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Review

The neuronal basis and ontogeny of empathy and mind reading: Review of literature and implications for future research

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Abstract

Social neuro-science has recently started to investigate the neuronal mechanisms underlying our ability to understand the mental and emotional states of others. In this review, imaging research conducted on theory of mind (ToM or mentalizing) and empathy is selectively reviewed. It is proposed that even though these abilities are often used as synonyms in the literature these capacities represent different abilities that rely on different neuronal circuitry. ToM refers to our ability to understand mental states such as intentions, goals and beliefs, and relies on structures of the temporal lobe and the pre-frontal cortex. In contrast, empathy refers to our ability to share the feelings (emotions and sensations) of others and relies on sensorimotor cortices as well as limbic and para-limbic structures. It is further argued that the concept of empathy as used in lay terms refers to a multi-level construct extending from simple forms of emotion contagion to complex forms of cognitive perspective taking. Future research should investigate the relative contribution of empathizing and mentalizing abilities in the understanding of other people's states. Finally, it is suggested that the abilities to understand other people's thoughts and to share their affects display different ontogenetic trajectories reflecting the different developmental paths of their underlying neural structures. In particular, empathy develops much earlier than mentalizing abilities, because the former relys on limbic structures which develop early in ontogeny, whereas the latter rely on lateral temporal lobe and pre-frontal structures which are among the last to fully mature.

Keywords: Social neuro-science; Theory of mind; Empathy; Pain; mPFC; Insula; ACC; Emotional processing

Contents

1. Introduction

Humans are intensely social creatures and one of the major functions of our brains is to enable us to interact successfully in social groups. One crucial capacity for successful interaction is our ability to understand other

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people and to predict their actions. Social cognitive neuroscience (Adolphs, 1999, 2003; Blakemore et al., 2004; Ochsner and Lieberman, 2001; Frith and Wopert, 2004) has recently started to provide insights into the neural mechanism underlying our capacity to represent others people's intentions and beliefs (referred to as "theory of mind" ToM or "mentalizing"), and the capacity to share the feelings of others (referred to as "empathy"). In everyday language as well as in the literature the terms empathy, perspective taking and ToM are often used as synonyms. Sometimes the term empathy is further differentiated by dividing it into two subcomponents, emotional and cognitive empathy. Indeed, at first glance these concepts are difficult to differentiate because they share similar features. Thus all these concepts refer to our ability to put ourselves in the shoes of another person, be it in their mental or emotional shoes. In the present paper the suggestion is made that the capacities to mentalize and to empathize are distinct and rely on different neuro-cognitive circuits. More specifically, it is argued that the process of mentalizing refers to the attribution of propositional attitudes to another person, that is, the attribution of desires, beliefs and intentions. For reasons of simplicity, the term "propositional attitude" will be sometimes replaced by the term "mental states", although the reader has to keep in mind that mental states could in principal also include feeling and emotional states. In the present paper we use the term "empathizing" to refer to the process which allows us to experience what it feels like for another person to experience a certain emotion or sensation (e.g., qualia). The capacity to understand other people's emotions by sharing their affective states is fundamentally different in nature from the capacity to mentalize. Thus, sharing the grief of a close friend feels fundamentally different than understanding what this person is having as thoughts and intentions, the latter lacking a bodily sensation.

First a short summary of the major findings of imaging studies in three interrelated but separate research streams will be provided: the neural basis of mentalizing, motor action imitation and empathizing. Then future directions for the study of empathizing and mentalizing will be discussed, focusing on how these abilities can be differentiated with regard to their relative contribution to the understanding of other people's mental and emotional states. Finally, possible implications of the outlined neuroscientific evidence for developmental science will be discussed. Specifically, it is suggested that our ability to reflect upon others and our ability to share their feelings should display different ontogenetic trajectories reflecting the differential development of the underlying brain structures.

2. Mind reading

For two decades now, research in developmental psychology, social psychology and cognitive neuro-science has focused on the human ability to have a "ToM" (Premack and Woodruff, 1978) or to "mentalize" (Baron-Cohen et al., 2000; Frith and Frith, 2003), that is, to make attributions about the propositional attitudes (desires, beliefs, intentions) of others. This ability is absent in monkeys and only exists in a rudimentary form in apes (Povinelli and Bering, 2002). Wimmer and Perner (1983) developed a new paradigm to study the ability to mentalize in children. In this so-called false-belief task a story is told which goes like this: Maxi has some chocolate and puts it into a blue cupboard. Maxi goes out. Now his mother comes in and moves the chocolate to a green cupboard. Maxi comes back to get his chocolate. Where will Maxi look for the chocolate? The answer can be given simply by pointing: Maxi will look in the blue cupboard because this is where he falsely believes the chocolate to be. Control questions checked that the child understood the sequence of events: Where is the chocolate really? Do you remember where Maxi put the chocolate in the beginning? A series of subsequent studies established that children from around age 4 but not before begin to understand this scenario and can verbally explain it when asked. At age 5, over 90%, and at age 6 all children could understand the task (Baron-Cohen et al., 1985; Perner et al., 1987). Other researchers used variants of this task with essentially similar results. Studies were also carried out in other cultures indicating the universality of this clear developmental phenomenon (Avis and Harris, 2005). Note, however, that Clements and Perner (1994, 2001) were able to show that the false-belief scenario with Maxi and the chocolate is already understood by 3-year-old children when the task is transformed into a little play and eye-gaze is measured instead of verbal report.

Research in the domain of psycho-pathology demonstrated that the explicit attribution of mental states such as false beliefs is severely delayed in autism. The lack of a ToM in most autistic children could explain their observed failures in communication and social interaction (Baron-Cohen et al., 1985, 2000; Frith, 2003).

Recent imaging studies on normal healthy adults have focused on the ability to "mentalize" and have used stories, cartoons, picture sequences and animated geometric shapes which differed in the degree to which they represented the intentions, beliefs and desires of others (for a review, see Gallagher and Frith, 2003). Other studies, for example, involved the brain imaging of subjects while they played strategic games (McCabe et al., 2001; Gallagher et al., 2002; Rilling et al., 2004) with another partner or alternatively with a computer outside the scanner room. All these studies have repeatedly given evidence for the involvement of three brain areas: the temporal poles, the posterior superior temporal sulcus (STS) and most consistently an area in the medial pre-frontal lobe (mPFC) which is illustrated in Fig. 1. This area has not only been found to be involved when mentalizing about the thoughts, intentions or beliefs of others but also when people are attending to their own mental states (Mitchell et al., 2005).

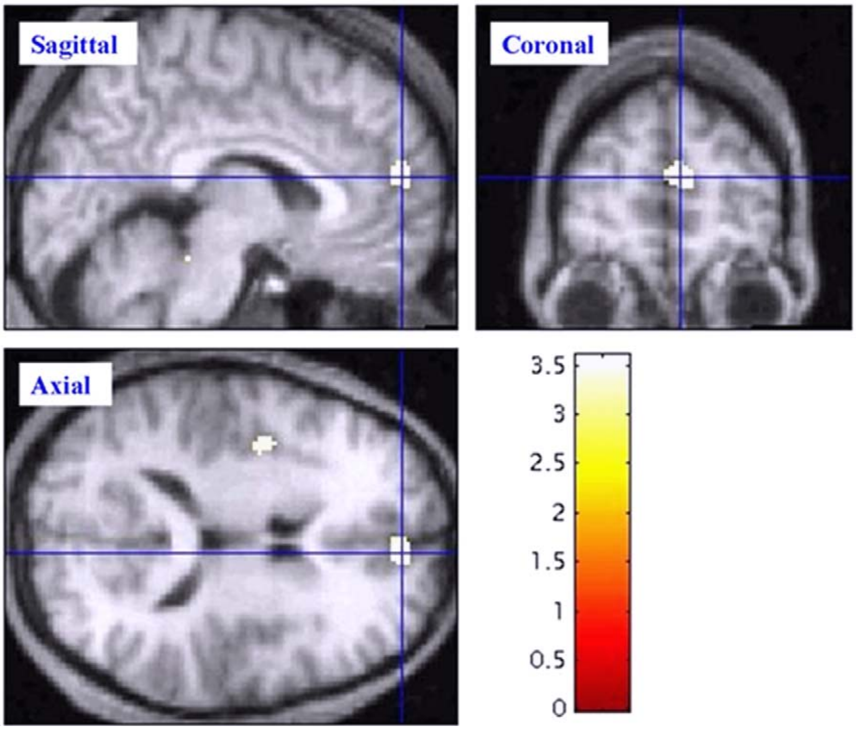

Fig. 1. Region of maximum activity in the region of the medial pre-frontal cortex, the area found to be reliably activated during mentalizing tasks. This activity was elicited when subjects adopted an ‘‘intentional stance’’ while they were playing a computerized version of the children’s game Rock Paper Scissors with either the experimenter or a computer. The figure illustrates activity specific to when subjects believed that they were playing against the experimenter compared to playing against a computer, and thus treated the other as an agent attributing to it beliefs and goals. The actual game sequence was identical in both conditions (adapted from Gallagher and Frith, 2003).

Frith and Frith (2003) suggested that this area may subserve the formation of decoupled representations of beliefs about the world, ‘‘decoupled’’ in the sense that they are decoupled from the actual state of the world and that they may or may not correspond to reality.

A related line of research has focused on the investigation of the neural mechanism underlying our ability to represent others’ goals and intentions by the mere observation of their motor actions. This notion stems from the finding that there are neurons in the pre-motor cortex of the macaque brain that fire both when the monkey performs a hand action itself and when it merely observes another monkey or a human performing the same hand action (Rizzolatti et al., 1996). It has been suggested that these ‘‘mirror neurons’’ represent the neural basis for imitation. Thus, when we imitate someone, we first observe the action and then try to reproduce it. But how do we transform what we see in terms of perceptual input into knowledge of what we need to do in terms of motor commands? The discovery of mirror neurons demonstrated that a translation mechanism is present in the primate brain and automatically elicited when viewing others’ actions. Moreover, Gallese and Goldman (1998) suggested that this mirror system might underlie our ability to understand other people’s intentions by providing us with an automatic simulation of their actions, goals and intentions.

Since the discovery of these ‘‘mirror neurons’’ a similar common coding of the production and perception of motor action has been demonstrated in the human brain using imaging techniques such as PET and fMRI (for a review, see Blakemore and Decety, 2001; Grezes and Decety, 2001). Typically, people were scanned while they saw movies depicting short motor actions. The observed activation was then compared with the activation elicited when the scanned subjects did the same motor action themselves. In line with the observation in monkeys, these studies revealed that the mere observation of another person performing an action recruited partly the same circuitry elicited by the execution of the same action. More specifically, this circuitry involves supplementary motor area (SMA), pre-SMA, pre-motor cortex, the supramarginal gyrus, intraparietal sulcus and the superior parietal lobe (Grezes and Decety, 2001).

3. Empathy

In addition to the ability to understand the mental states (propositional attitudes) of others, humans can also empathize with others, that is, share their feelings and emotions in the absence of any direct emotional stimulation to themselves. Humans can feel empathy for other people in a wide variety of contexts: for basic emotions and sensations such as anger, fear, sadness, joy, pain and lust, as well as for more complex emotions such as guilt, embarrassment and love. It has been suggested that empathy is the process that prevents us from doing harm to others and motivates altruistic behavior. An absence of empathy is what characterizes psychopaths who hurt others without feeling guilt or remorse (Blair, 2003). Empathy is crucial for the creation of affective bonds between mother and child, and later between partners and larger social groups. These examples exemplify that the lay term "empathy" refers to a complex and multi-level concept incorporating processes of affect sharing, mental state attribution and action control and initiation. As mentioned already in the introduction, we focus here on our capacity to understand emotions of others by sharing their affective states. At this point it is important to stress that although empathizing is defined as "affect sharing" the affective state in self and others is not simply shared but has to be induced in the self by the perception or imagination of an emotional state in another person and, even if it feels similar, is nevertheless distinguishable from the same feeling originated in ourselves.

Neuro-scientific research on empathy has been strongly influenced by action–perception models outlined earlier. Thus, the idea that there are neural mechanisms enabling the sharing of other people's states has been expanded to include the ability to share their *feelings and sensations* as well (Gallese, 2003; Gallese et al., 2004; Preston and de Waal, 2002). How can we understand what someone else feels when he or she experiences emotions such as sadness or happiness, or bodily sensations such as pain, touch or tickling, in the absence of any emotional or sensory stimulation to our own body? Influenced by perception–action models of motor behavior and imitation, Preston and de Waal (2002) proposed a neuro-scientific model of empathy, suggesting that observation or imagination of another person in a particular emotional state automatically activates a representation of that state in the observer with its associated autonomic and somatic responses. The term "automatic" in this case refers to a process that does not require conscious and effortful processing, but which can nevertheless be inhibited or controlled. Imaging studies in the past two years have started to investigate brain activity associated with different empathic responses in the domains of touch, smell and pain. The results have revealed common neural responses elicited by the observation of pictures showing disgusted faces and smelling disgusting odors oneself (Wicker et al., 2003), likewise by being touched and observing videos of someone else being touched (Keysers et al., 2004). Whereas the former study observed common activation in anterior insula (AI) cortex, a cortex which has been found to be associated with the processing and feeling of disgust, the latter study identified common activation in secondary somato-sensory cortex (SII), a part of the cortex involved in processing and feeling the sensation of touch.

Another study was able to identify shared and unique networks involved in empathy for pain (Singer et al., 2004a). In this study, couples were recruited allowing the assessment of empathy "in vivo" by bringing both partners into the same scanner environment. Brain activity was then measured in the female partner while painful stimulation was applied either to her own or to her partner's right hand via electrodes attached to the back of the hand. The male partner was seated next to the MRI scanner and a mirror allowed her to see both, her own and her partner's, hands lying on a tilted board in front of her. Flashes of different colors on a big screen behind the board pointed either to her hand or that of her partner, indicating which of them would receive the stimulation and whether it would be painful or non-painful.

This procedure enabled the measurement of pain-related brain activation (the so-called "pain matrix") when pain was applied to the scanned subject or to her partner (empathy for pain). The results suggest that some parts, but not the entire "pain matrix", were activated when empathizing with the pain of others. Activity in the primary and secondary somato-sensory cortex was only observed when receiving pain. These areas are known to be involved in the processing of the sensory-discriminatory components of our pain experience, that is, they indicate the location of the pain and its objective quality. In contrast, bilateral AI, the rostral anterior cingulate cortex (ACC), brainstem and cerebellum were activated when subjects either received pain or a signal that a loved one experienced pain (see Fig. 2). These areas are involved in the processing of the affective component of pain, that is, how unpleasant the subjectively felt pain is (Craig, 2002; Peyron et al., 2000). Thus, both the experience of pain to oneself and the knowledge that a loved partner is experiencing pain activates the same affective pain circuits. Further analyses also revealed that activity in these

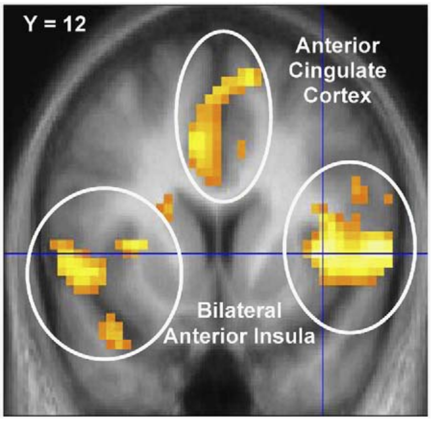

Fig. 2. Shared pain- and empathy-related networks observed when pain was applied to self or partner. The female volunteers activated anterior cingulated cortex (ACC) and bilateral anterior insula—the affective component of their own pain experience—when they observed their loved one receiving painful stimulation to his right hand. The figure illustrates results of a conjunction analysis between the contrasts pain–no pain in the context of self and other at $P<0.001$ (adapted from Singer et al., 2004b).

empathy-related pain-sensitive areas show individual variation and that these differences covary with interindividual differences in standard empathy questionnaires—the Empathic Concern Scale (IRI) by Davis (1980) and the Balanced Emotional Empathy Scale (BEES) from Mehrabian and Epstein (1972) and Mehrabian (1997). The higher the subjects scored on these questionnaires, the higher was their activation in ACC and AI.

In sum, these findings suggest that we use representations reflecting our own emotional responses to pain to understand how the pain of others feels. Moreover, our ability to empathize may have evolved from a system which represents our own internal feeling states and allows us to predict the affective outcomes of an event for ourselves and for other people. Consistently, activation in these regions has been observed in a wide range of imaging studies associated with emotional awareness of internal bodily states (Critchley et al., 2004), subjective feelings expressed by subjective ratings of trustworthiness in faces (Winston et al., 2002), in response to unfair offers during monetary exchange games (Rilling et al., 2002; Sanfey et al., 2003) or when confronted with the faces of fair players (Singer et al., 2004b). Interestingly, a special cell type, the so-called von Economo cell, has been observed exclusively in these two brain regions and only in humans and our closest relatives the great apes. John Allman has suggested that these large cells may provide a possible neural mechanism for fast social intuitions in uncertain situations of the like of "I feel or don't feel good about this" (Craig, 2003). In general, these structures have been suggested to subserve a subjective representation of internal bodily and subjective feeling states (Gallese et al., 2004; Craig, 2002, 2003; Critchley et al., 2004; Damasio, 1994).

Results of recent studies on empathy for pain indicate that similar empathic responses can be observed even if the "object" of empathy is unknown or unfamiliar (Jackson et al., 2005; Morrison et al., 2004). The magnitude of this activity, however, is modulated by the affective link to the "object" of empathy (Singer et al., 2006). Thus, activity in ACC and AI has also been observed when subjects watched still pictures depicting body parts involved in possibly painful situations (Jackson et al., 2005) or videos showing a needle piercing in the back of a hand (Morrison et al., 2004). The findings of a new study by Singer et al. (2006) indicate that overall empathy-related activation for unfamiliar persons in pain is lower than when empathizing with a loved one in pain. More importantly, however, this study gives first evidence for the modulation of activity in ACC and AI as a function of whether the subjects liked or disliked the other person in pain.

Finally, a number of studies have investigated the perception and evaluation of facial emotional expressions (for overviews, see also Blair, 2003; Adolphs, 2002; Haxby et al., 2002), mostly by presenting static pictures of faces with different emotional expressions ranging from fear, anger, disgust to happiness and surprise. These studies identified the involvement of a variety of brain regions, most prominently primary and higher-order visual areas, orbito-frontal cortex, amygdala, insula and basal ganglia. Although relevant, the focus of most of these studies was not on the study of empathy but on the investigation of threat detection, aversive conditioning, subliminal perception, inherent reward values or attentional modulation (for an exception, see Carr et al., 2003; Decety and Chaminade, 2003).

4. Future research perspectives: distinguishing mentalizing and empathizing

Clearly, neuro-scientific research on empathic understanding is in its infancy. In the experiments undertaken so far (Wicker et al., 2003; Keysers et al., 2004; Singer et al., 2004a, 2006; Morrison et al., 2004), subjects were neither required to make any explicit judgment about the feelings of the other person (for an exception see Avenanti et al., 2005, commented on by Singer and Frith, 2005) nor to engage in other-regarding behavior. As pointed out earlier the focus was primarily on our capacity for affect sharing, the capacity to automatically resonate with other people's feelings even when we are not aware of it. For example, when seeing someone else crying, we automatically start producing tears in our eyes, even in the absence of awareness.

The literature refers to these effects as emotional contagion, the human tendency to automatically mimic and synchronize facial expressions, vocalizations, postures and movements with those of another person (Hatfield et al., 1994). An example for such contagious effects can be observed already in newborns who respond significantly more with crying when hearing another newborn crying than when hearing the sound of white noise, their own cry, the cry of an older baby or a synthetic cry (Martin and Clark, 1987; Simner, 1971; Decety and Jackson, 2004).

However, affect sharing also occurs in the absence of any emotional stimuli to the subject. Even when subjects only see symbols which indicate by their color whether another person is in pain or not, activation in parts of the pain network involved in the processing of our own pain experience is elicited. As with emotional contagion this empathic response is still implicit in the sense that it was elicited without the requirement of any explicit, effortful perspective taking or judgment about the other people's emotional states.

The capacity for affect sharing—defined in this article as the capacity for empathy—is, however, only one aspect of what is called empathy in our everyday understanding. Thus, the term empathy usually refers to a complex and multi-level construct including simple forms of emotional contagion as well as complex forms of empathic perspective taking associated with other-regarding pro-social behavior (see also Decety and Jackson, 2004; Batson et al., 1997; Eisenberg and Fabes, 1990; Eisenberg, 2000; Preston and de Waal, 2002). Different authors have focused on different aspects of empathy, some focusing on the automatic component of affect sharing, others on the conscious process of perspective taking allowing the understanding of the others' feelings, and again others on the motivational aspect of empathy underlying the engagement in pro-social other-regarding behavior. Imagine, for example, being confronted with a close and usually quite peaceful friend who is in a stage of extreme rage because he is jealous that his girlfriend showed too much affection towards you during vacations together. Your capacity for affect sharing will help you to experience how it feels to be in rage and this will allow you to make more accurate predictions about possible actions your friend might take. At the same time, however, you will not confuse the rage and jealousy of your friend with your own motivational state. Moreover, you will engage in cognitive perspective taking (e.g., mentalizing) to understand the meaning of the feeling as well as your friend's thoughts and beliefs regarding this specific situation. Further, you will have to regulate and control your own feelings of distress resulting from the threat of the situation and you will probably try to engage in comforting helping behavior to appease the psychological pain of your friend. All these complex processes belong to what we commonly mean when we speak of empathy.

Future research will have to investigate in further detail these different levels of empathic responding and clarify when the abilities of mentalizing (understanding the propositional attitudes of others) and empathizing (sharing the affects of others) play unique and when they play common roles in the understanding of other people's states. An important component of this research will be to identify the neuronal circuitries underlying these different forms of empathic responses.

For purposes of illustration we will focus on the example of empathy research in the domain of pain. A first step for future research would be to compare implicit and explicit forms of empathy. For example, the comparison between brain activities during the mere perception of pain in others and that elicited when subjects are required to make explicit judgments about the unpleasantness or intensity of the painful stimulation as perceived by the other person should elicit different neural activation patterns: implicit forms of empathic responses should be associated with activation of affective representation of the pain network (AI and ACC) alone, whereas the explicit empathy conditions should involve additional activation in STS and mPFC, the areas which have been observed to be involved in cognitive perspective taking.

An interesting additional variation would be to test explicit empathic understanding in two conditions: (a) a condition in which there is congruency between one's own and the other's feeling and (b) a condition in which there is incongruency between one's own and the other's feeling. In the first case, subjects assess the effect of painful stimulation on another person who shares feelings with regard to pain similar to themselves. In the case of incongruency, subjects watch, for example, a masochist getting painful stimulation, i.e., a person that experiences pain partly as joyful and rewarding instead of solely aversive and unpleasant. In the latter condition, no affect sharing may take place because subjects lack the adequate affect representations. Accordingly, a lack of activation in pain-related networks and enhanced activation of STS and mPFC reflecting cognitive perspective taking should be observed. Finally, processes of inhibition and regulation of empathic responses are assumed to be associated with activity in brain areas known to be relevant for top-down control and emotion regulation, particularly the dorsolateral aspects of the pre-frontal cortex (Anderson et al., 2004; Miller and Cohen, 2001; Ochsner et al., 2002; Wager et al., 2004).

5. Implications for developmental neuro-sciences

So far, I have summarized evidence for neuronal correlates of mind reading and empathy, two abilities which allow human beings to represent the states of other people whether these are mental or emotional. These abilities enable people to predict others' behavior and, therefore, successfully engage in social interactions. Despite these common features and the difficulty of separating the two abilities in everyday situations, neuro-scientific evidence suggests that these abilities nevertheless can be distinguished and may rely on different neural circuitries. Thus, sharing sensations and emotions with others is associated with activation of circuitries involved in the processing of similar states in ourselves, involving the secondary somato-sensory cortices for touch, insular cortex and ACC for pain and disgust and amygdala for fear. Globally, these regions constitute the "emotional" (Dolan, 2002; Le Doux, 1998) or "social" brain (Adolphs, 1999) and most of these structures are usually referred to as limbic and para-limbic structures. They are crucial for emotional processing and developed early in phylogeny. By contrast, mentalizing abilities have been shown to be associated with activation in pre-frontal and temporal cortices, most importantly the mPFC and posterior STS, structures which belong to the neo-cortex and developed late in phylogeny.

Based on evidence from developmental brain science suggesting different developmental trajectories for different brain regions over the life span (Giedd et al., 1999; Gogtay et al., 2004; Sowell et al., 2003, 2004; Raz et al., 2005) it is suggested that introducing a developmental approach to the neuro-scientific study of mentalizing and empathizing may help to dissociate the two abilities and to generate a better understanding and prediction of the emergence of the proposed different levels of empathic responding. Note that there is a vast amount of existing behavioral data on the development of both empathy and ToM. This literature is summarized elsewhere and is not in the scope of the present article (Baron-Cohen et al., 2000; Mitchell et al., 2005; Decety and Jackson, 2004; Eisenberg and Fabes, 1990; Eisenberg, 2000). The prediction is made that the ability to understand the mental states of others should evolve later in ontogeny than the ability to share emotions because our ability to share affective states with others relies on phylogenetically old structures which develop early in ontogeny, whereas the capacity to understand mental states (beliefs, thoughts) relies on structures which emerged late in phylogeny and are also among those to mature latest in ontogeny.

Based on modern brain imaging techniques developmental neuro-sciences have indeed begun to give new evidence for nonlinear changes in gray matter (GM) density during childhood and adolescence. GM maturation is reflected in a loss of density over time with a simultaneous increase in synaptic pruning (Giedd et al., 1999; Gogtay et al., 2004; Sowell et al., 2003). Giedd et al. (1999) have shown that brain development between the ages of 4–21 years follows temporally distinct and functionally meaningful maturational trajectories in which higher-order association areas mature only after the lower-order sensorimotor regions have matured. Additionally, it appears that phylogenetically older cortical areas mature earlier than the newer cortical regions. Thus, within the frontal cortex, the primary sensorimotor cortices mature first whereas the pre-frontal cortex matures last; the dorsolateral pre-frontal cortex (DLPFC) loses GM only at the end of adolescence. The occipital lobes including primary visual cortex and the temporal poles involved in processing smell and taste mature very early, whereas the lateral temporal lobes mature very late. A small region of the posterior part of the superior temporal gyrus matures last; a finding which is interesting with respect to the crucial role of the STS in mentalizing (Apperly et al., 2004). Finally, phylogenetically, some of the oldest cortical regions, among those the limbic and para-limbic structures mentioned earlier, lie on the inferior brain surface in the medial aspects of the temporal lobe and develop earlier than the structures of the neo-cortex.

In sum, these findings suggest that levels of empathic responding that involve implicit affect sharing and are based on limbic and para-limbic structures as well as on somato-sensory cortices should develop earlier than our ability for cognitive perspective taking because the former rely on structures which develop early in brain development, whereas the latter rely on structures of the neo-cortex which are among the latest to mature, such as the pre-frontal cortex and lateral parts of the temporal cortex. The finding that the DLPFC has not fully matured up to an age of 25 is interesting with respect to its possible role in the modulation and control of affective responses and might suggest that the full capacity for effective and adaptive empathic responding is not developed until late adolescence. It would be interesting to investigate whether the maturation of the DLPFC parallels psychological maturation in the capacity to control and modulate empathic responses necessary to cope with contagious distress or engage in pro-social behavior.

6. Mentalizing and empathizing not only separate but also intertwined

Even though we have argued for separate developmental pathways for empathizing and mentalizing abilities with the latter developing much later than the former, we assume that (a) on both neuronal and psychological grounds the two developmental pathways also interact with each other and (b) both capacities undergo developmental changes throughout childhood and adolescence.

Thus, as discussed earlier, empathy refers to a multifaceted construct ranging from simple forms of emotion contagion to cognitive perspective-taking abilities. Contagious crying seems to be already present in newborns, before infants have developed self-awareness and the distinction between self and others, a capacity which develops only around 18–24 months of age, the period in which children also display the first manifestations of prosocial behavior towards others (Decety and Jackson, 2004). The ability to have empathic responses in the absence of any emotional cue develops probably even later and should parallel the maturation of memory systems and mental imagery. Moreover, explicit forms of empathy should coincide with the emergence of conscious representations of one's own feeling states allowing for statements such as "I feel sad or jealous". The capacity to understand other people's feelings when there is congruency between one's own and another person's feeling states probably develops earlier than the capacity to understand others' feeling in the absence of any representation of this feeling state in oneself. Whereas the former probably relies on a simulation based on one's own representation of a given feeling state in oneself (limbic structures), the latter probably relies purely on mentalizing capacities (pre-frontal and temporal structures). As outlined earlier, mentalizing abilities develop by about age 4 and are probably based on the development of mPFC and temporal structures. Thus, the basic capacity for mentalizing seems to be clearly in place long before the complete maturation of the neuro-circuitry subserving it. This suggests that not only empathizing but also mentalizing abilities may change in nature from early childhood to adolescence. Similar to emotional contagion preceding more complex forms of implicit and explicit empathy, explicit forms of mentalizing abilities are preceded by processes allowing implicit attribution of intentions and other mental states. For example, the ability of an infant to direct its attention/gaze towards the attentional focus of the mother (joint attention) already develops at around the age of 12–18 months or even earlier. Furthermore, explicit forms of mentalizing may differentiate and get more and more complex over the life span. The distinction between first-order (attributing a belief to another person) and second-order beliefs (attributing a belief about another person's belief), the former developing at about age 4, the latter developing later between the ages 6–10, points to a continuous development of mentalizing abilities throughout the life span.

Finally, it is important to stress that this paper has focused only on the first part of the life span and neglected possible implications of adult age changes in neuronal structures for emotional regulation and mind reading. The phase of old and very old age would be of special interest for testing the hypothesis of distinct neuronal networks underlying our abilities for affect sharing and mind reading. Similar to early childhood different brain areas show differential decline in old age [71] suggesting higher vulnerability to structures which develop later and are phylogenetically younger (e.g., PFC). It may therefore be that empathic responses are preserved up to very old age whereas mentalizing abilities show earlier decline. A challenge for future research will be to refine the use of functional imaging techniques in infants (Dehaene-Lambertz et al., 2002) and old age (Jones et al., in press) and to develop "interactive mind" paradigms suitable for infants, children and the aged to enable the assessment of the brain regions underlying our capacities for mind reading and empathizing over the entire life span.

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