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CHAPTER 22

Empathizing: neurocognitive developmental mechanisms and individual differences

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Abstract: This chapter reviews the Mindreading System model encompassing four neurocognitive mechanisms (ID, EDD, SAM, and ToMM) before reviewing the revised empathizing model encompassing two new neurocognitive mechanisms (TED and TESS). It is argued that the empathizing model is more comprehensive because it entails perception, interpretation, and affective responses to other agents. Sex differences in empathy (female advantage) are then reviewed, as a clear example of individual differences in empathy. This leads into an illustration of individual differences using the Empathy Quotient (EQ). Finally, the neuroimaging literature in relation to each of the neurocognitive mechanisms is briefly summarized and a new study is described that tests if different brain regions respond to the perception of different facial expressions of emotion, as a function of the observer's EQ.

Keywords: empathy; theory of mind; mindreading; neuroimaging; sex differences; psychopathology; individual differences; basic emotions

Introduction

In this chapter, we take the concept of empathy, and consider it in terms of neurocognitive developmental mechanisms and in terms of individual differences. The first part of the chapter deals with two conceptual approaches to the development of the empathizing ability. The second part of the chapter presents some empirical evidence on a quantitative trait measure of empathy. A simple definition of 'empathizing' is that it is the lens through which we perceive and process emotions. We therefore review the literature from neuroimaging studies, which suggests that perception of discrete basic emotions is processed in different neural regions and networks. Finally, we describe a recent study that reconciles these two approaches to empathy by investigating if an individual's level of empathy affects how their brain processes discrete emotions.

What is empathizing?

Empathizing is the drive to identify another person's emotions and thoughts, and to respond to these with an appropriate emotion (Davis, 1994). We use the term 'drive' but recognize that it also overlaps with the concept of a skill or an ability. We also focus on the definition of empathy given by Davis while recognizing that other authors may have a slightly different definition. Empathizing does not just entail the cold calculation of what someone else thinks and feels (or what is sometimes called mindreading). Psychopaths can do that much. Empathizing is also about having an appropriate emotional reaction inside you, an emotion triggered by the other person's emotion.

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Empathizing is done in order to understand another person, predict their behaviour, and to connect or resonate with them emotionally. Imagine you could recognize that ''Jane is in pain,'' but this left you cold, or detached, or happy, or preoccupied. This would not be empathizing. Now imagine you do not just see Jane's pain, but you also automatically feel concerned, wincing yourself, and feeling a desire to run across and help alleviate her pain. This is empathizing. And empathizing extends to recognizing and responding to any emotion or state of mind, not just the more obvious ones, like pain. Empathy is a skill (or a set of skills). As with any other skill, such as athleticism or mathematical or musical ability, we all vary in it. In the same way that we can think about why someone is talented or average or even disabled in these other areas, so we can think about individual differences in empathy.

Empathy is a defining feature of human relationships. Empathy stops you doing things that would hurt another person's feelings. Empathy also stops you inflicting physical pain on a person or animal. Empathy allows you to tune into someone else's world, setting aside your own world — your perception, knowledge, assumptions, or feelings. It allows you to see another side of an argument easily. Empathy drives you to care for, or offer comfort to, another person, even if they are unrelated to you and you stand to gain nothing in return. Empathy also makes real communication possible. Talking ''at'' a person is not real communication. It is a monologue. Real conversation is sensitive to this listener at this time. Empathy also provides a framework for the development of a moral code. Moral codes are built out of fellow-feeling and compassion.

Fractionating empathy

Philosophical (Stein, 1989) and evolutionary (Brothers, 1990; Levenson, 1996; Preston and de Waal, 2002) accounts have suggested that empathizing is not a unitary construct. Possible constituent 'fractions' of empathy include (1) 'emotional contagion/affective empathy', (2) 'cognitive empathy', and (3) sympathy.

Cognitive empathy is involved in explicit understanding of another's feelings and switching to take their perspective. Piaget referred to empathy as 'decentering', or responding nonegocentrically (Piaget and Inhelder, 1956). More recent developmental psychologists refer to this aspect of empathy in terms of using a 'theory of mind', or 'mindreading' (Astington et al., 1988; Whiten, 1991). Essentially, the cognitive component of empathizing entails setting aside your own current perspective, attributing a mental state (sometimes called an 'attitude') to the other person, and then inferring the likely content of their mental state, given their experience. The cognitive element also allows you to predict the other person's mental state or behaviour.

The second aspect to empathy is the 'affective' component (Hobson, 1993). A similar component in other accounts has been called 'emotional contagion', defined as the tendency to mimic and synchronise facial expressions automatically, vocalizations, postures, and movements with those of another person, to converge emotionally (Hatfield et al., 1992). This may be the most primitive component of empathy. For example, when witnessing someone else in a state of fear, if the observer 'catches' a similar state of fear, this acts as a 'quick-and-easy' route to alerting oneself to environmental dangers without having to face the dangers oneself.

A third component involves a 'concern mechanism' (Nichols, 2001) often associated with a prosocial/altruistic component, also termed 'sympathy'. This is distinct from emotional contagion in not necessarily involving matched states between the observer and the person experiencing the emotion, and being possibly specific to a certain class of emotions (sadness and pain, but not disgust or happiness) in the other person. It represents a case where the observer feels both an emotional response to someone else's distress and a desire to alleviate their suffering.

How does empathizing develop? The Mindreading System

In 1994, Baron-Cohen proposed a model to specify the neurocognitive mechanisms that comprise the

'Mindreading System' (Baron-Cohen, 1994, 1995). Mindreading is defined as the ability to interpret one's own or another agent's actions as driven by mental states. The model was proposed in order to explain (1) ontogenesis of a theory of mind and (2) neurocognitive dissociations that are seen in children with or without autism. The model is shown in Fig. 1 and contains four components: the intentionality detector (ID), the eye direction detector (EDD), the shared attention mechanism (SAM), and finally the theory-of-mind mechanism (ToMM).

ID and EDD build 'Dyadic' representations of simple mental states. ID automatically represents or interprets an agent's self-propelled movement as a desire or goal-directed movement, a sign of its agency, or an entity with volition (Premack, 1990). For example, ID interprets an animate-like moving shape as "it wants x" or "it has goal y." EDD automatically interprets or represents eye-like stimuli as "looking at me" or "looking at something else." That is, EDD picks out that an entity with eyes can perceive. Both ID and EDD are developmentally prior to the other two mechanisms, and are active early in infancy, if not from birth.

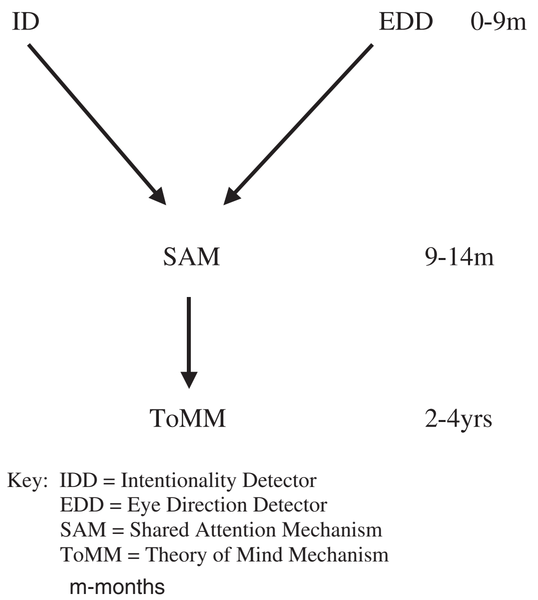

Fig. 1. Baron-Cohen's (1994) model of mindreading. Key: IDD = Intentionality Detector; EDD = Eye Direction Detector; SAM = Shared Attention Mechanism; ToMM = Theory-of-Mind Mechanism.

SAM is developmentally more advanced. SAM automatically represents or interprets if the self and another agent are (or are not) perceiving the same event. SAM does this by building 'triadic' representations. For example, where ID can build the dyadic representation "Mother wants the cup" and where EDD can build the dyadic representation "Mother sees the cup", SAM can build the triadic representation "Mother sees that I see the cup". As is apparent, triadic representations involve embedding or recursion. (A dyadic representation "I see a cup" is embedded within another dyadic representation "Mum sees the cup" to produce this triadic representation.) SAM takes its input from ID and EDD, and triadic representations are made out of dyadic representations. SAM typically functions from 9 to 14 months of age, and allows 'joint attention' behaviours such as protodeclarative pointing and gaze monitoring (Scaife and Bruner, 1975).

ToMM is the jewel in the crown of the 1994 model of the Mindreading System. It allows epistemic mental states to be represented (e.g., "Mother thinks this cup contains water" or "Mother pretends this cup contains water"), and it integrates the full set of mental-state concepts (including emotions) into a theory. ToMM develops between two and four years of age, and allows pretend play (Leslie, 1987), understanding of false belief (Wimmer and Perner, 1983), and understanding of the relationships between mental states (Wellman, 1990). An example of the latter is the seeing-leads-to-knowing principle (Pratt and Bryant, 1990), where a typical 3-year-old can infer that if someone has seen an event, then they will know about it.

The model shows the ontogenesis of a theory of mind in the first 4 years of life, and justifies the existence of four components on the basis of developmental competence and neuropsychological dissociation. In terms of developmental competence, joint attention does not appear possible until 9–14 months of age, and joint attention appears to be a necessary but not sufficient condition for understanding epistemic mental states (Baron-Cohen, 1991; Baron-Cohen and Swettenham, 1996). There appears to be a developmental lag between acquiring SAM and ToMM, suggesting that these two mechanisms are dissociable. In terms of neuropsychological dissociation, congenitally blind children can ultimately develop joint (auditory or tactile) attention (i.e., SAM), using the amodal ID rather than the visual EDD route. They can therefore go on to develop ToMM. Children with autism appear to be able to represent the dyadic mental states of seeing and wanting, but show delays in shared attention (Baron-Cohen, 1989b) and in understanding false belief (Baron-Cohen et al., 1985; Baron-Cohen, 1989a) — that is, in acquiring SAM and ultimately ToMM. It is this specific developmental delay that suggests that SAM and ToMM are dissociable from EDD.

Shortcomings of the Mindreading System model: the Empathizing SyStem

The 1994 model of the Mindreading System was revised in 2005 because of certain omissions and too narrow a focus. The key omission is that information about affective states, available to the infant perceptual system, has no dedicated neurocognitive mechanism. In Fig. 2, the revised model (Baron-Cohen, 2005) is shown and now includes a new fifth component: the emotion detector (TED). But the concept of mindreading (or theory of mind) makes no reference to the affective state in the observer triggered by recognition of another's mental state. This is a particular problem for any account of the distinction between autism and psychopathy. For this reason, the model is no longer of 'mindreading' but is of 'empathizing', and the revised model also includes a new sixth component: The Empathizing SyStem (TESS). (TESS is spelt as it is to playfully populate the Mindreading Model with apparently anthropomorphic components.) Where the 1994 Mindreading System was a model of a passive observer (because all the components had simple decoding functions), the 2005 Empathizing SyStem is a model of an observer impelled towards action (because an emotion is triggered in the observer which

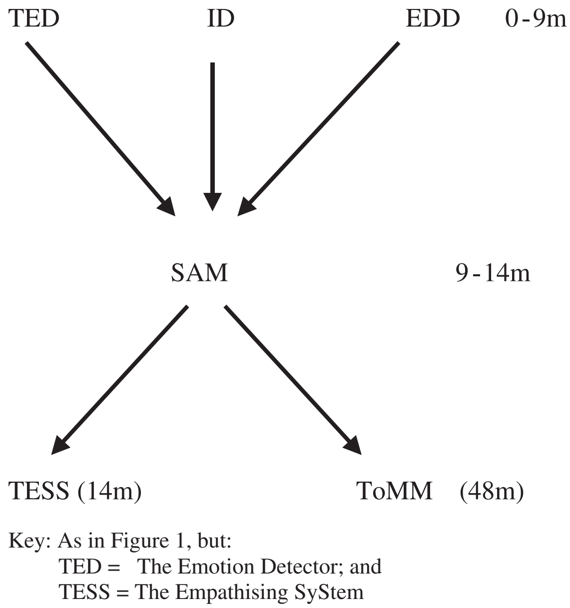

Fig. 2. Baron-Cohen's (2005) model of empathizing. Key: As in Fig. 1, with TED = The Emotion Detector and TESS = The Empathizing SyStem.

typically motivates the observer to respond to the other person).

Like the other infancy perceptual input mechanisms of ID and EDD, the new component of TED can build dyadic representations of a special kind, namely, it can represent affective states. An example would be "Mother — is unhappy" or even "Mother — is angry with me." Formally, we can describe this as agent-affective state proposition. We know that infants can represent affective states from as early as three months of age (Walker, 1982). As with ID, TED is amodal, in that affective information can be picked up from facial expression, or vocal intonation, 'motherese' being a particularly rich source of the latter (Field, 1979). Another person's affective state is presumably also detectable from their touch (e.g., tense vs. relaxed), which implies that congenitally blind infants should find affective information accessible through both auditory and tactile modalities. TED allows the detection of the basic emotions (Ekman and Friesen, 1969). The development of TED is probably aided by simple imitation that is typical of infants (e.g., imitating caregiver's expressions), which in itself would facilitate emotional contagion (Meltzoff and Decety, 2003).

When SAM becomes available, at 9–14 months of age, it can receive inputs from any of the three infancy mechanisms, ID, EDD, or TED. Here, we focus on how a dyadic representation of an affective state can be converted into a triadic representation by SAM. An example would be that the dyadic representation ''Mother is unhappy'' can be converted into a triadic representation ''I am unhappy that Mother is unhappy'', ''Mother is unhappy that I am unhappy'', etc. Again, as with perceptual or volitional states, SAM's triadic representations of affective states have this special embedded or recursive property.

TESS in the 2005 model is the real jewel in the crown. This is not to minimize the importance of ToMM, which has been celebrated for the last 20 years in research in developmental psychology (Leslie, 1987; Wimmer et al., 1988; Whiten, 1991). ToMM is of major importance in allowing the child to represent the full range of mental states, including epistemic ones (such as false belief), and is important in allowing the child to pull mentalistic knowledge into a useful theory with which to predict behaviour (Wellman, 1990; Baron-Cohen, 1995). But TESS allows more than behavioural explanation and prediction (itself a powerful achievement). TESS allows an empathic reaction to another's emotional state. This is, however, not to say that these two modules do not interact. Knowledge of mental states of others made possible by ToMM could certainly influence the way in which an emotion is processed and/or expressed by TESS. TESS also allows for sympathy. It is this element of TESS that gives it the adaptive benefit of ensuring that organisms feel a drive to help each other.

M-representations versus E-representations

To see the difference between TESS and ToMM, consider this example: ''I see you are in pain''. Here, ToMM is needed to interpret your facial expressions and writhing body movements in terms of your underlying mental state (pain). But now consider this further example: ''I am devastated — that you are in pain''. Here, TESS is needed, since an appropriate affective state has been triggered in the observer by the emotional state identified in the other person. And where ToMM employs M-representations[1] (Leslie, 1995) of the form agent-attitude-proposition (e.g., Mother — believes — Johnny took the cookie), TESS employs a new class of representations, which we can all E-representations[2] of the form self-affective state [agent-affective state-proposition] (e.g., ''I feel sorry that — Mom feels sad about — the news in the letter'') (Baron-Cohen, 2003). The critical feature of this E-representation is that the self's affective state is appropriate to and triggered by the other person's affective state. Thus, TESS can represent [I am horrified — that you are in pain], or [I am concerned — that you are in pain], or [I want to alleviate — that you are in pain], but it cannot represent [I am happy — that you are in pain]. At least, it cannot do so if TESS is functioning normally. One could imagine an abnormality in TESS leading to such inappropriate emotional states being triggered, or one could imagine them arising from other systems (such as a competition system or a sibling-rivalry system), but these would not be evidence of TESS per se.

Dissociations between TED, ToMM, and TESS from neuropsychiatry

Before leaving this revision of the model, it is worth discussing why the need for this has arisen. First, emotional states are an important class of mental states to detect in others, and yet the earlier model focused only on volitional, perceptual, informational, and epistemic states. Second, when it comes to pathology, it would appear that in autism TED might function, although this may be delayed (Hobson, 1986; Baron-Cohen et al., 1993, 1997c), at least in terms of detecting basic emotions. Even high-functioning people with autism or Asperger Syndrome have difficulties both in ToMM (when measured with mental-age appropriate tests) (Happé, 1994; Baron-Cohen et al., 1997b, 2001)

[1]M stands for mental.

[2]E stands for empathy.

and TESS (Attwood, 1997; Baron-Cohen et al., 1999a, b, 2003, 2004). This suggests that TED and TESS may be fractionated.

In contrast, the psychiatric condition of psychopathy may entail an intact TED and ToMM, alongside an impaired TESS. The psychopath (or sociopath) can represent that you are in pain, or that you believe — that he is the gas-man, thereby gaining access to your house or your credit card. The psychopath can go on to hurt you or cheat you without having the appropriate affective reaction to your affective state. In other words, he or she does not care about your affective state (Mealey, 1995; Blair et al., 1997). Lack of guilt or shame or compassion in the presence of another's distress are diagnostic of psychopathy (Cleckley, 1977; Hare et al., 1990). Separating TESS and ToMM thus allows a functional distinction to be drawn between the neurocognitive causes of autism and psychopathy.

Developmental dissociations

Developmentally, one can also distinguish TED from TESS. We know that at three months of age, infants can discriminate facial and vocal expressions of emotion (Walker, 1982; Trevarthen, 1989), but that it is not until about 14 months that they can respond with appropriate affect (e.g., a facial expression of concern) to another's apparent pain (Yirmiya et al., 1990) or show "social referencing." Clearly, this account is skeletal in not specifying how many emotions TED is capable of recognizing. Our recent survey of emotions identifies that there are 412 discrete emotion concepts that the adult English language user recognizes (Baron-Cohen et al., submitted). How many of these are recognized in the first year of life is not clear. It is also not clear exactly how empathizing changes during the second year of life. We have assumed the same mechanism that enables social referencing at 14-months-old also allows sympathy and the growth of empathy across development. This is the most parsimonious model, though it may be that future research will justify further mechanisms that affect the development of empathy.

Sex differences in empathizing

In the introduction to this chapter we promised to consider sex differences in empathizing. Some of the best evidence for individual differences in empathizing comes from the study of sex differences, where many studies converge on the conclusion that there is a female superiority in empathizing. Sex differences are best viewed as summated individual differences, on multiple dimensions that include genetic and epigenetic factors. Some of the observed behavioural differences are reviewed here.

(1) *Sharing and turn-taking*. On average, girls show more concern for fairness, while boys share less. In one study, boys showed 50 times more competition, while girls showed 20 times more turn-taking (Charlesworth and Dzur, 1987).
(2) *Rough and tumble play or "rough housing" (wrestling, mock fighting, etc)*. Boys show more of this than girls do. Although there is a playful component, it can hurt or be intrusive, so it needs lower empathizing to carry it out (Maccoby, 1999).
(3) *Responding empathically to the distress of other people*. Girls aged 1 year or more show greater concern through more sad looks, sympathetic vocalizations, and comforting. More women than men also report frequently sharing the emotional distress of their friends. Women also show more comforting, even of strangers, than men do (Hoffman, 1977).
(4) *Using a 'theory of mind'*. By three years of age, little girls are already ahead of boys in their ability to infer what people might be thinking or intending (Happe, 1995). This sex difference appears in some but not all studies (Charman et al., 2002).
(5) *Sensitivity to facial* expressions. Women are better at decoding nonverbal communication, picking up subtle nuances from tone of voice or facial expression, or judging a person's character (Hall, 1978).
(6) *Questionnaires measuring empathy*. Many of these find that women score higher than men (Davis, 1994).

(7) *Values in relationships*. More women value the development of altruistic, reciprocal relationships, which by definition require empathizing. In contrast, more men value power, politics, and competition (Ahlgren et al., 1979). Girls are more likely to endorse co-operative items on a questionnaire and to rate the establishment of intimacy as more important than the establishment of dominance. Boys are more likely than girls to endorse competitive items and to rate social status as more important than intimacy (Knight et al., 1989).

(8) Disorders of empathy (such as psychopathic personality disorder or conduct disorder) are far more common among males (Dodge, 1980; Blair, 1995).

(9) *Aggression, even in normal quantities, can only occur with reduced empathizing*. Here again, there is a clear sex difference. Males tend to show far more 'direct' aggression (pushing, hitting, punching, etc.) while females tend to show more 'indirect' (or relational, covert) aggression (gossip, exclusion, bitchy remarks, etc.). Direct aggression may require an even lower level of empathy than indirect aggression. Indirect aggression needs better mindreading skills than does direct aggression, because its impact is strategic (Crick and Grotpeter, 1995).

(10) *Murder is the ultimate example of a lack of empathy*. Daly and Wilson (1988) analysed homicide records dating back over 700 years, from a range of different societies. They found that 'male-on-male' homicide was 30–40 times more frequent than 'female-on-female' homicide.

(11) *Establishing a 'dominance hierarchy'*. Males are quicker to establish these. This in part may reflect their lower empathizing skills, because often a hierarchy is established by one person pushing others around, to become the leader (Strayer, 1980).

(12) *Language style*. Girls' speech is more co-operative, reciprocal, and collaborative. In concrete terms, this is also reflected in girls being able to keep a conversational exchange with a partner going for longer. When girls disagree, they are more likely to express their different opinion sensitively, in the form of a question rather than an assertion. Boys' talk is more 'single-voiced discourse' (the speaker presents their own perspective alone). The female speech style is more 'double-voiced discourse' (girls spend more time negotiating with the other person, trying to take the other person's wishes into account) (Smith, 1985).

(13) *Talk about emotions*. Women's conversation involves much more talk about feelings, while men's conversation with each other tends to be more object or activity focused (Tannen, 1991).

(14) *Parenting style*. Fathers are less likely than mothers to hold their infant in a face-to-face position. Mothers are more likely to follow through the child's choice of topic in play, while fathers are more likely to impose their own topic. And mothers fine-tune their speech more often to match what the child can understand (Power, 1985).

(15) *Face preference and eye contact*. From birth, females look longer at faces, and particularly at people's eyes, and males are more likely to look at inanimate objects (Connellan et al., 2001).

(16) *Finally, females have also been shown to have better language ability than males*. It seems likely that good empathizing would promote language development (Baron-Cohen et al., 1997a) and vice versa, so these may not be independent.

Leaving aside sex differences as one source of evidence for individual differences, one can see that empathy is normally distributed within the population. Figure 3 shows the data from the Empathy Quotient (EQ), a validated 60-item self-report questionnaire (Baron-Cohen and Wheelwright, 2004). It has been factor analysed to suggest the existence of three distinct components, which roughly correspond to the three-component model of empathy (Lawrence et al., 2004). Scores on the EQ show a quasi-normal distribution in several populations, with scores from

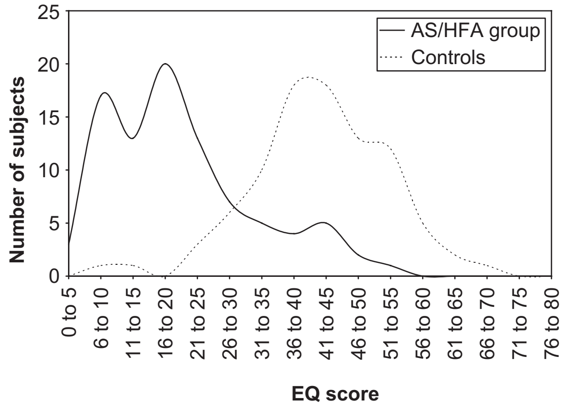

Fig. 3. The distribution of EQ in the general population (dotted line). Also shown is the distribution of empathy scores from people with Asperger Syndrome (AS) or High Functioning Autism (HFA). (From Baron-Cohen and Wheelwright, 2004.)

people with Autism Spectrum Conditions (ASCs) clustering toward the lower end (see Fig. 3). The EQ shows significant sex differences (Goldenfeld et al., 2006).

The search for the neural correlates of empathy has had two traditions of research, one focusing on theory-of-mind studies (involving largely intention attribution or emotion attribution) and another focusing on action understanding. The latter has gained considerable importance in recent years since the discovery of mirror neurons (Gallese et al., 2004).

On finding increasing evidence of sex differences in the EQ in the general population, we sought to investigate the neural correlates of this trait measure of empathizing across the population. Since empathizing can be viewed as a lens through which we perceive and process emotions, we attempted to marry the two fields of emotion perception and empathizing. The following section briefly introduces the current state of the literature on the neural bases of basic emotions and the results of a recent study from our lab.

Neuroimaging studies of empathizing and emotion

Neuroimaging studies have implicated the following different brain areas for performing tasks that tap components of the model of empathy proposed above, presented in order of their development.

1. Studies of emotional contagion have demonstrated involuntary facial mimicry (Dimberg et al., 2000) as well as activity in regions of the brain where the existence of 'mirror' neurons has been suggested (Carr et al., 2003; Wicker et al., 2003; Jackson et al., 2005).
2. ID has been tested (Brunet et al., 2000) in a PET study in a task involving attribution of intentions to cartoon characters. Reported activation clusters included the right medial prefrontal (BA 9), inferior frontal (BA 47) cortices, superior temporal gyrus (BA 42), and bilateral anterior cingulate cortex. In an elegant set of experiments that required participants to attribute intentions to animations of simple geometric shapes (Castelli et al., 2000), it was found that the 'intentionality' score attributed by the participants to individual animations was positively correlated to the activity in superior temporal sulcus (STS), the temporo-parietal junction, and the medial prefrontal cortex. A subsequent study (Castelli et al., 2002) demonstrated a group difference in activity in the same set of structures between people with Autism/Asperger Syndrome and neurotypical controls.
3. EDD has been studied in several neuroimaging studies on gaze direction perception (Calder et al., 2002; Pelphrey et al., 2003; see Grosbras et al., 2005 for a review) and have implicated the posterior STS bilaterally. This evidence, taken together with similar findings from primate literature (Perrett and Emery, 1994), suggests this area to be a strong candidate for the anatomical equivalent of the EDD.
4. A recent imaging study (Williams et al., 2005) investigated the neural correlates of SAM and reported bilateral activation in anterior cingulate (BA 32,24), and medial prefrontal cortex (BA 9,10) and the body of caudate nucleus in a joint attention task, when compared to a control task involving nonjoint attention (see Frith and Frith, 2003 for a review).
5. Traditional 'theory-of-mind' (cognitive empathy) tasks have consistently shown activity

in medial prefrontal cortex, superior temporal gyrus, and the temporo-parietal junctions (Frith and Frith, 2003; Saxe et al., 2004). This could be equated to the brain basis of ToMM.

6. Sympathy has been relatively less investigated, with one study implicating the left inferior frontal gyrus, among a network of other structures (Decety and Chaminade, 2003). Work on 'moral' emotions has suggested the involvement of a network comprising the medial frontal gyrus, the medial orbitofrontal cortex, and the STS (Moll et al., 2002).

Neuroimaging of discrete emotions

An increasing body of evidence from lesion, neuroimaging and electrophysiological studies suggest that these affect programs might have discrete neural bases (Calder et al., 2001). Fear is possibly the single most well investigated emotion. Passive viewing of fear expressions as well as experiencing fear (as induced through recalling a fear memory, or seeing fearful stimuli) activates the amygdala, orbitofrontal cortex and the anterior cingulate cortex (Morris et al., 1999; Damasio et al., 2000). There is considerable evidence from non-human primates (Kalin et al., 2001; Prather et al., 2001) and rats (LeDoux, 2000) to suggest a crucial role for these regions in processing fear. Visual or auditory perception of disgust expressions as well as experiencing disgust is known to activate the anterior insula and the pallidum (Phillips et al., 1997, 1998; Wicker et al., 2003). An increasing consensus on the role of the ventral striatum in processing reward from different sensory domains [receiving food rewards (O'Doherty et al., 2002), viewing funny cartoons (Mobbs et al., 2003), remembering happy events (Damasio et al., 2000)] concurs well with studies that report activation of this region in response to viewing happy faces (Phillips et al., 1998; Lawrence et al., 2004).

Perception of angry expressions have been shown to evoke a response in the premotor cortex and the striatum (Grosbras and Paus, in press) as well as the lateral orbitofrontal cortex (Blair et al., 1999). The results of studies on the processing of sad expressions are comparatively less consistent. Perception of sad face and induction of sad mood are both known to be associated with an increased response in the subgenual cingulate cortex (Mayberg et al., 1999; Liotti et al., 2000), the hypothalamus in humans (Malhi et al., 2004) and in rats (Shumake, Edwards et al., 2001) as well as in the middle temporal gyrus (Eugene, Levesque et al., 2003). There have been very few studies on the passive viewing of surprise. One study by (Schroeder et al., 2004) has reported bilateral activation in the parahippocampal region, which is known for its role in novelty detection from animal literature.

While the discrete emotions model holds well for these relatively 'simple' emotions, the dimensional models (e.g. see (Rolls, 2002)) become increasingly relevant as we consider the more 'socially complex' emotions, e.g. pride, shame and guilt – since it would not be very economical to have discrete neural substrates for the whole gamut of emotions. These two models, however, need not be in conflict, since the more complex emotions can be conceptualized as being formed of a combination of the basic ones (i.e. with each of the 'basic' emotions representing a dimension in emotion space).

Two major meta-analytic studies of neuroimaging literature on emotions highlight the role of discrete regions in primarily visual processing of different basic emotions (Phan et al., 2002; Murphy et al., 2003). Some studies using stimuli in other sensory modalities (olfactory (Anderson et al., 2003) gustatory (Small et al., 2003), auditory (Lewis et al., in press)) have shown the possibly dissociable role for the amygdala and the orbitofrontal cortex in processing emotions along the two dimensions of valence and arousal.

The relative absence of neuroimaging studies on 'complex' emotions could be possibly due to the increased cultural variability of the elicitors as well as the display rules that these expressions entail. Among the few exceptions, guilt and embarrassment have been investigated by Takahashi et al., 2004 who reported activation in ventromedial prefrontal cortex, left Superior Temporal Sulcus (STS) and higher visual cortices when participants read sentences designed to evoke guilt or embarrassment. This, taken together with the areas underlying the 'ToMM' system could possibly suggest an increased role of 'theory-of-mind' to make sense of these emotions.

'Empathizing' with discrete emotions?

Returning to the concept of individual differences in empathizing, this poses an interesting question for the brain basis of perception of discrete emotions. Do we use a centralized 'empathy circuit' to make sense of all emotions? If so, can one detect differences in how discrete emotions are processed in individuals who are at different points on the EQ continuum?

A direct approach to investigate individual differences in empathizing has been to test for sex differences in perception of emotions. Using facial Electromyography (EMG), one study (Helland, 2005) observed that females tend to show increased facial mimicry to facial expressions of happiness and anger when compared to males. In a metareview of neuroimaging results on sex differences on emotion perception, Wager et al. (2003) reported that females show increased bilaterality in emotion-relevant activation compared to males. This is not always found (Lee et al., 2002; Schienle et al., 2005). One of the reasons for this might have been the fact that sex differences are summated individual differences. Instead of such a broad category-based approach (as in sex-difference studies), an approach based on individual differences in self-report personality scores (Canli et al., 2002) or genetic differences (e.g., Hariri et al., 2002) may be more finely tuned.

To test this model of individual variability, we asked if an individual's score on the EQ predicted his/her response to four basic emotions (happy, sad, angry, and disgust). If empathizing were modulated by a unitary circuit, then individual differences in empathizing would correlate with activity in the same structures for all basic emotions. Twenty-five volunteers (13 female and 12 male) selected across the EQ space were scanned in a 3 T functional magnetic resonance imaging (fMRI) scanner on a passive viewing task using dynamic facial expressions as stimuli. It was found that activity in different brain regions correlated with EQ scores for different basic emotions (Chakrabarti et al., in press).

Different regional responses were found to correlate with the EQ for different emotions, suggesting that there is no unitary correlate of the personality trait of empathizing across these emotions. Specifically, for perception of happy faces, a parahippocampal-ventral striatal cluster response was positively correlated with the EQ. The role of this region in reward processing is well known (O'Doherty et al., 2004). This suggests that the more "empathic" a person is, the higher is his/her reward response to a happy face. Interestingly, the response from the same region correlated negatively with the EQ during perception of sad faces. This fits perfectly with the earlier results, i.e., the more empathic a person is, the lower is his/her reward response to a sad face.

For happy and sad faces therefore, empathizing seems to involve mirroring. The higher a person's EQ, the stronger the reward response to happy faces and vice versa for sad faces. This is in concordance with suggestions from earlier studies on pain perception (Singer et al., 2004) and disgust perception (Wicker et al., 2003), where observation and experience have been shown to be mediated by the same set of structures. One of the issues with the previous studies is a possible confound between 'personal distress' and empathizing. The novel element in our study is that we explicitly tested for the personality trait of empathizing in relation to perception of specific emotions.

However, empathizing does not appear to be purely an index of mirroring. For perception of angry faces, EQ correlated positively to clusters centered on the precuneus/inferior parietal lobule, the superior temporal gyrus, and the dorsolateral prefrontal cortex. The posterior cingulate region is known to be involved in self/other distinction (Vogt, 2005), and the superior temporal gyrus is known for its role in ToMM tasks (Saxe et al., 2004). This suggests that higher EQ corresponds to higher activation in areas related to the distinction of self versus other, as well as those that are recruited to determine another person's intentions. The dorsolateral prefrontal cortex is known for its role in decision making and context evaluation (Rahm et al., 2006). Higher EQ would therefore predict better evaluation of the threat from an angry expression. Since expressions of anger are usually more socially urgent for attention than those of either sadness or happiness, it is essential that highly empathic persons do not merely 'mirror' the expression. A high empathizer's perception of an angry face would therefore need to be accompanied by an accurate determination of the intentions of the person as well as an evaluation of the posed threat.

In response to disgust faces, a cluster containing the dorsal anterior cingulate cortex and medial prefrontal cortices is negatively correlated with EQ, suggesting that the areas involved in attribution of mental states (primarily required for deciphering the 'complex' emotions) are selectively recruited less by people of high EQ. This is what might be expected, since disgust as an emotion is less interpersonal than anger or sadness, so resources for decoding complex emotional signals need not be utilized. Another cluster that includes the right insula and Inferior Frontal Gyrus (IFG) is negatively correlated with EQ. Given the well-established role of this region in processing disgust, this was a surprising result. We expected that an increased ability to empathize would result in an increased disgust response to facial expressions of disgust. The negative correlation suggests that people with high EQ had a lower insula-Inferior Frontal Gyrus (IFG) response to disgust expressions. A re-examination of the behavioural literature on disgust sensitivity reveals a similar result since Haidt et al. (1994) suggested that increased socialization leads to lower disgust sensitivity. Individuals with high EQ may socialize more than those with low EQ.

Together, these results demonstrate variability among different basic emotions in how empathy interacts with them. This fits with the core idea that the different basic emotions have relatively independent evolutionary antecedents (Panksepp, 1998) and social communicatory functions (Izard and Ackerman, 2000). While some of the emotions involve more 'mirroring' (the same areas show activation during recognition and experience, e.g., the striatal response to happy faces correlating positively with EQ), others require an increased distinction between one's own emotional state and the other's emotional state (e.g., the Superior Temporal Gyrus (STG) and Inferior Perietal Lobule (IPL)/precuneus response to angry faces correlating with EQ).

This study provides support for the discrete emotions model discussed above, but reveals how empathy at the neural level is subtle and complex: Neural networks activated by perception of discrete emotions depend on the observer's EQ. Empathy is likely to be determined by other individual differences, such as fetal testosterone (Knickmeyer et al., 2005; Knickmeyer and Baron-Cohen, 2006), genetic variation (Skuse et al., 1997; Chakrabarti et al., 2006), as well as early care or neglect (Fonagy et al., 1997). We conclude that more basic neuroscience into empathy will enrich our understanding of this most fundamental human quality.

Abbreviations

EDD	Eye Direction Detector
EQ	Empathy Quotient
ID	Intentionality Detector
SAM	Shared Attention Mechanism
TED	The Emotion Detector
TESS	The Empathy SyStem
ToMM	Theory-of-Mind Mechanism

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