14

Social Neuroscience

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In this chapter, we take a key concept in neuroscience, namely empathy, and consider it in terms of neurocognitive developmental mechanisms and in terms of individual differences. The first part of the chapter deals with the development of empathy; the second part presents some empirical evidence on a quantitative trait measure of empathy. Trait empathy is intrinsically connected with our perception of, and response to, others' emotions. We therefore briefly review the literature on emotion processing from neuroimaging studies that suggest that discrete basic emotions are subserved by different neural regions and networks (Panksepp, 1998). Finally, we describe a recent study that investigates whether and how an individual's level of empathy affects the way in which 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 ability. We also focus on the definition of empathy given by Davis (1994), whilst 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 "mind-reading"). 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. Empathizing is done in order to understand another person, to predict their behavior, 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 only see Jane's pain, but you also automatically feel concern, wincing yourself, and feeling a desire to run across and help alleviate her pain. That 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 consider 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 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 & de Waal, 2002) accounts have suggested that empathizing is not a unitary construct. Possible constituent "fractions" of empathy include (a) "emotional contagion/affective empathy," (b) "cognitive empathy," and (c) 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 non-egocentrically (Piaget & Inhelder, 1956). More recent developmental psychologists refer to this aspect of empathy in terms of using a "theory of mind" or "mindreading" (Astington, Harris, & Olson, 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 behavior.

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 automatically mimic and synchronize facial expressions, vocalizations, postures, and movements with those of another person, and, consequently, to converge emotionally (Hatfield, Cacioppo, & Rapson, 1992). This may be the most primitive component of empathy. For example, if, when witnessing someone else in a state of fear, you "catch" a similar state of fear, this acts as a quick and easy route to alerting you to environmental dangers without having to face the dangers yourself. 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 as it does not necessarily involve matched states between the observer and the person experiencing the emotion, and is 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.

Development of Empathy

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 (a) the ontogenesis of a theory of mind, and (b) the neurocognitive dissociations that are seen in children with or without autism. The model is shown in Figure 14.1 and contains four components: ID, or the intentionality detector; EDD, or the eye direction detector; SAM, or the shared attention mechanism; and, finally, ToMM, or the theory of mind mechanism.

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.

SAM is developmentally more advanced. SAM automatically represents or interprets whether 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

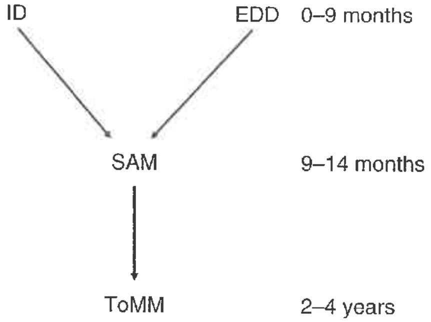

Figure 14.1 Baron-Cohen's 1994 model of mindreading. ID, intentionality detector; EDD, eye direction detector; SAM, shared attention mechanism; ToMM, theory of mind mechanism. *Note.* From "The Mindreading System: New Directions for Research," by S. Baron-Cohen, 1994, *Current Psychology of Cognition*, *13*, 724–750.

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 the cup"] is embedded within another dyadic representation ["Mother 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" behaviors such as protodeclarative pointing and gaze monitoring (Scaife & 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 2 and 4 years of age, and allows pretend play (Leslie, 1987), understanding of false belief (Wimmer & 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 & Bryant, 1990) where the 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 four 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 & 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 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, 1989a; Baron-Cohen, Leslie, & Frith, 1985)—that is, in acquiring SAM and ultimately ToMM. It is this specific developmental delay that suggests that SAM and ToMM are dissociable from EDD.

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 Figure 14.2, the revised model (Baron-Cohen, 2005) is shown and now includes a new, fifth component: TED, or the emotion detector. 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, TESS, or the empathizing system. (TESS is spelt as it is to playfully populate

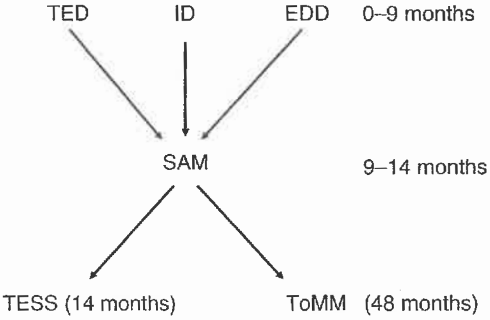

Figure 14.2 Baron-Cohen's 2005 model of empathizing. TED, the emotion detector; ID, intentionality detector; EDD, eye direction detector; SAM, shared attention mechanism; TESS, the empathizing system; ToMM, theory of mind mechanism. *Note.* From "The Empathizing System: A Revision of the 1994 Model of the Mindreading System," by S. Baron-Cohen, 2005, in B. Ellis and D. Bjorklund (Eds.), *Origins of the social mind* (pp. 468–492). New York: Guilford.

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 toward action (because an emotion is triggered in the observer which 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 3 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's affective state is presumably also detectable from their touch (e.g., tense versus 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 & Friesen, 1969). The development of TED is probably aided by the simple imitation that is typical of infants (e.g., imitating caregiver's expressions) which in itself would facilitate emotional contagion (Meltzoff & 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" or "Mother is unhappy that I am unhappy," and so on. 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 past 20 years in research in developmental psychology (Leslie, 1987; Whiten, 1991; Wimmer, Hogrefe, & Perner, 1988). 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 behavior (Baron-Cohen, 1995; Wellman, 1990). But TESS allows more than behavioral 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 the 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.

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 ("M" stands for "mental"; Leslie, 1994) of the form agent—attitude—proposition (e.g., Mother—believes—Johnny took the cookie), TESS employs a new class of representations, which we can call E-representations ("E" stands for "empathy") of the form self—affective state—(self—affective state—proposition); for example, "I feel sorry that—Mother 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.

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 may function, although this may be delayed (Baron-Cohen, Spitz, & Cross, 1993; Baron-Cohen, Wheelwright, & Joliffe, 1997; Hobson, 1986), 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; Baron-Cohen, Joliffe, Mortimore, & Robertson, 1997; Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001; Happé, 1994) and TESS (Attwood, 1997; Baron-Cohen, O'Riordan, Jones, Stone, & Plaisted, 1999; Baron-Cohen, Richler, Bisarya, Gurunathan, & Wheelwright, 2003; Baron-Cohen, & Wheelwright, 2004; Baron-Cohen, Wheelwright, Stone, & Rutherford, 1999). 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 gasman, thereby gaining access to your house or your credit card. The psychopath can go on to hurt you or to 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 (Blair, Jones, Clark, & Smith, 1997; Mealey, 1995). 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.

Developmentally, one can also distinguish TED from TESS. We know that at 3 months of age, infants can discriminate facial and vocal expressions of emotion (Trevarthen, 1989; Walker, 1982), 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, Kasari, Sigman, & Mundy, 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 (Golan, & Baron-Cohen, 2006). 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 that 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

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 behavioral differences are reviewed here:

1. *Sharing and turn-taking*. On average, girls show more concern for fairness, whilst boys share less. In one study, boys showed fifty times more competition, whilst girls showed twenty times more turn-taking (Charlesworth & Dzur, 1987).
2. *Rough and tumble play* or "rough housing" (wrestling, mock fighting, and so on). 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 from 1 year old 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 3 years old, girls are already ahead of boys in their ability to infer what people might be thinking or intending (Happé, 1995). This sex difference appears in some but not all studies (Charman, Ruffman, & Clements, 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 & Johnson, 1979). Girls are more likely to endorse cooperative 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, Fabes, & Higgins, 1989).
8. *Disorders of empathy* (such as psychopathic personality disorder or conduct disorder) are far more common among males (Blair, 1995; Dodge, 1980).
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.), whilst 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 & Grotpeter, 1995).
10. *Murder* is the ultimate example of a lack of empathy. Daly and Wilson (1988) analyzed 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 cooperative, reciprocal, and collaborative. In concrete terms, this is also reflected in the ability of girls 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, whilst 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, whilst 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, Baron-Cohen, Wheelwright, Ba'tki, & Ahluwalia, 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, Baldwin, & Crowson, 1997) 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 14.3 shows the data from the Empathy Quotient (EQ), a validated, 60-item, self-report questionnaire (Baron-Cohen & Wheelwright, 2004). It has been factor analyzed in two independent studies (Lawrence, Shaw, Baker, Baron-Cohen, & David, 2004; Muncer & Ling, 2006) to suggest the existence of three distinct components, which roughly correspond

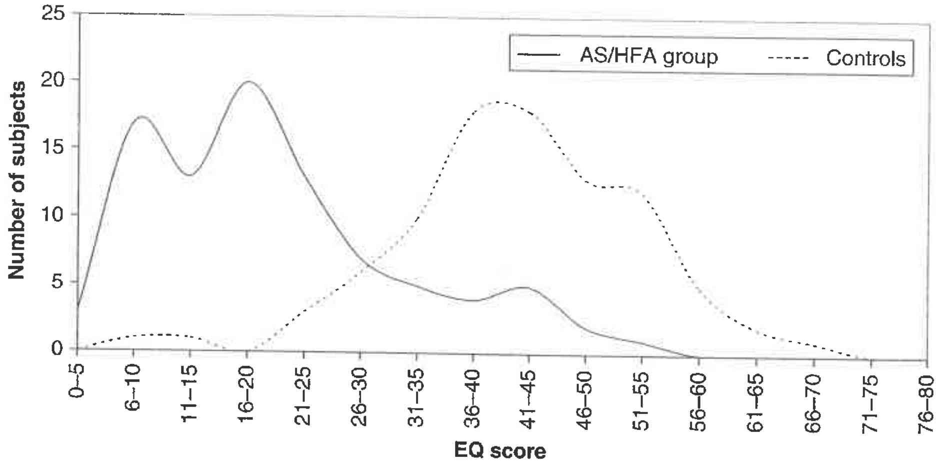

Figure 14.3 The normal distribution of empathy in the population (dotted line). Also shown is the distribution of empathy scores from people with Asperger syndrome (AS) or high functioning autism (HFA). *Note.* From "The Empathy Quotient (EQ): An Investigation of Adults with Asperger Syndrome or High Functioning Autism, and Normal Sex Differences," by S. Baron-Cohen and S. Wheelwright, 2004, *Journal of Autism and Developmental Disorders, 34*, 163–175.

to the three-component model of empathy. Scores on the EQ show a continuous distribution in several populations, with scores from people with autism spectrum conditions (ASC) clustering toward the lower end (see Figure 14.3). The EQ is associated with significant sex differences (Goldenfeld, Baron-Cohen, Wheelwright, Ashwin, & Chakrabarti, 2007).

The search for the neural correlates of empathy has had two traditions of research, one focusing on theory of mind studies (largely involving 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 (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996).

On finding increasing evidence of sex differences in the EQ in the "normal" population, we sought to investigate the neural correlates of this trait measure of empathizing across the population. Since trait empathy, by definition, influences how we perceive and respond to 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 as well as the different processes that contribute to the development of empathy. We then discuss a recent neuroimaging study from our laboratory that explicitly addresses this question.

Neuroimaging Studies of Empathizing and Emotion

Neuroimaging studies, conducted mostly on adults, 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 (see Plate 7).

(1) Studies of emotional contagion have demonstrated involuntary facial mimicry (Dimberg, Thunberg, & Elmehead, 2000), as well as activity in regions of the brain where the existence of "mirror" neurons has been suggested; for example, the inferior frontal gyrus, the inferior parietal lobule, and the superior temporal sulcus (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Jackson, Meltzoff, & Decety, 2005; Wicker et al., 2003). Dapretto and colleagues (2006) have recently demonstrated that children with ASC show a lower response in inferior frontal gyrus both during observation and explicit imitation of facial expressions of emotion, when compared to typically developing controls.

(2) ID has been tested in a PET study in a task involving attribution of intentions to cartoon characters versus predicting physical causality using the same set of characters (Brunet, Sarfati, Hardy-Bayle, & Decety, 2000). Significantly activated regions included the right medial prefrontal (BA 9) and 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, Happé, Frith, & Frith, 2000), it was found that the "intentionality" score attributed by the participants to individual animations was positively correlated to the activity in the superior temporal sulcus (STS), the temporoparietal

junction, and the medial prefrontal cortex. In a subsequent study (Castelli, Frith, Happé, & Frith, 2002), a group difference in activity in the same set of structures was demonstrated between people with ASC and typical controls.

(3) EDD has been studied in several neuroimaging studies on gaze direction perception (Calder et al., 2002; Grosbras, Laird, & Paus, 2005; Pelphrey, Singerman, Allison, & McCarthy, 2003), and have implicated the posterior STS bilaterally. This evidence, taken together with similar findings from primate literature (Perrett & Emery, 1994), suggests that this area is a strong candidate for the anatomical equivalent of the EDD.

(4) A recent imaging study (Williams, Waiter, Perra, Perrett, & Whiten, 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 non-joint attention (Frith & Frith, 2003).

(5) Traditional "theory of mind" (cognitive empathy) tasks have consistently shown activity in the medial prefrontal cortex, the superior temporal gyrus, and the temporoparietal junctions (Frith & Frith, 2003; Saxe, Carey, & Kanwisher, 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 & 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 suggests that these affect programs might have discrete neural bases (Calder, Lawrence, & Young, 2001). Fear is possibly the most well-investigated emotion. Passive viewing of fear expressions as well as experiencing fear (as induced through recalling a fear memory or seeing fear stimuli) reliably activates the amygdala, orbitofrontal cortex, and the anterior cingulate cortex (Blair, Morris, Frith, Perrett, & Dolan, 1999; Hariri, Mattay, Tessitore, Fera, & Weinberger, 2003). There is considerable evidence from nonhuman primates (Kalin, Shelton, & Davidson, 2001) and rats (LeDoux, 2000) to suggest a crucial role for these regions in processing fear. Passive viewing of disgust faces as well as experiencing disgust oneself is known to evoke a response in the anterior insula and globus pallidus as reported in several studies (Calder et al., 2001; Phillips et al., 1997; 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, Deichmann, Critchley, & Dolan, 2002; viewing funny cartoons: Mobbs, Greicius, Abdel-Azim, Menon, & Reiss, 2003; remembering happy events: Damasio et al. 2000) concurs well with studies that report activation of this region in response to viewing happy faces (Lawrence et al., 2004; Phillips, Baron-Cohen, & Rutter, 1998; Phillips et al., 1998).

Perception of angry expressions has been shown to evoke a response in the premotor cortex and the striatum (Grosbras & Paus, 2006) as well as the lateral orbitofrontal cortex (Blair & Cipolotti, 2000; Blair et al., 1999). The results of studies on the processing of sad expressions are comparatively less consistent. Perception of a sad face and induction of a sad mood are both known to be associated with an increased response in the subgenual cingulate cortex (Liotti et al., 2000; Mayberg et al., 1999), the hypothalamus in humans (Malhi et al., 2004) and in rats (Shumake, Edwards, & Gonzalez-Lima, 2001), as well as in the middle temporal gyrus (Eugene et al., 2003). There have been very few studies on the passive viewing of surprise. One study by Schroeder and colleagues (2004) 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 (Rolls, 2002) become increasingly relevant as we consider the more socially complex emotions—for example, pride, shame, and guilt—since it would not be 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 from 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 (Murphy, Nimmo-Smith, & Lawrence, 2003; Phan, Wager, Taylor, & Liberzon, 2002). Some studies using other sensory stimuli (olfactory: Anderson et al., 2003; gustatory: Small et al., 2003; auditory: Lewis, Critchley, Rothstein, & Dolan, 2005) have shown the possibly dissociable role of the amygdala and the orbitofrontal cortex in processing emotions along the two dimensions of valence and arousal.

The relative absence of neuroimaging studies of "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 and colleagues (2004), who reported activation in the ventromedial prefrontal cortex, the left superior temporal sulcus, and higher visual cortices when participants read sentences designed to evoke guilt or embarrassment. This, taken together with the areas underlying the ToMM system, suggests 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 among individuals at different points on the EQ continuum?

A direct approach to investigating individual differences in empathizing has been to test for sex differences in the perception of emotions. Using facial electromyography, 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 meta-review of neuroimaging results on sex differences in emotion perception, Wager and colleagues (Wager, Phan, Liberzon, & Taylor, 2003) report that females show increased bilaterality in emotion-relevant activation compared to males, though this is not always found (Lee et al., 2002; Schienle, Shafer, Stark, Walter, & Vaitl, 2005). One of the reasons for this might be 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, Sivers, Whitfield, Gotlib, & Gabrieli, 2002) or genetic differences (e.g., Hariri et al., 2002)) may be more finely tuned.

To test this model of individual variability, we asked whether an individual's score on the EQ predicted his or her response to four basic emotions (happy, sad, angry, disgust). If empathizing was modulated by a unitary circuit, then individual differences in empathizing would correlate with activity in the same structures for all basic emotions. Twenty-five adult volunteers (13 female, 12 male), selected across the EQ space, were scanned in a 3T 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, Baron-Cohen, & Bullmore, 2005).

Using a whole-brain analysis with permutation-based techniques (XBAMM, www-bmu.psychiatry.cam.ac.uk/software/docs/xbamm/), we found that different regional responses were correlated with the EQ for different emotions. Specifically, for the 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, 2004). This suggests that the more empathic a person is, the higher is his or her reward response to a happy face. Interestingly, the response from the same region correlated negatively with the EQ during the perception of sad faces. This fits perfectly with the earlier results; that is, the more empathic a person is, the lower is his or 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 (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 the perception of specific emotions.

However, empathizing does not appear to be purely an index of mirroring. For the 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 ToM 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 the 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-IFG response to disgust expressions. A re-examination of the behavioral literature on disgust sensitivity reveals a similar result since Haidt, McCauley, and Rozin (1994) suggested that increased socialization leads to lower disgust sensitivity. Individuals with high EQ may socialize more than those with low EQ.

The results suggest that empathizing with different basic emotions involves distinct brain regions. 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 another's (e.g., the superior temporal gyrus and precuneus/inferior parietal lobule response to angry faces correlating with EQ). While this explanation fits the discrete emotions model, it did not explicitly test whether there was any region that was common to all four correlation maps. To explore this, we performed a conjunction analysis for all four (emotion-neutral) versus EQ correlation plots. Using a hypothesis-driven region of interest analysis, we found a significant overlap in the left IFG-premotor cortex. This region was positively correlated with EQ for all four (emotion-neutral) contrasts.

The IFG-premotor cortex is a fundamental part of the "mirror systems" discussed earlier (Keysers & Perrett, 2004; Rizzolatti & Craighero, 2004). Several studies have shown involvement of "mirror systems" during perception of facial expressions (Buccino et al., 2001; Carr et al., 2003; Dapretto et al., 2006) and actions (Johnson-Frey et al., 2003; Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2005) in humans. This fits well with predictions from heuristic models that integrate perception and action (Hurley, 2005). The lower IFG-premotor response to all expressions as a function of trait empathy corroborates similar findings (Dapretto et al., 2006; Nishitani, Avikainen, & Hari, 2004). However, some studies (Carr et al., 2003; Dapretto et al., 2006) have used paradigms involving perception and explicit imitation of facial expressions and did not report any analysis for possible differences between emotions. Our analysis takes these possible differences into account and the IFG-premotor cluster emerges as a candidate region that correlates with empathy, independent of which emotion is being perceived.

This result provides a putative biomarker for empathy, a trait distributed continuously across the general population, with people with autism spectrum conditions (ASC) clustering toward the low end (Baron-Cohen & Wheelwright, 2004).

Common and Discrete Neural Substrates of Empathy

Comparing the results from the conjunction analysis (showing a common neural substrate of EQ across different emotions) with those from the whole-brain analysis (showing varying spatial patterns of correlation of EQ with different emotions) shows that there are both common regions that underlie empathy across different emotions and regions specific to certain emotions.

We interpret this using a model of face processing (Haxby, Hoffman, & Gobbini, 2000) applied to a discrete-emotions framework (see Figure 14.4a). At its simplest, the model proposes a core visual system for face perception. This constitutes the inferior occipital gyrus (IOG, for low level facial feature analysis), the lateral fusiform gyrus (FG, for higher order invariant aspects of faces such as identity), and the superior temporal sulcus (STS, for variable aspects of faces, such as lip movement and speech comprehension). This then interacts with an extended system, which involves different structures for different emotions (Haxby, Hoffman, & Gobbini, 2002). Focusing specifically on the perception of dynamic facial expressions of emotion, we propose that an intermediate module for action perception is involved, in line with similar suggestions from others (Gallese, 2003; Keysers & Perrett, 2004; Preston & de Waal, 2002; Rizzolatti & Craighero, 2004; see Figure 14.4b).

Focusing on the left of the dotted line in Figure 14.4b shows the processes that are equally influenced by trait empathy across all emotions. This includes the regions involved in face perception and the fundamental "mirror systems" used for action perception. This is revealed by the conjunction analysis, which shows a cluster that includes the IFG-premotor cortex. The common element in different facial expressions of emotion is the fact that they involve movement of eyes and mouth, which are possibly coded for by the generic "mirror systems" used for action perception. However, on investigating the interaction of each emotion with empathy, we move over to the right-hand side of the dotted line, which gives us emotion-specific correlation maps, in accordance with the discrete emotions model. We interpret these in light

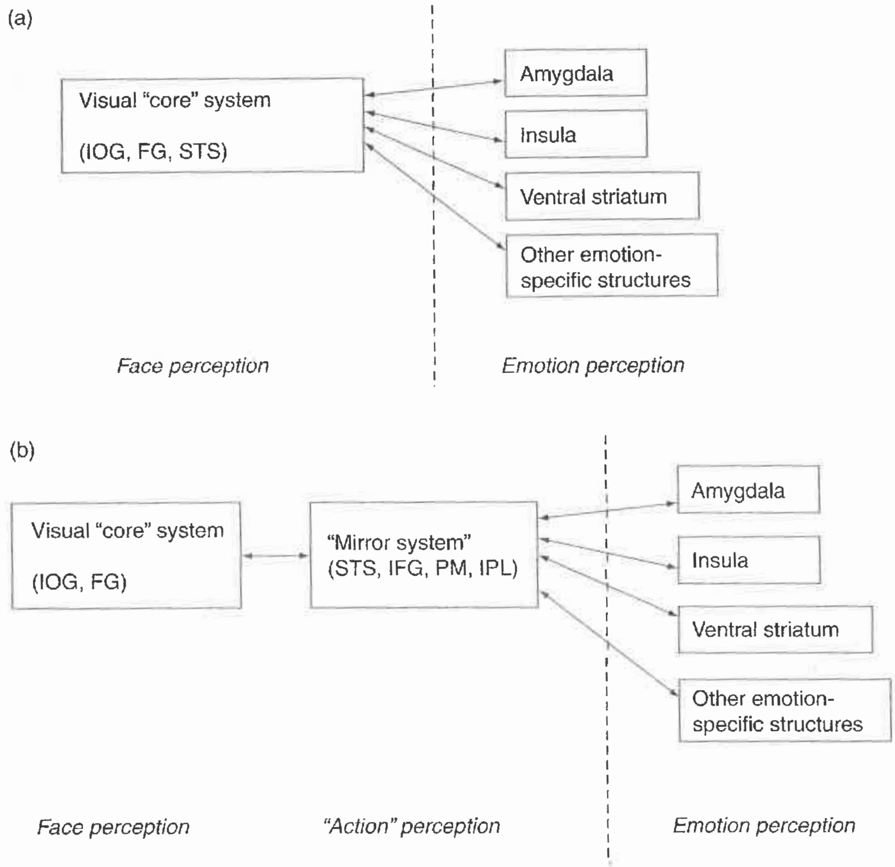

Figure 14.4 (a) The original model for face perception proposed by Haxby et al. (2000) applied to a discrete-emotions framework. (b) Suggested modifications to the model, specifically for perception of facial expressions of emotion, incorporating a module for "action perception." IOG, inferior occipital gyrus; FG, fusiform gyrus; STS, superior temporal sulcus; IFG, inferior frontal gyrus; PM, premotor cortex; IPL, inferior parietal lobule.

of their evolutionary function. It is worth noting, though, that we do not propose a strict temporal sequence of activation from left to right of this model; nor do we represent subcortical pathways from the visual areas to the emotion-related structures. As in the original model, several of these regions are reciprocally connected and the temporal progression of activation could be mediated through reafferent projections (Iacoboni et al., 2001). These can be investigated through methods that allow better temporal resolution (e.g., magnetoencephalography) and forward-model-based connectivity analysis (e.g., dynamic causal modeling: Friston, Harrison, & Penny, 2003).

This study 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.

At the molecular level, empathy is likely to be determined by other individual differences, such as fetal testosterone (Castelli et al., 2000; Knickmeyer, Baron-Cohen, Raggatt, & Taylor, 2005), genetic variation (Chakrabarti, Kent, Suckling, Bullmore, & Baron-Cohen, 2006; Skuse et al., 1997), as well as early care or neglect (Fonagy, Steele, Steele, & Holder, 1997). We conclude that more basic research into the neuroscience of empathy will enrich our understanding of this most fundamental human quality.

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