explicit processing, such as perspective taking, representing our own thoughts and feelings as well as those of others, and also some aspects of emotion regulation. It is unfortunately beyond the scope of this article to review the current knowledge of the neuroscience of emotion (see Davidson, Pizzagalli, Nitschke, & Kalin, 2003).

Each of these macrocomponents of empathy can further be fragmented into their constitutive elements as well as associated with their neural implementation. In the rest of the article, we address each of the macrocomponents separately; then, we review the evidence from various neurological disorders that can lead to a lack of empathy and discuss how these deficits enlighten our understanding of this process. Finally, we raise some questions for future research that we think can be best tackled by a multidisciplinary approach.

SHARED REPRESENTATIONS BETWEEN SELF AND OTHERS

Perception and Action Coupling

Investigations of the brain substrates involved in the perception of actions are directly relevant to the exploration of the mechanisms subserving empathy because bodily expressions constitute an external, perceivable indication of people's intentions and emotions. The notion of shared representations between self and other (Decety & Sommerville, 2003; Jeannerod, 1999) is at the core of our theoretical framework. This notion reflects the idea that the perception of a given behavior in another individual automatically activates one's own representations of that behavior (Knoblich & Flach, 2003; Preston & de Waal, 2002; Prinz, 1997). Such a view is grounded in the fundamental physiological properties of the nervous system regarding the continuity between action and cognition, which is primarily based on perception/action cycles. These processes are functionally intertwined—that is, perception is a means to action, and action is a means to perception, and they operate right after birth. Indeed, the vertebrate brain has evolved for the purpose of governing motor activity by transforming sensory patterns into patterns of motor coordination (Sperry, 1952). Spontaneous neural activity in developing networks of the vertebrate nervous system may well be at the very origin of these cycles. Research over the past 10 years has established that spontaneous activity (in many cortical and subcortical areas) is a characteristic feature of the embryonic nervous system (O'Donovan, 1999). Observations of preterm-born infants and fetuses show that sensory and motor activities are linked and that such linkages are prewired (Bloch, 1997). Thus, the human infant, like other young mammals, is born with instruments that can ensure relations with the external world. The newborn spontaneous motor activity provides the necessary and sufficient conditions for the natural interactions with others (Decety, 2002a).

Gibson (1966) proposed the metaphor of "affordance" to account for the direct link between perception and action. Affordances are properties of objects or events in the surroundings that respond to the needs of the perceiver. They are both physical and psychological, as well as ecological (see McArthur & Baron, 1983, for an ecological theory of social perception). Later, Shepard (1984) argued that as a result of biological evolution and individual learning, the organism is, at any given moment, tuned to resonate to the incoming patterns that correspond to the invariants that are significant for

it. These patterns, according to Shepard, have become most deeply internalized (i.e., represented), and even in the complete absence of external information, the system can be excited entirely from within (while imagining, for example). Thus, unlike Gibson, Shepard makes explicit reference to internal representation and, in our opinion, makes it possible to articulate the notion of resonance with that of shared representations. In addition, humans actively seek information about themselves and others. This aspect is compatible with contemporary theory of motor representation, which stresses the autonomy of the individual with respect to the external milieu and views his or her actions as a consequence of triggering by the environment or as a consequence of an internal process (Jeannerod, 1994).

The 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). This theory claims parity between perception and action. Its core assumption is that actions are coded in terms of the perceivable effects (i.e., the distal perceptual events) they should generate (Hommel, Müsseler, Aschersleben, & Prinz, 2001). This theory also states that perception of an action should activate action representations to the degree that the perceived and the represented action are similar (Knoblich & Flach, 2003). As such, 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 & Chaminade, 2003b).

There is both behavioral and neurophysiological evidence for shared representations between perception and action (see Viviani, 2002, for a review of psychophysics data demonstrating that the perception of biological actions is constrained by the observer's implicit knowledge of the movements that he or she is capable to produce). Imitation in neonates is the best evidence for this perception-action coupling functioning right from birth (Meltzoff & Decety, 2003, for a recent review). However, this early imitation cannot be explained solely by a simple motor resonance behavior mechanism—that is, a neural activity that is spontaneously generated during the perception of movements, gestures, and actions made by another person or a general arousal reaction. The work of Meltzoff and Moore (1994, 1997) and others (e.g., Kugiumutzakis, 1999; Nadel & Baudonnière, 1982) show that imitation is representationally mediated because the infant's response need not be temporally coupled to the stimulus and is not compulsory (see Table 1.1 in Meltzoff, 2002, for a complete list of the characteristics of early imitation). In addition, infants are not only

attracted to people, but they also identify with them (Hobson, 2002; Trevarthen, 1979). By 2 months, they imitate human actions but not those of objects because they implicitly understand other people to be like them (Legerstee, 1991). Taken together, these findings indicate that imitation is a social response.

This work with newborns has also led a number of developmental psychologists to propose that the understanding of the other person is primarily a form of embodied practice (e.g., Hobson, 1989; Legerstee, 1991; Meltzoff, 1990; Rogers & Pennington, 1991). Humans develop and maintain their self-concept through the process of taking action and then reflecting on what they have done—that is, the sensory consequences of their actions—and, later in life, what others tell about what they have done (Gallagher & Meltzoff, 1996). Meltzoff and Gopnik (1993) argued that the understanding of the other person emerges in part from being "like them" in action, through imitation, and that this provides the basic mechanism for empathy. However, the recognition of self-other equivalences would be the starting point for social cognition, not its culmination (Meltzoff, 2002).

Social psychologists have shown 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; Dijksterhuis & Bargh, 2001). One of the adaptive advantages of such behaviors is that they bind people together and foster empathy, liking, and smooth interaction. In an interesting series of recent experiments, Van Baaren, Holland, Kawakami, and Van Knippenberg (2004) demonstrated that participants who had been mimicked by the experimenter were more helpful and generous toward other people than nonmimicked participants. They also found that these beneficial consequences of mimicry were not restricted to behavior directed toward the mimicker but included behavior directed toward people not directly involved in the mimicry situation. The authors concluded that the effects of mimicry are not simply the result of an increased liking for the mimicker but are due to an increased prosocial orientation in general.

In neuroscience, evidence for this perception/action coupling ranges from electrophysiological recordings in monkeys, in which mirror neurons that fire both during goal-directed actions and observation of actions performed by another individual (Rizzolatti, Fogassi, & Gallese, 2001, for a review), to functional neuroimaging experiments in humans, which demonstrate that the neural circuit involved in action execution overlaps with that activated when actions are observed (Blakemore & Decety, 2001, for a review). This neural network includes the premotor cortex, the parietal lobule, the supplementary motor area, and the cerebellum (see Grèzes &
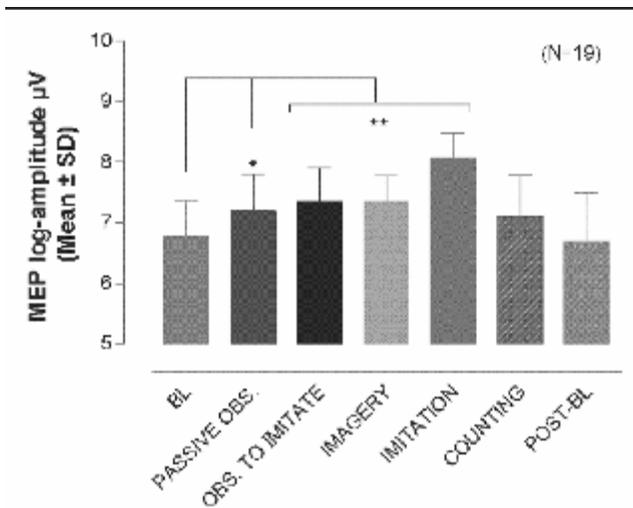
Figure 1: **Comparison of the mean changes in MEP log-amplitude in a group of participants during various experimental conditions including passive observation, observation to imitate, mental imagery, and imitation of hand actions.**
SOURCE: Clark, Tremblay, St.-Marie, 2003 (reprinted with permission).
NOTE: MEP = motor-evoked potentials.

Decety, 2001, for a meta-analysis). In addition, several neuroimaging studies have shown that similar brain areas, pertaining to the same network in the premotor and posterior parietal cortex, are activated during imagining one's own action (e.g., Decety et al., 1994; Hari et al., 1998), imagining another's action (Ruby & Decety, 2001), and imitating actions performed by a model (Decety, Chaminade, Grèzes, & Meltzoff, 2002; Decety et al., 1997; Iacoboni et al. 1999). Another strong evidence for the involvement of motor representation during observation comes from measurements of the corticospinal excitability by means of transcranial magnetic stimulation. One study found specific modulation of motor-evoked potentials (MEP) in participants asked to observed simple hand gestures (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). In another recent study, participants were asked to observe, imaging, or imitate hand actions while magnetic stimulation was delivered (Clark, Tremblay, & St.-Marie, 2003). Imitation produced the greatest MEP followed by the observation and imagery conditions (see Figure 1).

Such a shared motor-representations mechanism offers an interesting foundation for intersubjectivity because it provides a functional bridge between first-person information and third-person information (Decety & Sommerville, 2003). But as suggested by our model, this mechanism is necessary but not sufficient for empathic understanding. Moreover, it should be noted that the overlap between cortical areas involved in self-related actions and other-related actions is not complete. There are specific subcircuits within the premotor, prefrontal, and parietal cortices that account for either

the self or the other (e.g., Ruby & Decety, 2001). A recent functional magnetic resonance imaging (fMRI) experiment by Ramnani and Miall (2004) has shown that the motor system is engaged when participants use arbitrary visual cues to prepare their own actions and also when they use the same cues to predict the actions of other people. However, these two tasks activate separate subcircuits within the premotor cortex.

Emotion Sharing

Emotional expression and perception are an integral part of human interactions (Schulkin, 2004). 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.

The phenomenon of emotional contagion, defined as the tendency to automatically mimic and synchronize facial expressions, vocalizations, postures, and movements with those of another person and, consequently, to converge emotionally with the other (Hatfield, Cacioppo, & Rapson, 1994) is certainly the most simple expression of emotion sharing that does not need conscious awareness. There are a variety of ways in which happy people add color and life to our world and sullen people take it away (Chartrand, Maddux, & Lakin, in press).

The affective component of empathy may be conceptualized in its most rudimentary form as the ability to detect the immediate affective state of another person (Trevarthen & Aitken, 2001). This emotional arousal stems from the apprehension or comprehension of another's affective state. Developmental research indicates that we are, from birth, not only acting and thinking selves, but we also express an intuitive need to relate ourselves to other people. It has been shown that very young infants express what Trevarthen (1979) terms *intersubjective sympathy*—that is, they are innately predisposed to be sensitive and responsive to the subjective states of other people. This can be demonstrated through several means, including spontaneous face-to-face interaction between infants and their mothers and through more specialized "still-face procedures" (i.e., when mothers adopt a neutral face and stop responding to the infant), which can lead to withdrawal by the infant. Research performed by Field, Woodson, Greenberg, and Cohen (1982) has shown that neonates (aged 36 hours) can discriminate three facial expressions (happy, sad, and surprised) posed by a live model. This affective communica-

tion bridges the gap between an infant's grasp of other people's behavior and other people's experiences. Through the direct perception of feelings in the bodily expressiveness of others and through progressively more differentiated experiences of affective commonality with other people, an infant comes to understand something of what it means to be a person (Hobson, 1989; Rochat, 2001).

The infant affective state may be similar to or congruent with what the other person is feeling (Eisenberg & Strayer, 1987). For example, Simner (1971) investigated the phenomenon of neonatal crying in reaction to the distress cries of other newborns. He found that the sound of neonatal crying produced significantly more reactive crying in the newborn than did either white noise, a cry from a 5-month old, or a synthetic cry. These findings were later replicated by several groups (e.g., Sagi & Hoffman, 1976). Of special interest is the study by Martin and Clark (1987), who tested 1-day-old babies with, audiotapes of neonatal crying, the crying of an 11-month-old, and the newborn's own crying. Not only did they replicate Simner's results, but they also showed that newborns did not respond to the sound of their own cries. These latter results suggest that there is some self-other distinction already functioning right from birth.

Thus, it is clear that from very early on in development, infants are capable of emotional resonance, which is one important precursor of empathy (Hoffman, 2000). Another important foundation of the development of empathy is the affective synchrony in mother-infant play, which begins to occur regularly around 2 to 3 months of age. These play episodes, which each partner contributes through a repertoire of interactive behaviors, entail a sharing of affect between mother and baby (Stern, 1985; Trevarthen, 1979). Microanalyses of such social interactions conducted by Malatesta and Haviland (1982) showed that mothers were highly likely to imitate infant expressions of enjoyment and interest (which occurred most frequently), as well as expressions of surprise, sadness, and anger when they occurred. However, mothers rarely displayed negative emotions to their baby. Thus, infant-mother dyads exhibit considerable positive synchrony, partly as a consequence of the mother's contingent matching of positive infant emotional expressions. Field, Healy, Goldstein, and Guthertz (1990) have convincingly documented how depressed mothers can influence the subjective state of their babies through these interactions.

Another compelling evidence of infants' ability to discriminate among different facial expressions of emotion and to interpret them as emotional communication is known as "social referencing" (Campos & Stenberg, 1981). This process, which starts at about 10 months of age, reflects an active effort by infants to obtain emotion cues from others to assist in their own assessment of an uncertain or ambiguous situation (Rosen, Adamson, & Bakeman, 1992). However, it is difficult to interpret whether the child's referencing is genuinely empathic as the purpose of social referencing is to assess one's own circumstances rather than another's (Thompson, 1987). This process is best conceptualized as an integral, flexible aspect of the social construction of an infant's reality (Vygotsky, 1978).

It is around the 2nd year that empathy may be manifested in prosocial behaviors (e.g., helping, sharing, or comforting) indicative of concern for others. Studies of children in the 2nd year of life indicate that they have the requisite cognitive, affective, and behavioral capacities to display integrated patterns of concern for others in distress (Bretherton, Fritz, Zahn-Waxler, & Ridgeway, 1986). During this period of development, children increasingly experience emotional concern "on behalf of the victim," comprehend others' difficulties, and act constructively by providing comfort and help (Zahn-Waxler, Radke-Yarrow, Wagner, & Chapman, 1992).

The shared-representations mechanism may also account (at least partly) to emotion processing (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000). In this model, perception of emotion activates the neural mechanisms that are responsible for the generation of emotions (Adolphs, 2002). Such a system prompts the observer to resonate with the state of another individual, with the observer activating the motor representations and associated autonomic and somatic responses that stem from the observed target—that is, a sort of inverse mapping. For example, while watching someone smile, the observer activates the same facial muscles involved in producing a smile at a subthreshold level, and this would create the corresponding feeling of happiness in the observer. There is evidence for this mechanism in the recognition of emotion from facial expression. For instance, viewing facial expressions triggers expressions on one's own face, even in the absence of conscious recognition of the stimulus (Dimberg, Thunberg, & Elmehed, 2000; Wallbott, 1991).

Making a facial expression generates changes in the autonomic nervous system and is associated with feeling the corresponding emotion (Ekman, Levenson, & Friesen, 1983). 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 produced significant levels of subjective experience of the associated emotions as well as specific and reliable autonomic measures. In another study, Ekman and Davidson (1993) were able to demonstrate similar

patterns of electroencephalographic activity for spontaneous and voluntary forms of smiling. 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 superior temporal sulcus, the anterior insula, and the amygdala, as well as areas of the premotor cortex corresponding to the facial representation (Carr, Iacoboni, Dubeau, Mazziotta & Lenzi, 2003).

One may thus deliberately experience one's own emotion or use this mechanism to experience the emotion of the other, something that Edgar Allan Poe knew. In *The Purloined Letter* (1845/1990), he wrote:

> When I wish to find out how wise, or how stupid, or how good, or how wicked is any one, or what are his thoughts at the moment, I fashion the expression of my face, as accurately as possible, in accordance with the expression of his, and then wait to see what thoughts or sentiments arise in my mind or heart, as if to match or correspond with the expression.

Converging neurophysiological arguments in favor of this model are also supported by the finding of paired deficits between emotion production and emotion recognition. 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. The same authors also reported that there is an association between the impaired somatic sensation of one's own body and the impaired ability to judge other people's emotions. It has been reported that patients with Parkinson's disease may be impaired in expressing emotional faces and perceiving emotional facial affect (Jacobs, Shuren, Bowers, & Heilman, 1995). A study of brain-damaged individuals found that recognizing emotions from prosody draws on the right fronto-parietal cortex (Adolphs, Damasio, & Tranel, 2002). The authors stated that their results are consistent with 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 experiencing the emotion signaled in the stimulus.

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. Adolphs, Tranel, Damasio, and Damasio (1995) investigated S.M., a 30-year-old patient, whose amygdala was bilaterally destructed by a meta-
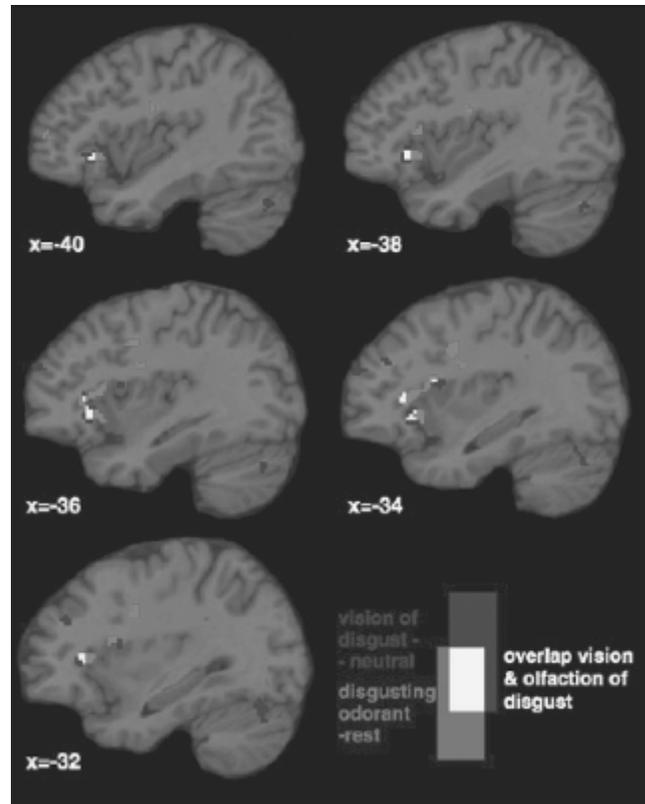

Figure 2:   **Overlap (white) between the brain activation elicited by the visual observation (blue) and the feeling (red) of disgust in a group of healthy volunteers.**
SOURCE: Wicker, Keyser, et al., 2003 (reprinted with permission).

bolic 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 when it came to recognizing fear from facial expressions and exhibited an equivalent deficit affecting fear recognition from body postures and emotional sounds (Sprengelmeyer et al., 1999). The patient reported reduced anger and fear in his everyday experience of emotion as well.

There is also evidence for paired deficits for the emotion of disgust. Calder, Keane, Manes, Antoun, and Young (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, nonverbal 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 a neuroimaging 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 (Wicker, Keysers, et al., 2003). It was found that observing such facial expressions and feelings of disgust activated the same sites in the anterior insula and anterior cingulate cortex (see Figure 2).

By virtue of its aversiveness, pain serves to promote the organism's health and integrity (Williams, 2002). The expression of pain provides a crucial signal, which can motivate helping behaviors in others. One does not feel the sensory aspects of another's pain, but one may understand her distress. Interestingly, a single-neuron recording study in neurological patients has 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, Davis, & Lozano, 1999). Jackson, Meltzoff, and Decety (2004) recently conducted an fMRI study to identify the whole neural network engaged in the perception of pain in other individuals. The participants were shown still photographs depicting right hands and feet in painful or neutral everyday-life situations and were asked to imagine the level of pain that these situations would produce. Significant activation in regions involved in the affective aspects of the pain-processing network—notably, the anterior cingulate cortex and the anterior insula—was detected, but there was no activity in the somatosensory cortex. Moreover, the level of activity within the anterior cingulate cortex was strongly correlated with subjects' mean ratings of pain attributed to the different situations. Another recent fMRI study demonstrated that the anterior cingulate cortex, the anterior insula, cerebellum, and brainstem were activated when subjects experienced a painful stimulus, as well as when they observed another person receiving a similar stimulus (Singer et al., 2004). Again, no activity was detected in the somatosensory cortex during the observation of pain in others. Together, these findings support the idea that part of the neural network mediating pain experience is shared when empathizing with pain in others.

A positron emission tomography study investigated 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 former condition also resulted in activation of the hypothalamus, the amygdala, the anterior temporal cortex, and the occipito-tempo-parietal junction, whereas the latter condition was specifically associated with activation in the anterior insula and orbitofrontal cortex. There is an overlap between externally and internally produced emotions, but this overlap is partial. It should be noted that the films and scripts included three emotions (happiness, sadness, and disgust), which were not analyzed separately.

Another recent neuroimaging study has demonstrated the involvement of shared representations (in both emotion processing areas, and fronto-parietal networks) when subjects feel sympathy for another individual (Decety & Chaminade, 2003a). 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. These stories were told with either congruent or incongruent motor expression of emotion. 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. This network was not activated when subjects watched incongruent social behavior. Indeed, the condition of mismatch between the narrative content of the stories and the motor expression of emotion elicited strong hemodynamic increase in the ventromedial prefrontal cortex and superior frontal gyrus, which are involved in monitoring conflict between expected and actual outcomes (e.g., Fink et al., 1999).

Altogether, shared representations between self and other at the cortical level have been found for action understanding, pain processing, and emotion recognition. This mechanism provides the neurophysiological basis for the operation of social cognition by means of the automatic activation of motor representations or emotions. 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.

SELF-OTHER AWARENESS

The shared-representations mechanism lends credence to the idea that the same representational form is used in coding embedded intentional relations, whether it involves the self as an agent or another agent (Gopnik, 1993). This idea is also consistent with the model stating that human consciousness is formed in the dynamic interrelation of the self and the other and therefore is inherently intersubjective in nature (Thompson, 2001). Knowledge of the self paves the way for achieving an inferential knowledge of the mental states of others. Yet, we do understand that self and other are similar but sep-

arate, and we usually do not confuse first-person knowledge from third-person knowledge.

As suggested earlier, in our model, empathy presupposes self-awareness. 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). 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). It is an adaptive trait that has evolved by natural selection because it confers some advantage on those individuals who possess it (Humphrey, 2002; Mandler, 2002). Moreover, the emergence of a self-representation in psychological development is vital for the empathic process (Lewis, 1999). We do not think that self-awareness relies on a specific brain region. Rather, it arises from the interaction between processes distributed in the brain, especially the prefrontal cortex and the inferior parietal lobule, and in which the right hemisphere plays a prominent role (Keenan, Gallup, & Falk, 2003).

The roots of the self begin early in infancy. Indeed, Gibson (1979) suggested that from birth, infants co-perceive themselves in acting and perceiving their environment. Neisser (1991) proposed this implicit self-knowledge may take two forms: an ecological self, formed through interactions with physical objects and bodily perception, and an interpersonal self, formed through infants' interactions with others.

Infants' representations of self- and other-actions are both overlapping and distinct (Rochat & Striano, 2000). Infants readily distinguish their own actions from those of others early on. For instance, Rochat and Hespos (1997) tested newborn infants within 24 hours of their birth to measure the frequency of rooting in response to either external tactile stimulation (the experimenter stroking the infant's cheek) or in response to tactile self-stimulation when the infants spontaneously brought one of their hands in contact with their cheek. They found that newborns tended to manifest rooting behavior three times more often in response to external compared to self-stimulation, suggesting some level of discrimination between these two sources of stimulation.

The awareness of others develops very early on in conjunction with an awareness of being the object of others' attention. The developmental psychologist Vasudevi Reddy suggested that infants are aware of the directedness of others' attention before evidence of joint attention. This is particularly well documented by the measure of a variety of emotional reaction during the first months (Reddy, 2003). She further argued that the development in awareness of attention during the first 2 years can be explained in terms of an expanding awareness of the objects of attention. Interestingly, measurements of cerebral metabolism in children (aged between 18 days to 12 years) indicate a right hemispheric predominance, which is mainly because of the neural activity in the posterior associative areas, and the fact that its functions develop earlier than the left hemisphere (Chiron et al., 1997). This latter finding led us to speculate that there is a functional relation (anatomically wired) between the parietal cortex and the implicit sense of self that infants manifest from birth. In addition, a number of studies have demonstrated that young infants are very sensitive to the contingent relationships between their motor behaviors and consequent stimulus events and that this capacity serves to distinguish the self from the external world (Gergely, 2001; Watson, 1972).

Moreover, infants also form shared representations of their own and others' actions. Asendorpf and Baudonnière (1993) have suggested that self-awareness and other-awareness develop in close synchrony during the 2nd year because both types of cognition are based on one common cognitive capacity: the capacity for secondary representation. Self-awareness requires a capacity for secondary representation because the self as an object of knowledge is a secondary representation. Similarly, other-awareness requires a capacity for secondary representation because other-awareness implies taking the perspective of another person into account. This framework would account for the dramatic increase in children's social-cognitive competence during the 2nd year.

Indeed, over the first several years of life, children acquire knowledge of both objective and subjective aspects of self and others. By 18 to 24 months of age infants begin to recognize their own mirror image, to display self-conscious emotions such as embarrassment or shame (Lewis, Sullivan, Stanger, & Weiss, 1989), to communicate with peers through the synchronic imitation of each other's activity (Asendorpf, Warkentin, Baudonnière, 1996), to cooperate with peers (Brownell & Carriger, 1990), and to react with empathic behavior to victims of distress (Zahn-Waxler, Radke-Yarrow, & King, 1979).

During the preschool years, children simultaneously develop the capacity to represent and report their own and others' mental states (e.g., Meltzoff & Gopnik, 1994). This development entails the ability to recognize when self- and other-perspectives and experiences are shared and thus congruent as well as under which circumstances they differ from one another.

Interestingly, the development of self- and other-mental-state understanding is functionally linked to that of executive functions (Russell, 1996)—that is, the processes that serve to monitor and control thought and actions, including self-regulation, planning, cognitive flexibility, response inhibition, and resistance to inter-

ference (Eslinger, 1996; Shallice, 1988). There is increasingly clear evidence of a specific developmental link between theory-of-mind development and improved self-control at around the age of 4 (Perner & Lang, 1999). Carlson and Moses (2001) have convincingly documented how executive functions, especially inhibitory control, play a crucial enabling role in both the emergence and expression of children's mental-state attribution. Furthermore, it has been demonstrated that the development of cognitive control is related to the maturation of the prefrontal cortex (Tamm, Menon, & Reiss, 2002). Bunge, Dudukovic, Thomason, Vaidya, and Gabrieli (2002) investigated interference and response inhibition with fMRI in children (ages 8 to 12) and adults. They found that children were more susceptible to interference and less able to inhibit inappropriate responses than were adults and that different brain regions were recruited between the two groups. Notably, the response inhibition in children was not associated with the right ventrolateral prefrontal cortex as it was in adults.

This is not to suggest that executive functioning can be equated with theory of mind. There is some evidence from neurological case studies indicating that theory of mind is dissociable from executive functioning (Blair & Cipolotti, 2000; Fine, Lumsden, & Blair, 2001; Lough, Gregory, & Hodges, 2001). In addition, executive function is a much broader construct than theory of mind (see the next section, Mental Flexibility and Self-Regulation).

In addition, there is evidence that a region around the paracingulate sulcus in the medial prefrontal cortex plays a specific role in attribution of intention (for a recent review, see Gallagher & Frith, 2003). 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, Hakeem, Erwin, Nimchinsky, & Hof, 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 (Baron-Cohen et al., 1999; Wicker, Perret, Baron-Cohen, & Decety, 2003), detecting the intention in simple dynamic animations (Castelli, Happé, Frith, & Frith, 2000), attributing intention to cartoons characters (Brunet, Sarfati, Hardy-Baylé, & Decety, 2000; Gallagher et al., 2000), comprehending stories (Fletcher et al., 1995; Vogeley et al., 2001), detecting social transgression (Berthoz, Armory, Blair, & Dolan, 2002), and appreciating humor (Goel & Dolan, 2001). It is also interesting that this region is not activated by individuals with mentalizing impairments, such as schizophrenics (Brunet, Sarfati, Hardy-Baylé, &

Decety, 2003) and high-level, functioning autistic individuals (Happé et al., 1996).

It is thus possible that executive functions are crucial for the development of theory of mind and that this latter process is specific and has a dedicated neural underpinning. Future research is needed to elucidate the functional relation between executive functions and mentalizing and how each can be fragmented into subcomponents with their respective neural implementation. For instance, Gallagher and Frith (2003) suggested that the activity in the medial prefrontal cortex occurs when cues are used to determine an agent's mental state that is decoupled from reality and to simultaneously handle these two perspectives on the world.

Neuropsychological research supports a preeminent role of the right frontal lobe in self-related processing. For instance, Keenan and his group (Keenan, Nelson, O'Connor, & Pascual-Leone, 2001) demonstrated that patients undergoing a Wada test were temporarily desensitized with regard to the recognition of their own faces when the right hemisphere was anesthetized. This was not the case when the left hemisphere was anesthetized. Right hemisphere damage is also found to be linked with impairments in autobiographical memory and self-evaluation. 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). Finally, severe deficits in personal autobiographical memory retrieval are also associated with damage to the right ventral prefrontal region (Levine et al., 1998).

Using fMRI measurements of subjects who were asked to categorize pictures of their own faces, Keenan, McCutcheon, and Pascual-Leone (2001) reported selective activation of the right inferior frontal gyrus on the border of the medial frontal gyrus. Fink et al. (1996) found activation of a right hemispheric network of temporomesial (including the amygdala and hippocampus), posterior cingulate, prefrontal right insula, and prefrontal regions during presentation of personal autobiographical memories versus impersonal statements. Two functional imaging studies have reported specific increase in activity in the medial prefrontal cortex and posterior cingulate during tasks that involved self-reflection (Gusnard, Akbudak, Shulman, & Raichle, 2001; Johnson et al., 2002).

Based on these numerous studies (and many others not reviewed here), Keenan et al. (2003) reasonably argued that the right hemisphere is a key player in self-awareness and mental-state attribution. Note that their original 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 distin-

guish between representations activated by the self and those activated by other (see Jackson & Decety, 2004). Yet, we have seen in the work reviewed above that the neural networks underlying self-processing and other-processing have some common components and some independent ones.

An influential cognitive-developmental model proposes that individuals represent their own (first-person knowledge) and others' activities (third-person knowledge) via a single conceptual system (Barresi & Moore, 1996). These authors also suggest that whenever an action is taking place, it activates an intentional schema, a structure internal to every person involved in that action. The intentional schema has the capacity of coordinating first- and third-person information; according to the input signals available, the action is attributed to the self or to the other person. Jeannerod (1999) suggested that conscious agency judgments are not directly based on explicit knowledge of the stimuli (external or internal) that have triggered the action or on the signals generated during its execution. Rather, several levels of processing are needed so that the level used for execution is distinct from the level of the conscious representations.

At the neural level, neuroscience research indicates that the right inferior parietal cortex in conjunction with prefrontal areas may be critical in distinguishing the self from the other and therefore navigating shared representations (Figure 2). 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). These multiple connections confer on this region a role in the elaboration of an image of the body in space and in time (Benton & Silvan, 1993) on which the sense of agency depends (see Gallagher, 2000, for a theoretical account about the sense of agency). Interestingly, not only the prefrontal but also the inferior parietal and temporo-parietal areas have evolved tremendously in humans as compared to nonhuman primates (Passingham, 1998).

Accumulating empirical evidence indicates that the parietal cortex plays a major role in the sense of agency— that is, in distinguishing between self-produced actions and actions generated by others (Blakemore & Frith, 2003; Jackson & Decety, 2004, for reviews). For instance, Farrer and Frith (2002) scanned individuals while watching a moving dot on a computer screen. In some trials, the participants were in control of the dot's movements, whereas in other trials, someone else controlled the dot. They found increased activity in the right inferior parietal cortex when the dot was controlled by the other, and
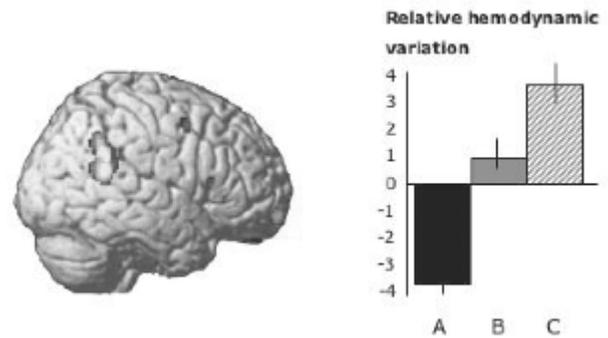

Figure 3: **Right inferior parietal lobule activation at the junction of the temporal cortex superimposed on a rendered MRI from the Montreal Neurological Institute. In this study, participants were scanned during a variety of object-directed actions, including self-action (A), imitation of actions demonstrated by an experimenter (B), and observation of their actions being imitated by the experimenter (C). Note the dramatic increase in this region in this latter condition.**
SOURCE: Adapted from Decety et al., 2002.

increased activity in the anterior insula when the dot was controlled by the self.

Another neuroimaging study varied the degree of concordance of the visual feedback provided to the participants about their movements with a joystick (Farrer et al., 2003). Activation of the right inferior parietal lobe was found to inversely correlate with the subjective sense of ownership in action execution; the more discordance between what the subjects did and what they saw, the more there was increase in this region. Similarly, activation in the right inferior parietal lobe was found in a reciprocal imitation paradigm when participants were aware (and observed) that their actions were being imitated online by another person (Chaminade & Decety, 2002; Decety et al., 2002; see Figure 3). The right inferior parietal cortex is also involved when subjects mentally simulate the actions of another person (Ruby & Decety, 2001). There are new findings suggesting that this mechanism is also at play during thinking about others. It has been demonstrated that when subjects are asked to adopt another person's perspective to evaluate their beliefs or imagine their feelings as compared to their own perspective, the right inferior parietal cortex is strongly involved (Ruby & Decety, 2003, 2004). Finally, an fMRI experiment recently demonstrated that the neurodynamic activity starts earlier in a number of cortical regions involved in motor control when participants made judgments about their own actions versus those of others (Grèzes, Frith, & Passingham, 2004). This latter finding shows 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. It can also be conjectured that the latency difference between the changes in activity elicited by the percep-

tion of self versus others' actions reflects the calibration process of shared representations. 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.

Importantly, it has been reported that some patients with right parietal lesions exhibit a denial of hemiplegia that extended to the motor deficits of other patients (Ramachandran & Rogers-Ramachandran, 1996). This suggests that availability of an efficient body schema is necessary not only for recognizing one's own actions but also for understanding the actions of others. We suggest that the inferior parietal cortex in conjunction with the prefrontal cortex plays a pivotal role in the sense of self by comparing the source of sensory signals. Such a role is crucial for empathy to maintain a distinction between the self and the other and keep track of the origin of the feelings.

MENTAL FLEXIBILITY AND SELF-REGULATION

Empathy may be initiated by 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 television report. However, in these conditions, empathy requires one to adopt more or less consciously the subjective point of view of the other. A more obvious instance is when a psychotherapist adopts the mental world of his client.

Perspective taking is acknowledged as an important source of human empathy (Batson, 1991a, 1991b; Batson et al., 2003; Eisenberg, Shea, Carlo, & Knight, 1991). Comparative studies performed with nonhuman primates and children seem to show that only the latter are able to adopt the point of view of another individual (Reaux, Theall, & Povinelli, 1999). Tomasello (1999) argues that this ability sets us apart from other primates and is an integral element in intersubjective communication.

An experiment by the social psychologist Ezra Stotland (1969) illustrates the effect of perspective taking to generate empathy. In his experiment, the participants watched someone else whose hand was strapped in a machine that they were told generated painful heat. One group of subjects was told just to watch the target person carefully, another group of subjects was asked to imagine the way the target was feeling, and one more group was told to imagine themselves in the target's place. Both physiological (i.e., palm sweating and vasoconstriction) and verbal measures of empathy showed that the deliberate acts of imagination produced a

greater response than just watching. Batson and his group conducted a variety a studies that demonstrate the effectiveness of perspective-taking instructions in inducing empathy. An important aspect of Batson's theoretical framework is that empathy-inducing conditions do not compromise the distinction between the self and other (e.g., Batson, Sager, et al., 1997, but see Cialdini et al., 1997, for a different account of empathy and self-other merging).

There is plenty of evidence from various disciplines to suggest that the mental flexibility to adopt someone else's point of view is an effortful and controlled process. In addition, the ability to take the conceptual perspective of the other is considered an indispensable element in the fully developed, mature theory of mind. Developmental research also indicates that perspective-taking ability develops gradually. In the affective domain, it is around 18 months that children demonstrate an emerging awareness of the subjectivity of other people's emotions. By that age, infants even seem to understand, for instance, that they should give an experimenter a piece of food that the experimenter reacts to with apparent happiness (e.g., broccoli) rather than one toward which the experimenter acts disgusted (e.g., cookies), even when they prefer the latter food; in contrast, 14-month-olds do not show this understanding (Repacholi & Gopnik, 1997). This finding appears to be the first empirical evidence that infants of this age have at least some limited ability to reason nonegocentrically about people's desires (Flavell, 1999).

This does not mean that adults reliably (and spontaneously) use the ability to adopt the perspective of others when reasoning about them. Indeed, even adults frequently make a less sharp distinction between what they know, or believe they know, and what they assume others do. Realizing that another can have a perspective that differs from one's own does not necessarily entail being able to adopt that perspective. A series of experiments performed by Keysar, Lin, and Barr (2003) revealed that adult subjects exhibit a tendency to infer that others have the same knowledge (and beliefs) as they do, even when they are aware that the others have a different point of view.

Several social and developmental psychologists have suggested, and documented through empirical work, that our default mode to reasoning about others is biased toward self-perspective, and this is a general feature of human cognition. Stated in other words, people are fundamentally egocentric and have difficulty getting beyond their own perspective when anticipating what others are thinking or feeling (Royzman, Cassidy, & Baron, 2003). For instance, humans have the tendency to believe that their actions and appearance are more likely to be noticed, judged, and remembered by others
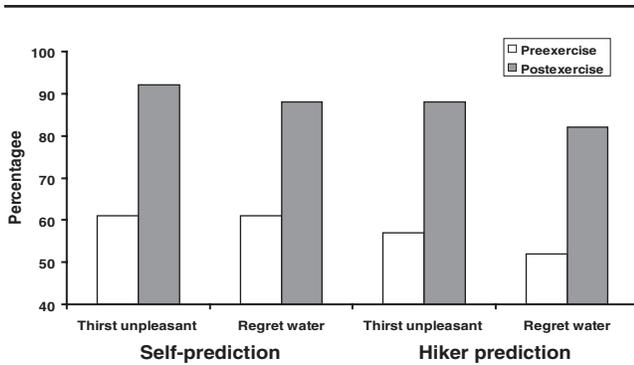
Figure 4: **In this study, participants were asked to predict the feelings of people in a situation that aroused drive states (three hikers lost in the woods with neither food nor water for several days). Participants made these predictions either immediately before or immediately after engaging in vigorous cardiovascular exercise, which made them thirsty and warm. The graph shows the percentage of participants before and after exercising who indicated that they and the lost hikers would be more bothered by thirst than hunger and would regret not bringing water more than food.**

SOURCE: Van Boven & Loewenstein, 2003 (reprinted with permission).

than is actually the case (Gilovich, Kruger, & Medvec, 2002). Humans are also inclined to impute their own knowledge to others and overestimate what they know (Nickerson, 1999). Recent research indicates that people's predictions of the feelings of others who are in a situation that arouses drive states (i.e., motivations caused by bodily needs such as exhaustion, hunger, and thirst) are based largely on their predictions of how they would feel in that situation. Van Boven and Loewenstein (2003) showed that people project their current drive states (i.e., motivations caused by physiological needs such as exhaustion, hunger, and thirst) when predicting how they and how other people would feel in a situation that arouses drive states (see Figure 4). It has been proposed that errors in such appraisal are rooted in a lack of suppression of the self-perspective (Hodges & Wegner, 1997; Vorauer & Ross, 1999).

This egocentric bias is also well documented in children. For instance, Taylor, Esbensen, and Bennett (1994) taught 4- and 5-years-olds a novel fact (e.g., that cats use their whiskers to determine whether they can fit in tight places) or told them about a novel process (e.g., how to make litmus paper change color on its own). Children were then asked whether they thought another child who was similar to them would know this fact. The vast majority of the children said that a similar child would also know that fact. Interestingly, this bias can be demonstrated with both children and adults and is found be relatively stable over age (Bernstein, Atance, Loftus, & Meltzoff, 2004).

We argue that the egocentric bias is compatible with the simulation theory, which states that we ordinarily understand and predict the behavior and mental states of others by simulation—that is, by using our own mental resources off-line as if we were in the situation of the other (Goldman, 1989; Gordon, 1986; Harris, 1991, 2000). For Harris (1991), the simulation of the experience of other persons is not a straightforward process, and the child often has to judge the simulation with his or her knowledge of the real situation from a first-person perspective. Consistent with this idea, Perner and Lopez (1997) found that children were better at predicting what another person would see in a particular situation if they had actually been in that situation first themselves.

Furthermore, we speculate that this view is coherent with the shared representations mechanism. One sees others through one's own embodied cognition. One uses one's own knowledge (including beliefs, opinions, attitudes, feelings) as the primary basis for understanding others. As suggested earlier, self-perspective may be considered as the default mode of the human mind because one experiences one's own point of view more directly. It is a very parsimonious and advantageous mechanism to understand and predict the behavior of others. Yet, there is a cost of making inappropriate psychological inferences about others. Many social misunderstandings are rooted in people's failure to recognize and take into account the degree to which their understanding of a situation may differ from those of others (Griffin, Dunning, & Ross, 1990). Flavell (1977) speculated that all people may be at risk for egocentric thinking throughout their life:

> We experience our own point of view more of less directly, whereas we must always attain the other person's in a more indirect manner. Furthermore, we are usually unable to turn our own viewpoint off completely when trying to infer the other's, and it usually continues to ring in our ears while we try to decode the other's. It may take considerable skill and effort to represent another's point of view accurately through this kind of noise, and the possibility of egocentric distortion is ever present. (p. 124)

For successful social interaction, then, and empathic understanding in particular, an adjustment must operate on these shared representations. Indeed, a complete merging or confusion of self- and other-feelings is not the goal of empathy (Batson 1987; Batson 1997; Ickes, 1997, 2003). An essential aspect of empathy is to recognize the other person as like the self while maintaining a clear separation between self and other. Hence, mental flexibility and self-regulation are important components of empathy. One needs to regulate one's own perspective that has been activated by the interaction with the others or even the mere imagination of such an interaction. Such a regulation is also important to modu-

late one's own vicarious emotion so that it is not experienced as aversive. Previous research has shown that emotion regulation is positively related to feelings of concern for the other person (Derryberry & Rothbart, 1988; Eisenberg et al., 1994). In contrast, people who experience their emotions intensely, especially negative emotions, are prone to person distress—that is, an aversive emotional reaction, such as anxiety or discomfort based on the recognition of another's emotional state or condition (Davis, 1983; Eisenberg et al., 1991).

We argue that empathy requires some form of active inhibitory mechanism (i.e., the deliberate suppression of a cognition or response to achieve an internally represented goal [Nigg, 2001]) and the contribution of the prefrontal cortex has an essential role in this regulation process (Fuster, 1989). A "self-regulatory disorder" has been coined by Levine and colleagues (Levine, Freedman, Dawson, Black, & Stuss, 1999) for the syndrome exhibited by these 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. 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. This may consequently lead to deficit of empathy (see also section titled The Lack of Empathy).

An association between executive functions and social competence has been shown by using self-report inventory in neurological patients with prefrontal cortex lesions (Grattan & Eslinger, 1989). Moreover, Rowe, Bullock, Polkey, and Morris (2001) tested neurological patients with unilateral frontal lobe lesion on theory of mind tasks as well as executive function tasks. They found that both patient groups exhibited significantly impaired performance on their ability to infer first- and second-order beliefs. Both frontal lobe groups also exhibited a range of deficits in tests of executive functions, but analyses revealed that these seemed to be independent of theory-of-mind impairments. A major study with frontal lobe patients with limited focal lesions tested for visual perspective taking and detecting deception (Stuss, Gallup, & Alexander, 2001). The authors reported dissociation of performance within the frontal lobes. Right frontal lobe lesions were associated with impaired visual perspective taking, and medial frontal lesions, particularly right ventral, with impaired detection of deception.

A series of three neuroimaging studies performed by our group 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 imaging the experimenter doing 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 network corresponds to the shared motor representations between the self and the other. Taking the perspective of the other to simulate his or her 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). Although not statistically significant, there was a tendency for response times to be slightly greater when the participants answered the question with the perspective of another person. 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 are emotionally neutral (Ruby & Decety, 2004). They were asked to imagine how they would feel if they were in those situations, and how their mother would feel in those situations. The mother was chosen as the target of empathy because she was the participants' best known person. Like in the previous experiment, a slight increase in the response times was observed when participants imagined the reaction of their mother elicited by neutral situations as compared to their own reactions. Reaction times were statistically greater when the subjects imagined emotional-laden situations, both from their own perspective and the perspective of their mothers. Activation was 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. The amygdala is acknowledged to be critical for normal judgments about the internal states of others (Adolphs, 2003). It is thus

Figure 5: Brain regions (frontopolar, medial prefrontal/anterior paracingulate, and posterior cingulate cortices) found activated when subjects overtly adopt the perspective of another individual versus self-perspective. The activated clusters, represented by yellow circles, are superimposed onto an MRI sagittal section. Numbers correspond to condition in which participants imagined actions (1: Ruby & Decety, 2001), knowledge (2: Ruby & Decety, 2003) or feelings (3: Ruby & Decety, 2004). Hemodynamic changes in these areas are more pronounced in the right hemisphere.

really interesting to detect its activation for both self and other imagined emotional reactions.

In a recent fMRI study, Seger, Stone, and Keenan (2004) asked participants 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.

One of the most striking findings of this series of studies that investigated self- versus other-perspective is the systematic involvement of the frontopolar cortex, medial prefrontal cortex, and posterior cingulate when the participants adopt the perspective of another person (see Figure 5).

Converging evidence from clinical neuropsychology (e.g., De Renzi, Cavalleri, & Facchini, 1996; Verfaellie & Heilman, 1987) and neuroscience (e.g., Brass, Zysset, & von Cramon, 2001; Fuster, 1989) points to the frontopolar cortex as being chiefly involved in inhibitory or regulating processing. Frontal damage may result in impaired perspective-taking ability (Price, Daffner, Stowe, & Mesulam, 1990) and a lack of cognitive flexibility (Eslinger, 1998). Interestingly, Anderson, Bechara, Damasio, Tranel, and Damasio (1999) reported the cases of two patients with early damage to the anterior prefrontal cortex (encompassing the frontopolar cortex

but not the gyrus rectus), who, when tested on moral dilemmas, exhibited an excessively egocentric perspective. The behavior of those patients reveals a lack of inhibition (or modulation) of self-perspective at the conceptual level. Hence, the study of Anderson et al. (1999) provides evidence for the role of the frontopolar cortex in inhibition at both conceptual and social levels. The results of the three neuroimaging studies of perspective taking support the hypothesis of such an inhibitory role of the frontopolar cortex for adopting the subjective viewpoint of others, whether the shared activated representations are motor, conceptual, or emotional in nature. Further support for this claim is provided by two recent fMRI studies in which involvement of the right lateral prefrontal cortex was detected when participants inhibited a prepotent response in a sensory motor task (Bunge et al., 2002) and also in a deductive-reasoning task (Goel & Dolan, 2003).

We argue that this inhibitory component is required to regulate and tone down the self-perspective to allow the evaluation of the other-perspective. This is necessary because the prepotent self-perspective, driven by the automatic link between perception and action, is the default mode, and this regulation allows cognitive and affective flexibility. Such a view is compatible with the role of the prefrontal cortex in top-down control of behavior (Miller & Cohen, 2001). It is also congruent with the empathy-altruism hypothesis, which claims that a distinction between self and other, rather than a merging between them, is required (Batson, 1991b).

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). Adopting the subjective perspective of another individual to understand his or her feelings is a self-generated process that operates on internally represented information fed by the internal activation of shared representations.

Empathy, as presented in our model, necessitates some level of emotion regulation to manage and optimize intersubjective transactions between self and other. Indeed, the emotional state generated by the perception of the other's state or situation needs regulation and control for the experience of empathy. Without such control, the mere activation of the shared representation, including the associated autonomic and somatic responses, would lead to emotional contagion or emotional distress.
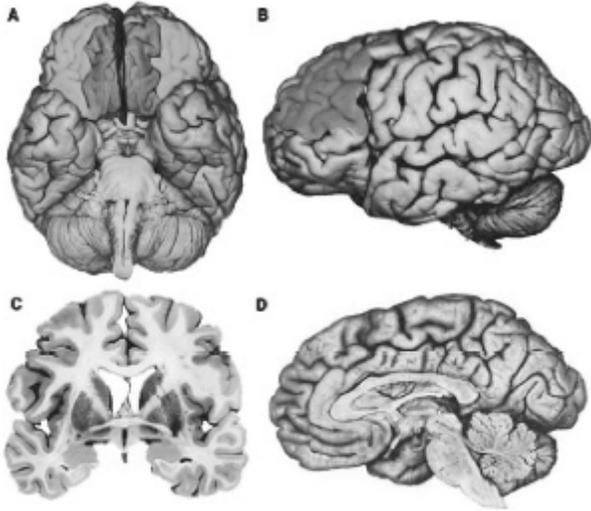
Figure 6: Key structures involved in emotional regulation: orbitofrontal (purple) and ventromedial prefrontal cortex (green) (A), dorsolateral prefrontal cortex (violet) (B), amygdala (orange) (C), and rostral anterior cingulate cortex (yellow) (D).
SOURCE: Davidson, Putnam, & Larson, 2000 (reprinted with permission).

Key structures in the circuitry underlying emotion regulation play an important role in empathy (Figure 6). Among these regions, the orbitofrontal-ventromedial and dorsolateral cortices have been reported in the neurological literature to be implicated in empathy. These two regions have separate anatomical pathways to communicate with subcortical regions and seem to mediate very different processes (Masterman & Cummings, 1997). The orbitofrontal is essential for regulating emotion, and its damage is associated with a wide range of social emotional deficits, including impaired social judgment and disinhibited behavior. 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 a special role in emotion regulation (Davidson, Putnam, & Larson, 2000). Damasio (1994) has proposed that somatic makers (i.e., stored memories of somatic states that are associated with particular experiences or outcomes) are stored in the ventromedial prefrontal cortex. It is likely that the ventromedial region is a crucial component in the neural network underpinning empathy (Shamay-Tsoory, Tomer, Berger, & Aharon-Peretz, 2003). Finally, the anterior cingulate cortex is part of a circuit involved in a form of attention that serves to regulate both cognitive and emotional processing (Bush, Luu, & Posner, 2000). Its lesion produces a host of symptoms, including apathy, inattention, dysregulation of autonomic functions, and emotional instability.

Finally, studies that investigate the cognitive and neural mechanisms involved in affective reappraisal (i.e., the cognitive regulation of social perception and emotional experience; Ochsner, 2004) are relevant to the understanding of empathy. An fMRI experiment has shown neural correlates of emotion reappraisal in the lateral prefrontal and medial prefrontal cortices and decreased activity in the medial orbitofrontal cortex and the amygdala (Ochsner, Bunge, Gross, & Gabrieli, 2002). Similar neural network was identified for voluntary suppression of sadness (Lévesque et al., 2003).

THE LACK OF EMPATHY

Although the loss of empathy has mainly been described after lesion of the frontal lobe, more specifically the prefrontal cortex, our model suggests that there may be distinct disorders related to empathy rather than a unique deficit. Furthermore, since our model assumes that empathy relies on dissociable components, it predicts a variety of structural or functional dysfunctions depending on which aspect is disturbed. We believe that this view is more coherent with the broad range of disorders that are related to empathy and with the multidimensional nature of this behavior. Indeed, we do not think it is reasonable to assume a single source of empathy deficit in very different conditions, such as sociopathy, conduct disorders, narcissistic personality disorder, Asperger's syndrome, stroke, or traumatic brain injury.

It is well accepted that empathic processing may be impaired after focal lesions of the prefrontal cortex (Eslinger, 1998). Patients with bilateral lesions of the orbitofrontal cortex were found to be impaired in the "faux pas" task (Stone, Baron-Cohen, & Knight, 1998). This task requires both an understanding of false or mistaken belief and an appreciation of the emotional effect of a statement on the listener (Baron-Cohen, O'Riordan, Stone, Jones, & Plaisted, 1999). 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, several other patient studies reported a relationship between the deficit in empathy and performance of cognitive flexibility tasks among patients with lesions in the dorsolateral lesions, whereas those with orbitofrontal cortex lesions were more impaired in empathy but not in cognitive flexibility (Grattan, Bloomer, Archambault, & Eslinger, 1994; Shamay-Tsoory et al., 2003). Furthermore, the study by Shamay-Tsoory et al. (2003) demonstrated that among patients with posterior lesions, only those with damage to the right hemisphere (parietal cortex) were impaired in empathy. Another recent study by the same group tested patients with lesions of the

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Box 1.   Measurements Used in the Evaluation of Empathy Ability Across Different Studies (note that this list is not intended to be exhaustive).

- *Emotional attribution task:* The participant is presented with short stories describing emotional situations and asked what the protagonists might feel in those situations (e.g., Blair & Cipolotti, 2000).
- *Faux pas task:* The participant is read a story with the occurrence of a faux pas and asked if she or he detected the faux pas—that is, a socially awkward situation (e.g., Stone, Baron-Cohen, & Knight, 1998).
- *Interpersonal Reactivity Index (Davis, 1983):* The participant is asked to fill in self-report scales that contain a number of items to assess various psychological aspects of cognitive and emotional empathy.
- *Balance Emotional Empathy Scale (Mehrabian & Epstein, 1972):* A 33-item questionnaire targeting emotional empathy.
- *Hogan's (1969) Empathy Scale:* Measures an individual's cognitive ability to understand another's viewpoint using a 64 true-false statements.
- *Measures of autonomic nervous system responses:* Skin conductance, heart rate, heart period, respiration rate are used to monitor the changes during a given task—for instance, watching emotion-laden pictures or listening to short stories (e.g., Blair, 1999; Decety & Chaminade, 2003b).
- *Dyadic interaction (Ickes, Stinson, Bissonnette, & Garcia, 1990):* For instance, after two people have been seated in a "waiting room," their interaction is unobtrusively videotaped. Then, in a second phase, the participants are shown the videotape and asked to report their own thoughts and feelings during the interaction and infer each of their interaction partner's reported thoughts and feelings.
- Behavioral measures in empathy-eliciting situations, such as latency to respond to the feigned distress of another (e.g., Zahn-Waxler, Radke-Yarrow, Wagner, & Chapman, 1992).
- Participants are assigned to groups that differ in terms of perspective-taking instructions (e.g., imagine how the person feels vs. imagine how you would feel in this situation) before watching videotape or listening to an emotionally laden story. Then, they complete reaction questionnaires using Likert-type scales to measure their emotional response to the stimuli (e.g., Batson, 1997).

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ventromedial prefrontal cortex or dorsolateral prefrontal cortex with three theory-of-mind tasks (second beliefs and faux pas) differing in the level of emotional processing involved (Shamay-Tsoory, Tomer, Berger, Goldsher, & Aharon-Peretz, in press). The authors found that patients with ventromedial lesions were most impaired in the faux pas task but presented normal performance in the second-belief tasks. They further argued that 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. Unfortunately, there is no clear indication of the lesion sites in these studies. Also the ventromedial prefrontal region of interest encompasses both the orbitofrontal, the ventromedial, as well as medial aspects (including the paracingulate gyrus). Nevertheless, this study shows that it is possible to distinguish within the same group of patients quite specific deficits of social cognition.

From these patient studies aforementioned, it can be tentatively concluded that different parts of the right prefrontal cortex are involved in the capacity to reason about the feelings of others, including the ability to adopt the perspective of others. It is not yet clear what specific process each subregion subserves. Moreover, as described in Box 1, one of the most challenging limits to comparison between studies of empathy stems from the use of different tools and methods.

Some researchers have theorized that there is a relation between aggressive behavior and a lack of empathy. The tendency to have low concern for the needs of other and the consequences of one's own actions seems to be a common characteristic of disruptive behavior disorders (Zahn-Waxler, Cole, Welsh, & Fox, 1995). A recent study by Gill and Calkins (2003) that examined situational empathy behaviors, including physiological measures in 2-year-olds identified as either high or low in aggressive/ destructive behaviors, produced mixed results that do not fully support prior research.

Empathy deficit in antisocial personality disorder has been suggested to come from a reduced ability to feel other people's emotional state and more so for sadness and fear (Blair, 1995). This deficit has been ascribed to a dysfunction in the amygdala of developmental origin (Blair, 2001). This is also compatible with the fact that individuals with this disorder have generally intact executive functions and can successfully complete theory-of-mind tasks (Hare, 1993). Therefore, their lack of empathy would be related to disrupted affective processing rather than an inability, for instance, to adopt the perspective of others. In fact, people with antisocial personality disorders are probably good at perceiving others' intentions while disregarding the emotional content and may thus take advantage of it. This is precisely what the research of Mealey (1995) suggests. The psychopath cannot simulate emotions he cannot experience and must rely exclusively on cognitive inputs to his theory-of-mind mechanism.

A very interesting single case of acquired sociopathy has been investigated by Blair and Cipolotti (2000). The authors investigated an individual, J.S., with orbito-

frontal cortex and left amygdala damage, with an impressive battery of measures including skin conductance response (SRC), tests of executive functions, emotion recognition, and social cognition tasks. While J.S. showed executive impairments but no reversal learning impairment, he was significantly impaired on most of the social cognition tasks. Notably, he was both impaired in the recognition of emotional expressions (happiness, anger, disgust, and sadness) and in the attribution of emotional states to others (fear, anger, and embarrassment). His ability to attribute mental states to others was preserved. His SRC responses to negative emotional expressions were reduced. Blair and Cipolotti argued that the distinctive features of the acquired sociopathy of J.S. were the result of impairment of a system that responds to angry expressions/expectations of others' anger and that this system is particularly involved in the suppression of socially aberrant behavior.

Antisocial personalities are often reported to perform poorly on neuropsychological tests of executive functioning (e.g., Séguin, Pihl, Harden, Tremblay, & Boulerice, 1995). Executive functions are considered necessary for socially appropriate conduct, and in our model, they contribute to empathy through self-regulation. Morgan and Lilienfeld (2000) conducted a meta-analysis of 39 studies (yielding a total of 4,589 participants) to clarify the relation between antisocial behavior and executive functions. The results of this meta-analysis indicate that there is a robust and statistically significant relation between executive functions and antisocial behavior. The authors were unable to subdivide executive function measure in terms of their associations with different brain regions (e.g., dorsolateral, orbitofrontal) because of the lack of knowledge concerning the neuroanatomical substrates of most executive functions tasks. Interestingly, Blair (1995) proposed that people with antisocial personalities have a disruption of a violence inhibition mechanism that is normally triggered by distress cues of others, and this aspect belongs to executive functioning.

Clinical and forensic research distinguish "affective" or "reactive" aggression, which is a response to physical or verbal aggression initiated by others with violence that is relatively uncontrolled and emotionally charged, from a "predatory" or "instrumental" cold-blooded aggression, which is a controlled, purposeful aggression lacking in emotion that is used to achieve a desired goal (Blair, 2001; Dodge, Lochman, Harnish, Bates, & Petit, 1997). Our model of empathy predicts that the former type of personality would lack executive control (particularly self-control), whereas the latter personality would have some dysfunctions in sharing feelings with others. Interestingly, measurements of glucose metabolism in two groups of affective and predatory murderers have shown that the first group has lower prefrontal activity, and the second group has similar prefrontal activity as compared to controls but lower activity at the subcortical level, including the amygdala (Raine et al., 1998).

Children with autism, a neurodevelopmental disorder, display a broad range of social communication deficits, and most scholars agree that a lack of empathy prominently figures amongst them (Frith, 2001). The underlying cause of the empathy deficit is, however, more controversial. Baron-Cohen, Leslie, and Frith (1985) proposed the hypothesis that the social impairment in autism arises from a failure of a mentalizing mechanism (a theory-of-mind module). Other authors believe that children with autism have a hard time feeling and expressing emotion and that this basic deficit prevents them from engaging in social interactions (e.g., Hobson, 1989). Others still, such as Russell (1996), argue that deficits in executive functions are the major cause for the social/communicative disorders observed in autism. Rogers and Pennington (1991) suggested a cascade model of autism in which the lack of certain aspects of interpersonal development at every previous stage disrupts certain developments in the following stage. These authors view early imitation skills, emotion sharing, and theory of mind as increasingly complex expressions of the ability to form and coordinate certain representations of self and other. These representations are then used to guide the planning and execution of one's own behavior. Finally, Dawson (1991) proposed that autism involves impairment in attentional functioning for social stimuli (e.g., facial expressions, speech, gestures). She hypothesized that because social stimuli are complex, variable, and unpredictable, children with autism have difficulty processing and representing them, and therefore, their attention is not naturally drawn to such stimuli (Dawson, Meltzoff, Osterling, Rinaldi, & Brown, 1998). These different views (imitation/emotions sharing vs. executive functions) are not incompatible with our model of empathy, as it remains possible that empathy deficits in autism are related to disruption of either emotion sharing or mental flexibility/self-regulation components or even both.

When compared with developmentally delayed children, 20-month-old infants with autism were found to be specifically impaired on empathy tasks, joint attention, and imitation (Charman et al., 1997). Imitation deficits have been proposed to explain the difficulty of autistic children in establishing social relationships and identifying with others (Meltzoff & Gopnik, 1993; Rogers, 1999). For instance, a study by Hobson and Lee (1999) demonstrated that autistic children can imitate the goal of actions displayed by an experimenter but that they failed to imitate the affective style with which the actions were

carried out. This suggests that these children cannot readily adopt the experimenter's perspective entirely. It has also been demonstrated that long before children with autism show theory-of-mind deficits, they show deficits in joint attention and attention monitoring (Osterling & Dawson, 1994). A study examined 30- to 70-month-old autistic and normal children's social behavior, affect, and use of gaze during naturalistic interactions with their mothers (Dawson, Hill, Spencer, Galpert, & Watson, 1990). Both autistic and normal children responded with smiles more frequently to social events than to nonsocial events. However, when autistic children's responses to the mother's smiles were examined, the authors found that they never smiled in response to the mother's smile. In other words, they do not exhibit the biologically based ability to respond empathically to others (Hobson, 1989).

Several studies have examined behavioral and autonomic responses of children with autism who look at adults depicting facial emotional expressions (see Blair, 2003, for a critical review). Although most studies report that children with autism look less frequently at the adult faces than control subjects in empathy-eliciting situations, the remaining findings are equivocal. For instance, one study did not find a reduction of heartbeat rate during the observation of someone in distress (Corona, Dissanayake, Arbelle, Wellington, & Sigman, 1998). Another study has shown that the autonomic responses of these children change according to the distress of the target, if the emotions displayed are not ambiguous and if they are presented under conditions with reduced distraction (Blair, 1999). Moreover, and contrary to what is often claimed, children with autism can make moral/conventional distinction (Blair, 1996). It is likely, however, that these children present a difficulty in taking the perspective of others, which requires executive resources, but they seem to have the physiological substrate to display affective sharing abilities. Altogether, both impairment in executive functions and emotion sharing may account for the empathy deficit in autism.

FUTURE DIRECTIONS

Given the complexity of human empathy, many areas of research and theory are necessary for its understanding, including evolutionary psychology, comparative psychology, developmental science, social psychology, neuropsychology, and cognitive neuroscience. Each discipline contributes valuable information, especially if the data can be integrated into a functional model.

Is it possible to identify at the computational level primitive constructs that are recruited in empathic understanding? Psychological models use hypothetical representations and processes that operate on those representations. What is the psychological reality of the constructs people employ to account for empathy? A construct is composed of process and representation working together to serve a particular function (Willingham & Dunn, 2003). Self-awareness, executive functions, theory of mind, affective reappraisal, and perspective taking are all psychological constructs, but none of these constructs can be described as a primitive one. They further need to be reduced, and each is likely to be implemented by a complex neural machinery. Thus, as stated by Cacioppo et al. (2003), the most powerful tool in achieving sound social neuroscience research remains the expertise, intelligence, and creativity of the investigators and not a higher field strength magnet.

One important theoretical aspect is whether there is partial overlap between theory-of-mind and empathic-understanding processes. Should these two psychological constructs be separated—one for emotion and affect processing and the other for other mental-states attribution? Most neuroimaging studies using theory-of-mind tasks have detected specific activation in the medial prefrontal cortex around the paracingulate sulcus (Gallagher & Frith, 2003; Happé, 2003, for recent reviews). Our model of empathy includes explicit processing of the mental states of self and others and thus requires anterior cingulate computing resources similar to that of mentalizing tasks. Conversely, Farrow and colleagues (2001) argued from the results of an fMRI study in which subjects were required to predict and experience the emotions of others, the neural basis of empathy is distinct from that subserving inference of other's intentions. It is therefore an important task in the future to explore the respective computational role of every key region of the prefrontal cortex (including the medial prefrontal cortex, the anterior paracingulate sulcus, and the ventromedial prefrontal cortex) in mental, affective state attribution, as well as in executive functions, in relation to how humans navigate the social world. Passingham, Stephan, and Kötter (2002) have argued that each cytoarchitectonic area has unique patterns of cortico-cortical connections that determine its function, and differences in neural activity during distinct tasks are produced by distributed subsystems of brain regions. Even though there is massive parallel processing, the temporal dynamics of activation in these regions are also an important aspect to be investigated further.

Another interesting issue is whether there are gender differences in empathy. If so, are they learned or related to hormonal and innate differences in the way our brain is shaped? The work in social psychology, although not entirely conclusive, has seriously questioned the alleged female-superiority in empathic understanding, suggest-

ing motivational differences between the genders instead (Ickes, 2003). But perhaps certain, more specific differences are biologically based, as suggested by the results of a recent fMRI study that investigated neural response in men and women to infant crying and laughing and showed significant differences between the two groups (Seifritz et al., 2003). Women but not men, independent of their parental status, showed neural deactivation in the anterior cingulate cortex in response to infant crying and laughing. In addition, the response pattern in the amygdala and interconnected limbic structures changed fundamentally with parental experience in both men and women. Nonparents showed stronger activation from laughing, whereas parents showed stronger activation for crying. These results seem to demonstrate that the emotion-sharing component may be subjected to personal experience and/or emotion regulation is prepared biologically different in men and women.

Some people have greater empathic ability than others, as demonstrated by the work of Marangoni, Garcia, and Ickes (1995) and Ickes et al. (2000). Could these differences be related to individual differences in personality traits, and how do they fit into this multicomponent model of empathy? Can social neuroscience help to better understand the origins of these individual differences? An interesting and testable personality difference related to emotion regulation is that of temperament. It is a moderately stable psychological profile in quality and intensity of emotional reaction, attention, and self-regulation under some genetic constraints that emerges during childhood (Kagan, 1998; Rothbart & Bates, 1998). In addition, research with adults shows that there are a number of different strategies people use to regulate emotion. For example, reappraisal and suppression are both effective ways to regulate emotion, but they have quite distinct mechanisms and side effects. In general, these strategies can be classified as being either response focused or antecedent focused (Gross, 2001). How do these different strategies modulate empathy, and how are they expressed in the nervous system?

Lesion studies are needed to further elucidate a causal role of any given structure in the neural systems involved in empathy. Nonetheless, it is not easy to evaluate empathic disorder in clinical settings, and often patients with different etiologies are pooled into separate groups provided that their lesions fall into a predefined category. If possible, more discrete subdivision of the prefrontal cortex is necessary because each subregion is likely to play a specific role in empathy behavior. For instance, ventromedial, orbitofrontal, and medial prefrontal cortices subserve distinct functions in social-emotional cognition. Also, too often, empathy abilities in patient populations are measured only with self-report and rating inventories. A combination of physiological measures and empathy-eliciting tasks would provide deeper knowledge into the mechanisms of this behavior.

Finally, of special interest will be the understanding of what motivates us to feel empathy in the sense of caring for the other (see Batson et al., 2003). Indeed, empathy is a motivated behavior and does not so often get automatically triggered. Most of the time, this behavior is regulated by top-down processing involving cultural values, concepts, and the like. For instance, although a large number of people were apparently devastated by the Challenger disaster and expressed a lot of sympathy (especially for the children who witnessed the dramatic death of their school teacher), it seems that fewer people have expressed concern for the 800,000 individuals, including newborns, that have been slaughtered in the 1994 Rwanda genocide. Is it a matter of psychological identification or just a difference as the result of a disparity in media coverage? It is certainly easier to identify with one individual than with many. This idea is supported by the findings that judgments in response to personal moral dilemmas compared with impersonal ones involve greater activity in brain areas associated with emotion and social cognition (Greene, Sommerville, Nystrom, Darley, & Cohen, 2001). But is this the sole explanation of such an asymmetry between the reactions to those dramatic events, knowing that beliefs, opinions, suppositions, attitudes, cultural norms, and related states of mind have a top-down modulatory influence on empathic processing? For instance, Nelson and Baumgarte (2004) have shown that individuals experience less emotional and cognitive empathy for a target experiencing distress stemming from an incident reflecting unfamiliar cultural norms and that this reduction of empathy is mediated by a lack of perspective taking on the part of the observer. These findings suggest that modulatory mechanisms incorporate internal representations of prior experience as well as similarity between self and other.

CONCLUSION: EMPATHY BEYOND MENTAL SIMULATION OF THE SUBJECTIVITY OF THE OTHER

The way our nervous system is organized and tailored by evolution provides the basic mechanism for resonating with others, as well as the capacity to simulate our own actions, their consequences, and also the actions of others (Jackson & Decety, 2004). This shared-representations mechanism (i.e., distributed neural patterns temporarily activated by actual perception or evoked from memory), driven by the common coding between perception and action, provides the default

mode of self-processing (or tendency) to relate implicitly to others. Humans come prepared with the innate motivation to seek engagements of conspecifics and implicitly learn that others are similar to themselves (Meltzoff, 2002). It is through bodily activity that one first grasps the presence of others and then gains insight into their subjective lives (Gallagher, 2001). It is thus not productive to disentangle cognition and affects from actions.

We argued that the shared-representations mechanism is responsible for the human projective tendency, which needs to be regulated (or calibrated) when sharing emotions or when adopting the perspective of others to understand their feelings. This requires additional processing mechanisms, including monitoring and manipulation of internal information generated by the activation of the shared representations.

One of the main components of empathy is based on a mental simulation of the subjectivity of others, which can be initiated in two ways: automatically or intentionally. The idea of an unconscious and automatic simulation is far from new (see Gallese, 2001; Gallese & Goldman, 1998; Goldman, 1993). For instance, Lipps (1903) suggested that an involuntary, instinctual, "kinesthetic" imitation of the observed vital activity of another occurs in empathy. When empathy produces this "physical mimicry" in the spectator, the intentional focus does not remain on the spectator's body but is projected into the other. Later, Ax (1964) suggested that empathy might be thought of "as an autonomic nervous system state, which tends to simulate that of another person." In psychoanalysis, 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. This 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). This view was further developed by Levenson and Ruef (1992), who 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 idea that the knowledge about emotions expressed by others relies on a simulation of how the emotion would feel in the perceiver was also proposed by Damasio (1994, 2003). The presumed mechanism for such a simulation involves an internal brain simulation that consists of rapid modification of ongoing body maps. The discovery that the somatosensory cortex is involved in the recognition of emotions provided the first direct evidence in favor of such an unconscious simulation process (Adolphs et al., 2000). Recently, Goldman and Sripada (in press) have provided several detailed cognitive models for a simulational approach to face-based emotion recognition marshaling neurological evidence for paired deficits between emotion production and emotion perception.

However, this simulation is not exclusively under automatic management, and it falls, at least in humans, under conscious control. This makes empathy, as described here, an intentional capacity. In many cases, the outcome of the simulation mechanism is not empathic feeling. In addition, without self-awareness and emotion-regulation processing, there is no true empathy. Indeed, the activation of shared representations would lead to anxiety or discomfort. This formulation is consistent with the observation that prosocial behaviors, which stem from empathy, emerge in parallel with self-conscious emotions. These emotions require self-evaluation and comparison with other selves, as well as some form of regulation.

Forming an explicit representation of another person's feeling as an intentional agent therefore necessitates additional computational mechanisms beyond the shared representation level. This requires that second-order representations of the other are available to the consciousness (a decoupling mechanism between first-person information and second-person information), for which the anterior paracingulate cortex plays a unique function (Frith & Frith, 2003). Thus, empathy is not a simple resonance of affect between the self and other. It involves an explicit representation of the subjectivity of the other. It is a consciously experienced phenomenon. Recent neuroimaging investigations of the perception of pain in others support such a view (Jackson et al., 2004; Morrison, Lloyd, di Pellegrino, & Roberts, in press; Singer et al., 2004). All these studies have shown that only part of the network mediating pain experiences (including the anterior cingulate cortex and the insula) is shared when empathizing or evaluating the pain in others. Most importantly, 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. Once again, we do not assume that there is a unitary empathy system (or module) in the brain. Rather, we consider multiple dissociable systems to be involved in the experience of empathy.

Finally, as suggested earlier, empathy is a motivated process that more often than commonly believed is trig-

gered voluntarily. This makes empathy a flexible human capacity as well as a method of gaining knowledge of understanding another, and it is susceptible to social-cognitive intervention, such as through training or enhancement programs for targeting various goals (e.g., reeducation of antisocial personalities, training of psychotherapists or physicians, and training early at-risk-children).

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