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Empathy from the Perspective of Social Neuroscience

Olga Klimecki & Tania Singer

Empathy, which can be broadly defined as the capacity to share and understand other people's emotions (for comprehensive reviews, see Batson, 2009a; Decety & Jackson, 2006; de Vignemont & Singer, 2006; Eisenberg, 2000; Hoffman, 2000; Singer & Lamm, 2009; Singer & Leiberg, 2009), has recently become an important focus of attention in the field of social neuroscience. What motivates the quest for the neural substrates underlying our understanding of emotions in others?

After many years in which neuroscientific research mainly focused on cognitive and sensory processing, attention has increasingly turned to understanding how the human brain tackles emotions and social interactions, which after all are both phenomena at the core of our existence as social beings. Thus, the field of social neuroscience has started to investigate the neural mechanisms underlying social cognition and emotions, such as our ability to empathize. In addition to the basic understanding of the biological mechanisms underlying social emotions and empathy in healthy individuals, research on the neural substrates of empathy may also help us understand clinical phenomena related to a lack of affective and social skills such as autism, which is characterized by impairments in social interaction and communication (American Psychiatric Association, 2000), or alexithymia, a subclinical phenomenon associated with difficulties in identifying and describing emotions (Nemiah, Freyberger, & Sifneos, 1976).

The importance of empathy in our everyday lives becomes clear when we try to imagine what it would be like to live in a world completely devoid of empathy. Take the following scenario, for instance: A baby starts crying while her mother is reading a book. Without empathy, the mother would probably continue reading and not look after the baby. Her capacity to empathize, however, enables her to realize the baby's needs and react to them appropriately. As this example illustrates, empathy does not only motivate other-related prosocial behavior but also enables us to better predict the behavior of others and adapt our reactions accordingly. Finally, empathy also plays a crucial role in observational learning – by witnessing the emotional reaction of others in different

circumstances, we learn which situations are good for us and which situations are better avoided.

In this chapter, we start out by revisiting the definition of empathy and delineating it from other routes to social understanding; namely, theory of mind and action understanding. We then examine the theoretical and neural underpinnings of concepts such as emotion contagion and mimicry, which can be thought of as antecedents of empathy, and compassion and empathic distress, which are introduced as consequences of empathy. Before turning our focus to how research in social neuroscience has advanced our understanding of empathy in the human brain, we review the major contributions of psychological research to our understanding of empathy and its relation to prosocial behavior. Because the neural underpinnings of empathy have been examined most prominently in the domain of empathy for pain, we begin by summarizing this line of research and discussing the reported results in light of the shared network hypothesis. In this context, we stress the specific role of the insula as a neural structure that processes both, interoception and empathy. Subsequently, we describe factors that modulate the experience of empathy for pain along with their neural underpinnings, before turning to neural correlates of empathy in other domains such as touch or smell. Finally, we show initial findings from social neuroscience research focusing on more positive aspects of empathy, such as compassion. We conclude the chapter by outlining outstanding questions in the field.

Defining Empathy and Related Concepts

Empathy is commonly defined as the human capacity to understand and share another person's emotion without confusing it with one's own emotional state (for comprehensive reviews, see Batson, 2009a; Decety & Jackson, 2006; de Vignemont & Singer, 2006; Eisenberg, 2000; Hoffman, 2000; Singer & Lamm, 2009; Singer & Leiberg, 2009). In other words, we empathize with another human being when we vicariously share their affective state, but at the same time are aware that the other person's emotion is causing our response.

In this section, we first point out the conceptual difference among *empathy, mentalizing,* and *action understanding,* which can be conceived of as different routes to the understanding of others. After showing that the psychological distinction among these three concepts is paralleled by differences in the underlying neural networks, we take a closer look at the "sisters of empathy" – *emotion contagion, mimicry, sympathy and compassion* – all of which are concepts closely related to empathy.

Mentalizing and Action Understanding as Alternative Routes for Understanding Others

In addition to *empathy,* which can be seen as the emotional route for understanding others, there are at least two other ways of putting oneself into another person's shoes. On the one hand, we have the cognitive ability to understand the thoughts, beliefs, and intentions of others, which is called *mentalizing, perspective-taking,* or *theory of mind* (ToM; Frith and Frith, 2003; Premack and Woodruff, 1978). On the other hand, we have the capacity to understand the motor intentions of others, which has been associated with the discovery of mirror neurons (see Rizzolatti & Sinigaglia, 2010, for a review). Although all three often occur simultaneously in everyday social cognition, the psychological and neural processes underlying these distinct routes to understanding others can be clearly distinguished (for reviews, see de Vignemont & Singer, 2006; Preston & de Waal, 2002; Singer & Lamm, 2009). Cognitive processes related to theory of mind have been associated with activations in the medial prefrontal cortex (mPFC), superior temporal sulcus (STS), and the adjacent temporoparietal junction (TPJ; for reviews, see Amodio & Frith, 2006; Frith & Frith, 2006; Mitchell, 2009; Saxe, 2006; Saxe & Baron-Cohen, 2006), whereas

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the neural correlates of *action understanding* are found in a neural network spanning the inferior parietal lobe (IPL), the inferior frontal gyrus, and ventral premotor areas (see Rizzolatti & Sinigaglia, 2010, for a recent review). In monkeys, recordings from so-called *mirror neurons* in corresponding areas have revealed that these neurons encode both the execution of an action and the observation of the same action in others (Gallese et al., 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Paralleling the establishment of this mirror network in monkeys, recent research has extended these findings to humans by means of magnetoencephalography, (MEG; Hari et al., 1998), transcranial magnetic stimulation (TMS; Cattaneo, Sandrini, & Schwarzbach, 2010; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995) and functional magnetic resonance imaging (fMRI) studies (Iacoboni et al., 2005). Together, these studies suggest that monkeys as well as humans may use the same neural structures to encode their own actions and to understand the actions of others (for a review, see Rizzolatti & Craighero, 2004, or Rizzolatti & Sinigaglia, 2010). In a meta-analysis, Grèzes and Decety (2001) compared the activation foci of a variety of studies and found that overlapping activations for execution, simulation, and observation of actions are located in the supplementary motor area, dorsal premotor cortex, supramarginal gyrus, and superior parietal lobe. Finally, as discussed in detail later, the neural correlates of empathy are mainly observed in limbic and paralimbic areas such as the anterior insula (AI) and anterior cingulate cortex (ACC; for recent reviews, see Lamm & Singer, 2010; Singer & Lamm, 2009; Singer & Leiberg, 2009). Together, theory of mind, action understanding, and empathy allow us to infer the thoughts, motor intentions, and emotions of others, thereby facilitating social interactions.

Different Components of Empathy

After having introduced theory of mind, action understanding, and empathy as three

complementary routes to the understanding of others relying on distinct neural networks, we now describe the different facets of empathy-related phenomena. They range from rather automatic and primitive reactions, such as mimicry and emotional contagion (which can be thought of as precedents of empathy), to states like compassion or empathic distress that follow from empathy and are, themselves, important determinants of behavior (Figure 23.1; Batson, 2009b; de Vignemont & Singer, 2006; Eisenberg, 2000; Goetz, Keltner, & Simon-Thomas, 2010; Klimecki & Singer, 2012; Singer & Lamm, 2009).

Mimicry and Emotional Contagion

Mimicry can be described as an automatically elicited response mirroring another person's emotional expression conveyed by facial, vocal, or postural expressions or by movements (see Hatfield, Rapson, & Li, 2009, for a recent review). In the domain of facial mimicry, for instance, electromyographic (EMG) recordings reveal that the visual presentation of emotional faces elicits corresponding emotional facial expressions in the observer (see Dimberg & Öhman, 1996, for a review); the perception of happy faces evokes increased activity in the zygomatic major muscle (which raises the corners of the mouth during smiling), whereas the perception of angry faces leads to increased activity in the corrugator supercilii muscle (which is associated with frowning). The short latency between stimulus onset and facial reaction (300–400 ms) supports the claim that facial mimicry is elicited automatically and occurs preattentively. Complementing these findings in the domain of facial mimicry, researchers observed that people also tend to synchronize their vocal expressions and adopt the postures and movements of others (reviewed, for example, by Hatfield et al., 2009).

Emotional contagion goes one step further than mimicry in that the automatic imitation and synchronization of displayed emotions – whether at the level of facial expressions, vocalizations, postures, or
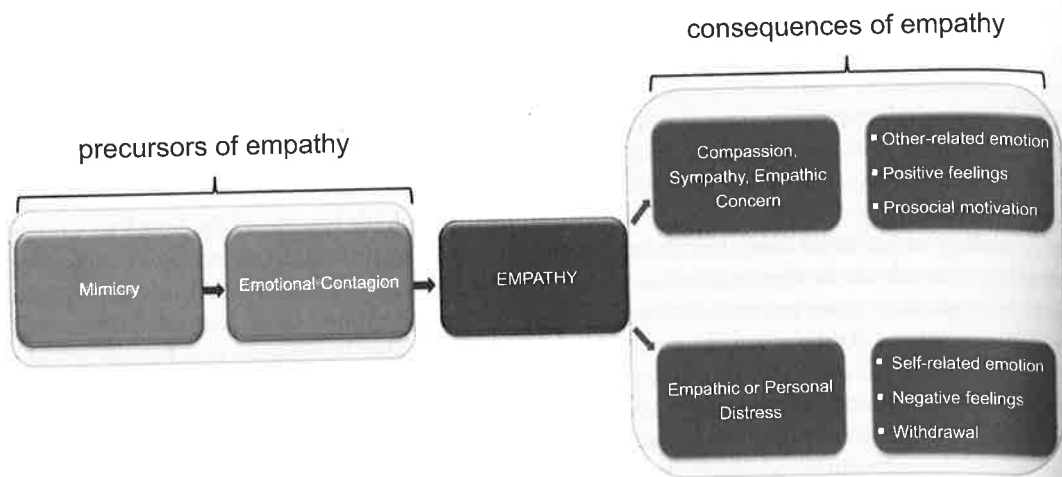
Figure 23.1. Schematic model showing the precursors and consequences of empathy.

movements – result in a convergence in the actual emotional experience (see Hatfield et al., 2009, for a recent review or Dimberg & Öhman, 1996). This is in line with the claim that peripheral-physiological feedback shapes our emotional experience (e.g., Adelmann & Zajonc, 1989) and the finding that perceiving another person in a certain emotional state can induce a congruent state in the observer (e.g., Gottman & Levenson, 1985; Harrison, Singer, Rotshtein, Dolan, & Critchley, 2006; Neumann & Strack, 2000). More concretely, this finding suggests that seeing another person smile makes us smile, which in turn makes us feel happy. Mimicry and emotional contagion can thus be regarded as precursors of empathy. In contrast to emotional contagion and mimicry, however, which can occur without self-other distinction, empathy crucially relies on the capacity to distinguish between oneself and the other. In other words, an empathic observer is aware that he or she is experiencing feelings vicariously and that these feelings were induced by emotions experienced by another person, not by his or her primary experience (de Vignemont & Singer, 2006).

Empathic Distress

Whereas mimicry and emotion contagion can be regarded as precursors of empathy, empathy may, in turn, lead to two opposing consequences: empathic distress and compassion. *Empathic distress*, which is also referred to as *personal distress*, is an aversive and self-oriented emotional response to the suffering of others. It often results in withdrawal behavior, which is motivated by the desire to protect oneself from negative emotions (Batson, O'Quin, Fultz, Vanderplas, & Isen, 1983; Eisenberg et al., 1989). In this light, empathic distress, although regarded as a consequence of empathy, falls somewhat between emotion contagion and empathy as the self-other distinction becomes blurred when the secondary empathic experience triggered by another person's suffering becomes so overwhelming that it turns into distress. This concept is particularly important for people working in health care sectors, where repeated encounters with suffering may lead to burnout (for a review, see Klimecki & Singer, 2012). Therefore, it is vital to find alternative ways of dealing with the suffering of others: Empathy does not necessarily have to take the route of empathic distress, but can instead lead to more adaptive positive emotions of compassion.

Compassion, Empathic Concern, and Sympathy

Compassion, empathic concern, and sympathy' all denote affective states that can be experienced as a consequence of empathy

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- Positive feelings
- Prosocial motivation

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and that are not shared *with* someone, but felt *for* someone (Batson, 2009a; Singer & Lamm, 2009). Empathy or *"feeling with"* denotes a state in which the feelings of someone else are vicariously shared so that the empathizer feels an isomorphic state (de Vignemont & Singer, 2006): On witnessing a sad person, the empathizer becomes sad him- or herself. In contrast, *"feeling for"* someone refers to an emotional state that is not necessarily isomorphic to the target's affective state, but instead relies on feelings of concern for the other. More precisely, compassion can be defined as *"the emotion one experiences when feeling concern for another's suffering and desiring to enhance that individual's welfare"* (Keltner & Goetz, 2007). In other words, compassion consists of two main components. First, there is a caring feeling for the suffering of others that secondly motivates behavior aimed at relieving the other's suffering. As described in detail later, research in social and developmental psychology has demonstrated that empathic concern actually motivates prosociality and helping behaviors (see Batson, 2009b, or Eisenberg, 2000, for a review). In sum, whereas empathy is a vicarious emotion isomorphic to the emotional experience of the other, the experience of compassion, sympathy, or empathic concern denotes an affective state experienced with regard to the other that does not encompass the sharing of negative affect, but instead relies on a feeling of care and concern that motivates prosocial behavior. Before turning to empirical evidence for the promotion of prosocial behavior by compassion, we provide an overview of measures developed by psychologists to assess empathy and its different components.

Empathy Research in Psychology

Psychologists from various fields have investigated empathy and its relation to prosocial behavior. In this section, we first describe self-report, behavioral, and physiological measures of empathy before summarizing how research in developmental and social

psychology established the link between empathy and prosocial behavior. Theodor Lipps (1903) first introduced the concept of empathy by proposing that we imitate the gestures and actions of others in order to understand their inner states. To measure empathy, Davis (1980) developed a questionnaire called the Interpersonal Reactivity Index (IRI) that includes four distinct components: perspective-taking, empathic concern, personal distress, and fantasy. Perspective-taking is very close to the earlier mentioned notion of theory of mind, because it measures the tendency of people to cognitively adopt the perspective of others. Empathic concern, however, is related more closely to the concept of sympathy or compassion as discussed earlier, whereas the personal distress subscale measures how prone individuals are to experiencing discomfort as a result of witnessing distress in others. Finally, the fantasy scale asks people how well they tend to identify with fictional characters in books or movies. The Balanced Emotional Empathy Scale (BEES; Mehrabian, 1997; Mehrabian & Epstein, 1972), which includes subscales such as "susceptibility to emotional contagion" or "sympathetic tendency," is another questionnaire that measures the emotional aspects of empathy.

These self-report measures are complemented by the assessment of empathic accuracy. Levenson and Ruef (1992), for instance, presented subjects with videotaped marital interactions. By comparing the subjects' ratings of positive and negative emotions displayed in the video with the self-report of the actual target, an empathy accuracy score is obtained that assesses the degree to which subjects correctly identify the emotional state of others. Additionally, physiological measures such as skin conductance and heart rate can be compared with respect to the level of physiological linkage between the target and the subject empathizing with the target (see also Gottman & Levenson, 1985). Ickes and colleagues (Ickes, 1993, for a review) used a similar approach to determine to what degree subjects succeed in inferring another person's thoughts and the content of their emotions.

Empathy and Its Relation to Prosocial Behavior

To establish the link between empathy and prosocial behavior, researchers in developmental and social psychology have conducted studies that suggest that empathy can have two opposing consequences depending on the nature of the empathic experience. In the field of social psychology, Batson and colleagues conducted several experiments (see Batson, Duncan, Ackerman, Buckley, & Birch, 1981; Batson, Fultz, & Schoenrade, 1987; Batson et al., 1983) that established that participants experiencing empathic concern feel the urge to help people in need, regardless of whether the adverse situation is easy or difficult to escape. On the contrary, participants suffering from empathic distress tend to be more self-oriented and to withdraw from negative experiences whenever possible; thus they only choose to help when the aversive situation is difficult to escape. This tendency to escape might result from aim to protect oneself by reducing one's own negative affect.

The link between empathic concern vs. empathic distress and prosocial behavior has been extended to children by research in developmental psychology, which, in addition, has established a relationship between the physiological correlates of emotional reactions and helping behavior (for a review, see Eisenberg, 2000). Eisenberg and colleagues (1989), for instance, found that adults' self-reports and facial display of sympathy predicted prosocial behavior. In children, however, the propensity to offer help was not predicted by their verbal reports of distress and sympathy. Instead, children's facial display of distress was negatively related to helping. This difference between adults and children may indicate that children's capacity to report their emotional experience reliably is underdeveloped. In sum, these results indicate that although there are differences between adults and children, empathic concern (or sympathy) promotes prosociality, whereas empathic distress is associated with withdrawal tendencies. Interestingly, a recent study revealed that prosocial behavior toward strangers can be increased by short-term training of compassion (Leiberg, Klimecki, & Singer, 2011). These findings have broad implications for the implementation of compassion training in schools and other public organizations, because compassion was shown to be a trainable and generalizable skill, motivating prosocial behavior that even extends toward strangers.

Empathy in Social Neuroscience

After having reviewed the various methods employed by social and developmental psychologists to study empathy and related concepts, we turn to the paradigms developed by social neuroscientists. Because a vast majority of empathy studies in the fMRI setting are based on variations of the empathy-for-pain paradigm, we begin this section by describing the main methods, findings, and implications of empathy-for-pain research. Subsequently, we integrate these findings with neuroscientific studies on empathy in various other domains.

Empathy for Pain

Given that empathy is a highly social phenomenon, researchers were (and still are) faced with the difficulty of coming up with a paradigm that is compatible with fMRI measurements while at the same time being ecologically valid. To reconcile both aims, Singer and colleagues (Singer et al., 2004) designed an empathy-for-pain paradigm in which two participants who are present in the same scanner environment alternately receive painful stimuli administered through electrodes attached to the back of their hand. More specifically, both the person lying in the scanner and the person sitting next to the scanner receive painful and nonpainful electric stimulation. This setup allows for the comparison between brain responses elicited when the scanned subjects experience painful stimulation versus neural activations related to witnessing

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another person experiencing pain. During the brain scan, arrows in different colors that can be seen by the participant through the help of a mirror system indicate who is going to be stimulated next and whether the stimulation is going to be painful or not. Under the assumption that people in a very close relation feel strong empathy for each other, Singer and colleagues (2004) started out by examining empathy for pain in couples. Intriguingly, the results of this study show that the neural signature of empathy for pain is very similar to the neural processes underlying the self-experience of pain (for brain circuits mediating pain perception, the so-called pain matrix, see Chapter 9). More specifically, empathy for pain activated selective parts of the neural pain matrix including the AI and the anterior cingulate cortex (ACC), which both are key regions in processing bodily and feeling states (see also Singer, Critchley, & Preuschoff, 2009, and Chapter 3). These findings have been replicated by several studies using similar paradigms (Bird et al., 2010; Hein, Silani, Preuschoff, Batson, & Singer, 2010; Singer et al., 2006, 2008). Converging evidence for the involvement of AI and, less consistently, the ACC in empathy for pain also has been obtained from several other studies (some of which are discussed in more detail later) using various paradigms ranging from simultaneous pain administration in the scanner to the presentation of photographs or videos depicting painful events (e.g., Botvinick et al., 2005; Cheng, Chen, Liu, Chou, & Decety, 2010; Chen et al., 2007; Danziger, Faillenot, & Peyron, 2009; Decety, Echols, & Correll, 2010; Gu & Han, 2007; Jackson, Brunet, Meltzoff, & Decety, 2006; Lamm, Batson, & Decety, 2007; Lamm & Decety, 2008; Lamm, Nusbaum, Meltzoff, & Decety, 2007; Moriguchi et al., 2007; Morrison, Lloyd, di Pellegrino, & Roberts, 2004; Ogino et al., 2007; Saarela et al., 2007; Zaki, Ochsner, Hanelin, Wager, & Mackey, 2007).

In support of the claim that the observed neural activation patterns are closely related to the concept of empathy developed by psychologists, Singer and colleagues (2004)

showed that higher self-reports of empathy as measured by the BEES and the IRI were accompanied by increased neural activity during empathy for pain in the left AI and ACC, thereby supporting the external validity of the empathy-for-pain paradigm. Further evidence for the link between the observed brain responses and empathic experience stems from studies in which neural activation patterns in specific empathy-related regions were shown to correlate with self-reported impressions and actual helping behavior (Hein et al., 2010), as well as with individual unpleasantness ratings (e.g., Jabbi, Swart, & Keysers, 2007; Lamm, Nusbaum, et al., 2007; Saarela et al., 2007; Singer et al., 2008). Importantly, the existence of a shared neural network for self-experienced pain and empathy for pain is supported by a recent meta-analysis of Lamm, Decety, and Singer (2011), which showed consistent overlaps in AI and ACC across nine independent fMRI studies and is discussed in more detail later. Although the studies described here point to a shared neural representation of self-experienced and vicariously experienced pain, the question still remains whether activations in the AI and the ACC overlap on the level of neuronal subpopulations and single neurons (e.g., Singer & Lamm, 2009).

Shared and Distinct Neural Networks in Empathy for Pain

In addition to confirming an overlap between first-hand and vicarious pain experience in the AI and ACC, the meta-analysis of Lamm and colleagues (2011) suggests that this shared network can be accessed via several routes depending on the paradigm employed. Whereas the use of picture-based empathy paradigms is linked to additional activation increases in the inferior parietal, ventral premotor, and dorsomedial cortex (a neural circuitry typically observed in action understanding), cue-based paradigms induce activation in networks typically linked to theory of mind, such as the mPFC, precuneus, STS, and TPJ.

Distinct connectivity patterns of the AI and ACC with other brain regions during self-experienced pain versus empathy for pain have been examined by Zaki and colleagues (2007), who reported that self-experienced pain is associated with stronger connectivity between the AI and regions involved in the transmission of painful sensations, such as clusters in the midbrain, periaqueductal gray, and mid-insula. Conversely, empathy for pain has been shown to be associated with higher connectivity of the ACC and AI with brain regions implicated in social cognition and affect processing, such as the medial prefrontal cortex.

Converging evidence for the activation of sensory brain structures during self-pain stems from the earlier mentioned meta-analysis (Lamm et al., 2011), where the direct experience of pain recruited mid- and posterior insula, as well as primary sensory cortices in addition to the AI and ACC (see Figure 23.2 for illustration). The stronger involvement of brain regions processing sensory information in self-experienced pain suggests that we share the pain of others by accessing the neural structures representing our own affective states, while leaving aside sensory and nociceptive components.

Moreover, the meta-analysis on empathy for pain showed that contralateral primary somatosensory cortex (SI) activation, which most likely encodes somatosensory aspects of painful sensations, is restricted to self-experienced pain in cue-based studies. Picture-based studies, on the contrary, evoke bilateral SI activations during both empathy for painful and nonpainful situations, thus pointing to an unspecific role of the SI in empathy for pain that is presumably related to seeing body parts being touched. Interestingly, activity in somatosensory cortices can also be increased when subjects are instructed to evaluate the sensory consequences of painful stimuli, suggesting that attention can influence the quality of the empathic experience and that this shift in focus is accompanied by corresponding brain activations (Lamm, Nusbaum, et al., 2007). Complementing these findings, sensorimotor reso-

nance with empathy for visually depicted pain has been shown by studies using TMS (Avenanti, Bueti, Galati, & Aglioti, 2005; Avenanti, Pauuello, Bufalari, & Aglioti, 2006) and EEG (Bufalari, Aprile, Avenanti, Di Russo, & Aglioti, 2007; Valeriani et al., 2008). Taken together, these results point to a core shared network for self-experienced pain and empathy for pain in the ACC and AI that varies in its connectivity with other brain regions. Thus, the AI and ACC are coactivated with areas involved in processing self-related components of nociceptive experience when experiencing pain in oneself. However, when empathizing with others, the AI and ACC are co-activated with networks involved in social cognition (ToM and action observation). This finding suggests that the information available in the task and the situational demands determine which of the social cognition networks will be predominantly engaged.

With regard to the quality of the empathic experience, the reported studies suggest that we primarily share painful experiences by simulating the affective and not so much the sensory and nociceptive components of pain. Note, however, that there seems to be a graded activation of the neural pain matrix, such that activations in the posterior insula and secondary somatosensory cortex can be observed, even without the administration of pain, if subjects adopt a first-person perspective (Jackson et al., 2006) or simply imagine a painful event (Ogino et al., 2007). Because these activation patterns do not include the primary somatosensory cortex, there seems to be a continuum between directly and vicariously experienced pain that is reflected in the underlying neural substrates.

The Role of the Insula in Empathy and Interoception

The posterior-anterior gradient of the insula in self-experienced pain and empathy for pain is mirrored by research showing that primary nociceptive information is first processed in dorsal posterior parts of the insula
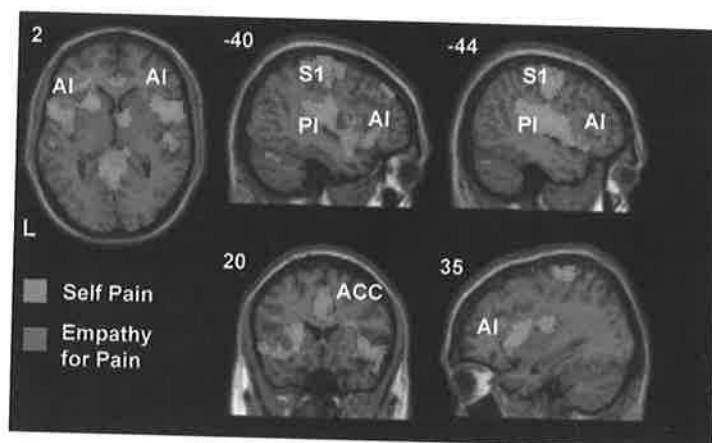
Figure 23.2. Shared and distinct neural networks for self-experienced pain and empathy for pain. Depicted functional neural activations are the result of a meta-analysis based on nine fMRI studies investigating empathy for pain (Lamm et al., 2011). Activations related to self-experienced pain (green) encompass a large portion of the insula, including the middle and posterior insular cortex, whereas activations related to empathy for pain (red) are restricted to the most anterior parts of AI, where they overlap with activations related to self-experienced pain. Functional activation maps are overlaid on a high-resolution structural MRI scan in standard stereotactic space (MNI space). White labels indicate slice number in stereotactic space, L = left hemisphere, AI = anterior insula, ACC = anterior cingulate cortex, PI = posterior insula, S1 = primary somatosensory cortex. With permission from Springer Science+Business Media: Brain Structure and Function, The role of anterior insular cortex in social emotions, 214, 2010, p. 581, Lamm, C., & Singer, T., Figure 1. See color plate 23.2.

before being remapped and integrated with other information in the AI where emotions access consciousness (Craig, 2002, 2009). These results fit into the general notion of the insula as a key player in processing interoceptive information from the body (Craig, 2002; Damasio, 1994; Ostrowsky et al., 2000, 2002; see Chapter 3) and emotions more generally (shown by a meta-analysis by Kober et al., 2008). Given these findings, Singer et al. (2004, 2009) proposed that the insula fulfills a dual role: (1) processing bodily information, such as heart beat or temperature-related sensations, which are then integrated into global feeling states, and (2) predicting the affective states of others in the process of empathizing. In other words, we use our own bodily and affective representation to understand the emotional experiences of others. This interpre-

tation implies that a deficit in understanding our own feelings should entail difficulties in empathizing with the feelings of others. Indeed, this claim was confirmed in studies focusing on people with alexithymia, a subclinical phenomenon characterized by difficulties in identifying and describing emotions (Nemiah et al., 1976). Silani and colleagues (2008) demonstrated that activity in the AI during interoception on emotional stimuli diminished with increasing alexithymia scores, whereas activation in the AI during interoception was positively related to trait empathy. Furthermore, this study showed that a higher degree of alexithymia was accompanied by lower levels of trait empathy. Extending these results, Bird and colleagues (2010), using the Singer et al. (2004) empathy-for-pain paradigm, found that AI activations also decrease when highly

alexithymic participants are asked to empathize with others in pain.

Modulation of Empathy

In this section, we discuss findings indicating that empathic brain responses in the AI are not only modulated by person-specific characteristics, such as alexithymia, but can also be affected by the relation to the target (e.g., liking or disliking), contextual and attentional factors, and the appraisal of the situation (for recent reviews, see de Vignemont & Singer, 2006; Singer & Lamm, 2009). Several studies have shown that stimuli that under normal circumstances lead to empathic responses fail to induce empathy in certain situations and may even evoke the opposite; namely what has been referred to as "Schadenfreude" – the joy of witnessing another person's misfortune.

Relationship between Empathizer and Target

Singer and colleagues (2006) observed such a reversal of emotional response to the pain of others when they studied how perceived fairness affects empathy for pain. In their experiment, participants first played an economic game with two other volunteers, one of whom played fairly while the other played unfairly. When the participant was subsequently scanned, the fair and unfair players (who were actually confederates) were sitting next to the scanner, and all three alternately received painful or nonpainful stimulation on the back of their hands. In line with previous findings, Singer and colleagues observed that both the first-hand experience of pain and empathy for pain experienced for the fair person rely on shared neural representations in the AI and the ACC. However, when empathizing with the pain of the unfair player, only female subjects showed greater activations in these regions. Male subjects, by contrast, showed a decline in AI activation while witnessing the unfair, as opposed to the fair, player in pain. This reduction

in the men's neural empathy response was accompanied by increased activation in the nucleus accumbens – a region known to be crucially involved in reward processing (for recent reviews, see Knutson & Cooper, 2005; Schultz, 2000; Chapter 19). Moreover, the extent of nucleus accumbens activation was positively correlated to the subjectively expressed desire of revenge. In other words, activity in this reward-related brain structure was higher when men reported a stronger desire for revenge toward the unfair player. This activation pattern may imply that men actually experienced "Schadenfreude" when witnessing the unfair player being punished.

In another study, Hein and colleagues (2010) extended these findings by showing a relationship between empathy-related brain responses in the AI and subsequent prosocial behavior. The authors examined ingroup-outgroup biases in male soccer fans while they witnessed a fan of their favorite team (ingroup) or a fan of a rival team (outgroup) receiving painful electric shocks. As expected, the observation of ingroup members receiving pain was linked to greater AI activations. More importantly, the intensity of AI activation actually predicted the degree to which subjects would later help their ingroup member by taking the painful shocks themselves. In contrast, nucleus accumbens (NAcc) activation elicited by witnessing an outgroup member suffering predicted a refusal to help and reflected how negatively the subject evaluated the outgroup member. These findings imply that empathy-related insula activation drives altruistic behavior, whereas an antagonistic signal in the NAcc reduces the propensity to help. Other examples of factors that influence the nature of social relationships, and thereby the degree of empathy and its neural correlates, are ethnicity (Xu, Zuo, Wang, & Han, 2009) and closeness to the other person (Cheng et al., 2010).

Characteristics of the Empathizer

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link between high alexithymia (Silani et al., 2008) and low empathy, as well as the decrease of AI activations during empathy for pain in alexithymic participants (Bird et al., 2010), the characteristics of the empathizer have also been shown to influence empathic experiences in other domains. Cheng and colleagues (2007), for instance, showed that, when observing needles being inserted into different body parts, participants without experience in acupuncture showed activations in the neural network involved in empathy for pain, whereas physicians who practice acupuncture themselves did not show such a neural response.

Situational Context, Attention, and Appraisal

The role of contextual appraisal in relation to empathy has been examined in relation to the attribution of responsibility. Decety and colleagues (2010), for example, tested the degree to which empathic responses to videos of pain in AIDS patients differed as a function of the target's responsibility (infection through transfusion or drug taking). The self-report measures and the neural activations of the subjects both conveyed that attributed responsibility influences the extent of empathic response. Participants reported higher pain and empathy ratings toward the pain of transfusion targets as compared to drug targets, and these reports were accompanied by greater activation of the neural networks involved in processing pain (AI and ACC).

Another factor that has been shown to influence empathy is attention. Gu and Han (2007) reported lower ACC activity when participants were asked to count neutral stimuli in images displaying painful events compared to rating the intensity of the pain. Finally, Lamm, Nusbaum, et al. (2007) investigated the effects of cognitive appraisal and perspective-taking on empathic responses by presenting video clips of painful facial expressions during a medical treatment. Perspective-taking was varied by instructing the participants to imagine themselves in the depicted situation

versus imagining the feelings of the patient during the medical treatment. To manipulate cognitive appraisal, subjects were told either that the medical treatment had been beneficial or unsuccessful. When subjects were told that the treatment had not been successful, they provided higher ratings of pain and unpleasantness than in the condition in which the treatment had been beneficial. Brain data corroborate these findings by showing stronger activations in the perigenual ACC for the ineffective treatment condition. With regard to the different perspectives adopted, results show that participants reported higher personal distress when they imagined themselves in the patient's situation (self-perspective), whereas participants reported more empathic concern when they cognitively differentiated between the patient and themselves (other-perspective). The observed increase in empathic distress when adopting a self-perspective fosters the claim that empathic distress arises due to an over-identification with the suffering of others. On the neural level, adopting a self-perspective was associated with increased activations of the neural pain matrix. This finding speaks for a stronger sharing of pain in distress and underscores the important distinction between empathic distress and empathic concern as two opposing outcomes of empathy associated with different qualities of emotional experience.

Empathy for Touch, Smell, and Taste

As reviewed earlier, a majority of neuroscience studies on empathy have focused on pain. However, an early study focused on the examination of shared representations for smell and disgust (Wicker et al., 2003). In their experiment, Wicker and colleagues studied how processing the actual experience of disgusting olfactory stimuli differs from processing others' visual display of disgust. The results of this fMRI study show that both self- and other-related disgust are accompanied by overlapping activation in the AI and ACC. Further support for this

finding comes from a study by Jabbi and colleagues (2008), who showed AI activation regardless of whether subjects tasted an unpleasant substance, viewed disgusted facial expressions, or read disgusting scenarios. Finally, Keysers and colleagues (2004) reported that, whereas the sensory experience of being touched is specifically linked to activation in the contralateral primary somatosensory cortex, the neural signatures of being touched and observing touch overlap in the secondary somatosensory cortex. In summary, these studies parallel findings on empathy in the domain of pain by providing evidence for the involvement of a shared neural network underlying empathy in other modalities such as touch, smell, and taste.

The Compassionate Brain

Although social neuroscience has so far mostly focused on finding evidence for shared networks and their modulation, the field has recently moved forward to the investigation of positive consequences of empathy such as empathic concern, sympathy, or compassion. In a recent intervention study, Klimecki and colleagues (Klimecki, Leiberg, Lamm, & Singer, 2012) investigated how training compassion over several days changes neural function and subjective emotional experience. To this end, the researchers specifically developed a new paradigm, the Socio-affective Video Task (SoVT) in which participants witness the distress of others. At pre-training, this stimulus material elicited strong empathy and strong negative emotions. Consistent with findings from a recent empathy for pain meta-analysis (Lamm et al., 2011), empathy ratings in response to other's distress were accompanied by activations in anterior insula and ACC. Training compassion over several days changed this response pattern: participants reported feeling more positive emotions towards the suffering of others and showed increased activations in medial orbitofrontal cortex, ventral tegmental area/ substantia nigra (VTA/SN), putamen and pallidum. The involvement of

these brain areas in compassion is also supported by cross-sectional studies on compassion and love. Kim and colleagues (2009), for instance, showed that adopting a compassionate attitude towards pictures of sad faces augmented activations in ventral striatum and VTA/SN. Moreover, romantic as well as maternal love (Bartels and Zeki, 2000; 2004) have been associated to activations in the middle insula, the dorsal part of the ACC, and the striatum (comprised of the putamen, globus pallidus, and caudate nucleus). Similar results were reported by Beauregard and colleagues (2009) who observed increased activations of the middle insula, the dorsal ACC, the globus pallidus, and the caudate nucleus when their participants adopted a stance of unconditional love toward pictures of individuals with intellectual disabilities. Finally, a cross-sectional study revealed that expert meditators, but not novice meditators had augmented activations in middle insula when listening to distressing sounds (Lutz, Brefczynski-Lewis, Johnstone, & Davidson, 2008).Given that the observed regions are linked to reward processing and show a high density of oxytocin and vasopressin receptors – neuropeptides that play a crucial role in attachment and bonding (for a review, see Depue & Morrone-Strupinsky, 2005; Zeki, 2007), the described results might be interpreted as reflecting the rewarding nature of experiencing love and warmth, even when faced with the suffering of others.

Taken together, these results suggest that the previously introduced distinction between empathic distress and compassion as the two consequences of empathy is paralleled by the involvement of different neural substrates. Whereas distressing empathic experiences have been shown to be associated with the AI and ACC, compassionate or loving experiences seem to involve the medial orbitofrontal cortex, as well as midinsular and striatal regions. Because of the scarcity of research in this field, many more studies are needed to refine the delineation of the neural networks involved in the positive emotions of compassion and love and

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Conclusion

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Conclusion

The field of social neuroscience is evolving quickly and the studies described in this chapter have (among others) greatly advanced our understanding of the neural bases of empathy. Most importantly, the development and use of ecologically valid paradigms could show that self-experienced and vicariously experienced pain rely on shared neural substrates in the AI and ACC. Together with the finding of distinct activation patterns in self-experienced affective states, this suggests that we understand the feelings of others by simulating the affective component of the observed states. In this context, the insula plays a specific role, because it generally serves as an interoceptive cortex supporting representations and predictions of feeling states for oneself and for others. Despite the major advances in our understanding of the empathic brain, many questions remain to be answered while at the same time new questions arise with newly gained insights.

Outstanding Questions and Future Directions

- In light of the findings speaking to a shared network for self-experienced and vicariously experienced emotions, how far are the neural substrates shared on the level of single neurons? Can these phenomena be distinguished by functional gradients in structures like the insula?
- By which mechanisms can empathic experiences be influenced so that, instead of resulting in empathic distress, empathy leads to compassion? Which neural changes accompany these interventions, and how do neural pathways underlying compassion differ from neural signatures of negative experiences associated with sharing someone else's pain?

- What role do neurotransmitters like oxytocin and vasopressin play in empathy, and how do they interact in the circuitry of emotion processing?
- Given that the acquisition of empathic and compassionate skills probably depends on the maturation of certain cortical structures, which neural changes accompany the development of empathy and related concepts from early childhood to adolescence? How do these findings tie in with emotional plasticity over the life-span?

Acknowledgments

Notes

1 Because these three terms are often used to denote the same underlying concept (Batson, 2009a) – with Batson primarily using the term empathic concern (Batson, 2009b), whereas Eisenberg instead speaks of sympathy (Eisenberg, 2000) – we use these terms interchangeably throughout the chapter.

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