Understanding Other Minds: Perspectives from developmental social neuroscience (3rd edn)

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CHAPTER

13   Neural sources of empathy: An evolving story 🔓

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Abstract

The ability to feel what others are feeling is basic to human social life. In recent years, neuroscientists have begun to study empathy as distinct from other affective phenomena or mentalizing. Together this research demonstrates that empathy occurs in a variety of domains and is modulated by both context and dispositional differences. Research further suggests that vicarious feeling relies upon many of the same neural networks that represent direct experience. This chapter provides an overview of the field. Focusing on empathy for pain, we describe different experimental methods and their findings. We hone in on several cortical regions that are frequently associated with empathy, the anterior insula and the cingulate cortex. We further present evidence for the link between empathy and prosocial behavior. Throughout the chapter, we highlight unanswered questions and propose future avenues for research.

Keywords: social neuroscience, empathy, pain, insula, cingulate cortex

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Compared with many other animals on the planet, human beings are small, slow, soft, and weak. Yet, we have unequivocally won the cross-species competition for global domination. What allowed us, as physical underdogs, to claim this unlikely victory? In other words, what makes humans special?

While many disciplines have addressed this question in some way, psychologists' answer has evolved over time. Until recently, the dominant view held that human uniqueness was bound up in our *intrapersonal* abilities, such as the use of arbitrary symbols (Deacon, 1997; Pinker, 1994; Pinker & Bloom, 1990), and recursive syntax (Chomsky, 1980; Hauser, Chomsky, & Fitch, 2002) in language, or our ability to mentally "time travel" in reflecting on past experiences and planning future actions (Suddendorf & Corballis, 1997, 2007; Tulving, 2002. Although these faculties are undoubtedly critical, in the last decade human specialness has come to be seen as much more **interpersonal**: embodied, for example, in our abilities to understand (Brothers, 1997; Leslie, 1994), learn from (Csibra & Gergely, 2006; Moll & Tomasello, 2007), and share intentions with others (Tomasello, 2000; Tomasello, Carpenter, Call, Behne, & Moll, 2005).

Together, such abilities contribute to the multi-faceted construct of empathy. Empathy is thought to comprise multiple related, but distinct processing steps, including (1) vicariously sharing others' internal states, (2) explicitly considering (and perhaps understanding) others' states and their sources, and (3) expressing motivation to improve others' experiences (e.g. by reducing their suffering). Together, these components of empathy support our abilities to cooperate on everything from hunting trips to the development of scientific theory (Tomasello, 2009), and motivate us to protect each others' well being (Batson, 2011; de Waal, 2008).

Given empathy's enormous importance, psychologists of all stripes have developed new tools and techniques, ranging from time data in infants (Hamlin, Wynn, & Bloom, 2007; Thomsen, Frankenhuis, Ingold-Smith, & Carey, 2011) to cross-species comparative studies (Flombaum & Santos, 2005; Silk, Brosnan, Vonk, Henrich, Povinelli, Richardson, et al., 2005), to explore empathic abilities. Human neuroscience has been no different. Since the spread of tools like fMRI for measuring task-related brain activity two decades ago, researchers have called for these tools to be used in characterizing the neural bases of empathy, and many more researchers have answered this call. The resulting avalanche of data has clarified some of the myriad ways in which **perceivers** (individuals paying attention to, thinking about, or responding to another person) represent the experiences of social **targets** (individuals who are the focus of perceivers' attention).

Here, we don't aim to exhaustively review this vast literature, but rather to offer a three-part survey and glimpse of the future. The first section will describe extant neuroscience work on empathy, which has

p. 215 largely focused on localizing and characterizing the neural systems underlying two ↳ components of empathy: **experience sharing** (perceivers' tendency to vicariously experience targets' sensorimotor, visceral, and affective states) and **mental state attribution** (perceivers' explicit consideration of targets' internal states), each of which has been explored by dozens of studies. This work has provided a powerful, mechanistic snapshot of some features of empathy.

The second section will explain why extant neuroscientific models of empathy remain incomplete, and as such, this domain of research is at a critical turning point. This is because a description of individual social cognitive processes—the "pieces" that make up empathy—is far removed from a holistic picture of how the human brain puts those pieces together, and allows perceivers to understand and respond to targets. This is not always appreciated in social cognitive neuroscience: researchers often treat processes such as experience sharing and mentalizing as though they were separate "processing streams" operating in isolation.

The third and last section of this chapter will focus on a critical shift in the field away from this modular view of empathy, and suggest some direction for future research. Here, we will describe how the first stage of empathy research is now giving way to a second stage that focuses on the **interactions** between multiple cognitive and neural mechanisms that constitute empathy, especially when perceivers encounter complex, ecologically valid social cues. This second stage of evolution is ongoing, and the way it plays out will determine the course of research on the neuroscience of empathy—and the issues this field will be able to address—in the coming decades.

A tale of two systems

Understanding and responding to others' internal states are enormously complex tasks. Luckily, perceivers have access to a number of methods for accomplishing them. They can stereotype social targets (Devine, 1989; Quadflieg, Turk, Waiter, Mitchell, Jenkins, & Macrae, 2009), project their own internal states onto targets (Gilovich, Medvec, & Savitsky, 2000; Ross, Greene, & House, 1977), apply analysis of variance to others' behaviors to derive underlying traits and preferences (Kelley, 1973), and avail themselves of any number of other social cognitive "tools" (Ames, 2004). That said, the lion's share of neuroscientific research on empathy has focused on two of these tools—experience sharing and mental state attribution. Neuroscientists have explored these processes and their underlying neural systems through starkly independent lines of research. Here, we will discuss each of these empirical programs in turn.

Experience sharing

The first line of research deals with the mechanisms through which one person comes to vicariously experience others' internal states. Psychologists and neuroscientists posit that experience sharing occurs because perception (e.g. of a target in pain) and experience (e.g. a perceiver feeling pain themselves) are deeply linked, and as such observing targets will naturally cause perceivers to take on those targets' states (Dijksterhuis & Bargh, 2001; Preston & de Waal, 2002). Perception–experience coupling is a centuries-old idea in philosophy (Smith, 1790/2002), and more recently has been supported by observations that perceivers indeed take on the postures (Chartrand & Bargh, 1999), facial expressions (Dimberg, Thunberg, & Elmehed, 2000), autonomic arousal (Vaughan & Lanzetta, 1980), and moods (Neumann & Strack, 2000) that they observe in others. In many ways, the idea of experience sharing follows from the more general theory of **embodied cognition**, which posits that concepts related to physical states (including, presumably, those of other people) are processed through sensory and motor representations (Barsalou, 2008; Decety, 1996; Kosslyn, Thompson, & Alpert, 1997; Niedenthal, Barsalou, Ric, & Krauth-Gruber, 2005; Zaki, Davis, & Ochsner, 2012).

p. 216 Over the last 20 years, neuroscientists have characterized several regions of the human brain that exhibit a property consistent with experience sharing, which we will refer to as **neural resonance**. These regions respond to both perceivers' experience of a state and to their observation of targets experiencing that same state. As it turns out, neural resonance is widespread, and its localization depends on the type of internal state perceivers experience or observe. For example, perceivers engage the putative "mirror neuron system," encompassing premotor, inferior frontal, and inferior parietal cortex (Rizzolatti & Craighero, 2004), both when executing and observing motor acts. When experiencing and observing non-painful touch, perceivers engage somatosensory cortex (Keysers, Kaas, & Gazzola, 2010; Keysers, Wicker, Gazzola, Anton, Fogassi, & Gallese, 2004). When experiencing pain and observing targets in pain, perceivers also engage somatosensory cortex (Avenanti, Bueti, Galati, & Aglioti, 2005), but additionally recruit activity in regions related to the interoceptive and affective components of pain, including the anterior insula and anterior cingulate cortex (Jackson, Meltzoff, & Decety, 2005; Morrison, Lloyd, di Pellegrino, & Roberts, 2004; Ochsner, Zaki, Hanelin, Ludlow, Knierim, Ramachandran, et al., 2008; Singer, Seymour, O'Doherty, Kaube, Dolan, & Frith, 2004). Newer data suggest that even the hippocampus and posterior medial frontal cortex exhibit resonant properties during action imitation (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). Hereafter, we will refer to brain regions that exhibit neural resonance as the **experience sharing system (ESS)**, with the understanding that this is a loose, functional definition, and not one based on cytoarchitectonic properties or connectivity.

Regardless of the specific states being observed and experienced, neural resonance has generated a great deal of excitement, for at least two reasons. First, resonance has been put forward as the likely neural basis

of shared representations. Second, resonance often has been nominated as the primary driver of empathy (Gallese & Goldman, 1998; Gallese, Keysers, & Rizzolatti, 2004).

The first of these claims is plausible and well supported. Neural resonance is highly consistent (Keysers & Gazzola, 2009; Rizzolatti & Sinigaglia, 2010) across studies and can be modulated by the same factors that modulate experience sharing, such as social context and perceiver motivations (Singer, Seymour, O'Doherty, Stephan, Dolan, & Frith, 2006; Xu, Zuo, Wang, & Han, 2009). Furthermore, one criticism often leveled at work on the ESS is that voxels represent relatively large patches of neural "real estate," and as such it is difficult to know whether neural resonance findings actually reflect overlapping activation in cellular populations or the activation of distinct populations that co-exist within single voxels. One extant study has addressed this concern by using multivariate techniques that hone in on multi-voxel patterns of activation while perceivers experienced pain and observed targets in pain. This relatively sensitive measure replicated the main finding of neural resonance across the two conditions (Corradi-Dell'acqua, Hofstetter, & Vuilleumier, 2011).

The second of these claims—that neural resonance is the primary mediator of empathy—is much less well supported. This is because virtually all studies of neural resonance focus on observation and experience of relatively "low-level" states that include strong sensorimotor and visceral components, such as pain, disgust, motor intentions, and facial expressions. However, empathy involves sharing not only such low-level states with targets, but also sharing "higher level" affective states and understanding the sources of those states. Critically, high level states are often irreducible to lower level visceral or sensorimotor states; for example, the identical motor program of pushing someone could be employed for the very different high level purposes of starting a fight or saving someone from an oncoming bus (Jacob & Jeannerod, 2005). Furthermore, there are many instances in which a target's state diverges from that of a perceiver (e.g. when a target falsely believes something that a perceiver does not or is trying to hide or control expression of their true ↳ feelings); in these cases, assuming one's own internal states are shared by a target can hinder interpersonal understanding (Epley, Keysar, Van Boven, & Gilovich, 2004; Gilovich et al., 2000).

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Mental state attribution

Errors arising from imputing one's own internal states onto others, in fact, spurred early research in a very different tradition: the study of so-called "theory of mind." Since Premack & Woodruff's (1978) pioneering work with chimpanzees, scientists have studied the ability of humans (and some other animals) to ascribe unique mental states to others, and to utilize inferences about mental states during social interactions (an ability we will refer to as **mental state attribution**). Mental state attribution, in various forms, has been a major topic of research for decades, with special attention being paid to its developmental trajectory (Flavell, 1999), and its breakdown in autism spectrum disorders (Baron-Cohen, Leslie, & Frith, 1985).

Cognitive neuroscience research on mental state attribution over the last 15 years has borrowed a number of paradigms from these developmental and clinical traditions, usually asking perceivers to draw inferences about the beliefs, knowledge, intentions, and emotions of others based on written vignettes, pictures, or cartoons. Related work has adapted social psychological paradigms on person perception by asking perceivers to judge the stable traits (as opposed to transient states) of themselves and of targets. Regardless of the type of judgment being made about others or the medium in which target cues are presented, such tasks produce a strikingly consistent pattern of activation in a network that includes medial prefrontal cortex (mPFC), temporoparietal junction (TPJ), posterior cingulate cortex (PCC), and temporal poles. As with the ESS, we will refer to this set of regions as the mental state attribution system (MSAS), understanding that this categorization is loose and functional (for more descriptions of the MSAS and its functions, see Baron-Cohen, Ring, Wheelwright, Bullmore, Brammer, & Simmons, 1999; Castelli, Frith, Happé, & Frith, 2002; Fletcher, Happe, Frith, Baker, Dolan, Frackowiak, et al., 1995; Goel, Grafman, Sadato,

& Hallett, 1995; Mitchell, 2009a; Mitchell, Heatherton, & Macrae, 2002; Ochsner, Knierim, Ludlow, Hanelin, Ramachandran, Glover, et al., 2004; Olsson & Ochsner, 2008; Peelen, Atkinson, & Vuilleumier, 2010; Saxe & Kanwisher, 2003). The specific roles of these cortical regions are, it seems, not limited to MSA-related computations. For example, the TPJ is likely related to orienting attention based on exogenous cues (Corbetta, Patel, & Shulman, 2008; Mitchell, 2008), the PCC's position as a convergence point for both sensory and motor information may support a role in assessing the salience of social stimuli (Vogt, Vogt, & Laureys, 2006), and the mPFC is often engaged by making non-social decisions under conditions of uncertainty (Daw, O'Doherty, Dayan, Seymour, & Dolan, 2006). Overall, the MSAS likely supports a suite of sub-processes that underlie a broader ability to "project" one's self into distal scenarios or points of view (including the past, future, and uncertain or counterfactual concepts, as well as targets' non-observable mental states; see Buckner, Andrews-Hanna, & Schacter, 2008; Mitchell, 2009b; Spreng, Mar, & Kim, 2009).

Isolated systems as a red herring

At first blush, it may seem that experience sharing and mental state attribution should be functional cousins, intimately linked as processes that support the broader construct of empathy. A close look reveals that—at least at the level of the brain—there is a striking lack of family resemblance, however. As readers may have noticed, the brain regions making up the ESS and the MSAS are almost completely non-overlapping (Figure 13.1). This dissociation holds up under meta-analytic scrutiny: studies engaging one system rarely concurrently engage the other (van Overwalle & Baetens, 2009). Even within individual

studies, the types of cues typically engaging one system often do not ↳ engage the other. Specifically, the ESS is often responsive to **sensorimotor** cues (e.g. facial expressions of emotion) that suggest internal states, whereas the MSAS is more responsive to *contextual* cues that describe the likely sources of those states (Gobbini, Koralek, Bryan, Montgomery, & Haxby, 2007; Wheatley, Milleville, & Martin, 2007; Zaki, in press).

Figure 13.1
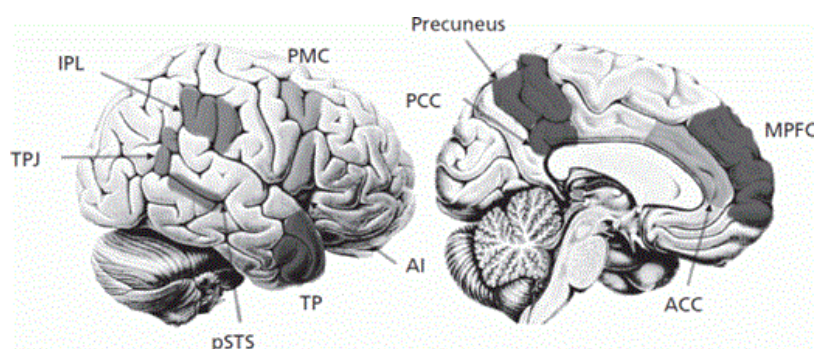
Brain regions comprising the ESS (light gray) and MSAS (dark gray). IPL = inferior parietal lobule; TPJ = temporoparietal junction; pSTS = posterior superior temporal sulcus; TP = temporal pole; AI = anterior insula; PMC = premotor cortex; PCC = posterior cingulate cortex; ACC = anterior cingulate cortex; mPFC = medial prefrontal cortex.

Furthermore, the ESS and MSAS sometimes "compete" for control over behavior. For example, perceivers asked **not** to imitate the movements of targets attenuate activity in the mirror neuron system, but increase activity in the mPFC and TPJ (Brass, Ruby, & Spengler, 2009). Similarly, when sensorimotor and contextual cues about a target's emotion conflict (imagine, for instance, seeing someone crying, but understanding that he has just won an Olympic gold medal), perceivers' can rely on either type of cue in judging what they believe a target truly feels (Aviezer, Hassin, Ryan, Grady, Susskind, Anderson, et al., 2008; Carroll & Russell,

1996). Recently, we found that, in such situations, reliance on sensorimotor cues engaged activity in the ESS and dampened activity in the MSAS, whereas reliance on contextual cues produced the opposite pattern of activity (Zaki, Hennigan, Weber, & Ochsner, 2010).

Thus, the ability to empathically connect with and understand another person seems to fractionate into two disparate social "information processing streams," supported by two dissociable neural systems. Yet ostensibly, both of these processes and neural systems serve the same ends: understanding and sharing targets' internal states. If this is true, then what specific role does each system play in supporting empathy more broadly? Typically, reviews of this literature hold that these processes provide relatively independent contributions to empathy (Decety & Jackson, 2004; Shamay-Tsoory, 2010; Singer, 2006). Others suggest avenues through which these processes could interact with each other (Keysers & Gazzola, 2007; Uddin, Iacoboni, Lange, & Keenan, 2007).

However, until recently it was difficult to answer questions about whether and how multiple neural systems combine to support empathy, because empathy—as a multi-component phenomena—was rarely studied in neuroscience. Instead, as the review of extant data above suggests, the "first stage" of empathy research focused on characterizing single processes by engaging them in relative phenomenological isolation through the use of highly controlled unimodal, static, and artificial social cues and tasks (e.g. viewing pictures of actors posing a canonical emotional expression, imitating isolated target movements, or
p. 219   answering questions about vignettes describing ↳ mental states). The reasons for beginning with such paradigms were powerful; so little was known about the neural bases of empathy that maximal experimental control was critical to gaining any insights about its constituent processes. Indeed, the control offered by simplified social paradigms was foundational in allowing scientists to build a functional architecture of empathy's building blocks.

This approach, however, also had the side effect of stacking the deck in favor of a viewing empathy's sub-processes as isolated. This is because the tasks and stimuli used to study the ESS and MSAS were typically designed to engage these processes in isolation. For example, when viewing a context-free picture of an emotional facial expression, perceivers have access only to sensorimotor cues, and as such are likely to draw heavily on experience sharing, especially because studies of the ESS rarely require perceivers to draw explicit inferences about target states. On the other hand, studies of mentalizing ask perceivers to draw just such inferences, based on heavily contextualized stimuli (e.g. vignettes describing the sources of targets' false beliefs). In other words, studies of the ESS and MSAS often employ tasks and stimuli that are "optimized" to each system and its relevant cognitive process. As such, it is unsurprising that perceivers respond by deploying the system called on by the experimental setting, in a manner consistent with modular separation between experience sharing and mental state attribution.

These differences between tasks suggest that the historical division between studies of the ESS and MSAS is both helpful and unhelpful to understanding empathy. On the one hand, it is useful to the extent that a careful approach to exploring the specific contexts in which each system is engaged can provide useful model of when and how social cues will trigger different forms of information processing. On the other hand, this approach is unhelpful if focusing on the ESS or MSAS in isolation leads to overly constrained theories of empathy (Zaki & Ochsner, 2012). Even worse, models that draw a bright line between experience sharing and mental state attribution may be overlooking a potentially central stimulus and task confound. As we will discuss below (see "Coactivation of ESS and MSAS"), the neural systems underlying these processes may be responsive to specific perceiver goals: for example, the ESS is engaged when perceivers attend to **how** a target is expressing an emotion, whereas the MSAS is engaged by perceivers' attention to *why* targets feel the emotions they are expressing. Furthermore, differing classes of social stimuli likely draw perceiver attention naturally towards the "how" or "why" of targets' actions and expressions, and these are typically the types of cues that studies of the ESS and MSAS have employed. Similarly, different tasks, e.g. imitating a targets' facial expression vs. judging how a target likely feels based on that expression

—orient perceivers towards different goals and engage different neural systems, even when based on nearly identical stimuli (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Mitchell et al., 2002).

"First stage" empathy research typically—though not always—divided programs of research along more than one of these dimensions. Studies of the ESS typically used low level sensorimotor cues and either passive viewing or imitation tasks, whereas studies of the MSAS often used more contextualized cues and drew perceivers' attention towards explicit judgments of target states. Do the resulting findings necessarily mean that experience sharing and mental state attribution are isolated in natural contexts? It is quite difficult to answer this question, because we do not know whether differences in neural activity in studies of the ESS and MSAS reflect stimulus type, task, or perceiver attentional set, as opposed to true distinctions between information processing streams.

Critical here is the fact that the social cues perceivers encounter outside the laboratory are often substantially different than those employed by the lion's share of extant research. Specifically, "real-world" social cues are typically dynamic (unfolding over time), multimodal (including concurrent sensorimotor and contextual information), and contextually embedded (such that ↳ interpretations of any one cue are often altered or constrained by other cues or a perceiver's prior knowledge; see Keysers & Gazzola, 2007; Zaki & Ochsner, 2009). The gulf separating laboratory and naturalistic social cues would not be problematic if these cues produced the same patterns of brain activity, and only differed in, for example, the intensity of this activity (i.e. differing **quantitatively**). However, early evidence suggests this is not the case. Indeed, naturalistic social information seems to produce patterns of information processing and brain activity that differ **qualitatively** from those produced by simplified cues like those used in typical social cognitive neuroscience studies, including engaging both the ESS and MSAS, and producing interactions between these systems.

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This is important, in part, because it is under-acknowledged in much of the neuroscience literature on empathy. Resulting theoretical models, in turn, may over-emphasize the ability to understand empathy as a whole based on tasks examining isolate pieces of typical social experiences. By way of analogy, this may be something like drawing inferences about the way that the brain processes the sound of an orchestra based on data describing how the brain processes the sound of each individual instrument, ignoring the unique types of information (e.g. harmonies across instruments) that emerge at the orchestral level in the real world stimulus of interest (Zaki, under revision).

Theories emphasizing the dissociability of the MSAS and ESS run the risk of either missing or glossing over this complexity, and as a consequence, formulating models of empathy that rest too heavily on single processes. For example, two competing and well-known theories have claimed that interpersonal cognition can be largely localized to **either** the ESS **or** MSAS (Gallese et al., 2004; Saxe, 2005). The resulting debate, while provocative, is probably misguided, because each side bases its argument on evidence derived from studies examining only one piece of the larger social puzzle.

Putting the pieces together

So far, we have chronicled the work researchers have done in characterizing the neural bases of two empathic sub-processes—experience sharing and mental state attribution—and described some conceptual limitations that hinder the ability of descriptions of single social cognitive "pieces" to translate into descriptions of empathy as it likely operates in more ecologically valid contexts (cf. Neisser, 1980).

This second point is not meant to discredit work on single social cognitive processes. Quite the opposite— such research is not only important, but also constitutes the only reasonable starting point for building a neuroscience of empathy. That said, we (Zaki, in press; Zaki & Ochsner, 2009) and others (e.g. Keysers &

Gazzola, 2007) have advocated for following this research with a "second stage" of work focusing not on single processes in isolation, but on how perceivers put these pieces together, by deploying multiple, interactive empathic processes when encountering complex social cues.

Luckily, this second stage is well underway. Largely in the last 3 years, researchers have updated their approach to examine the brain's response to just the type of complex social information we have described above. This work capitalizes on first stage characterizations of the ESS and MSAS to study how these systems respond when pieces of social information (e.g. dynamic biological movement and linguistic cues about beliefs or emotions) are joined to form a coherent whole.

This work has produced a sea change in the way neuroscientists view empathy. Instead of conceiving of experience sharing and mental state attribution as isolated social cognitive processing streams, we now have a picture of these processes as intimately tied in at least 3 ways: As reviewed below (1) the ESS and MSAS are concurrently engaged by naturalistic social cues, (2) these neural ↳ systems become functionally coupled with each other during complex social cognitive tasks, and (3) activation of both of these systems predict empathy-related outcomes, including accuracy about targets' internal states and perceivers' motivation to engage in prosocial behavior towards targets.

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Coactivation of the ESS and MSAS

Early data led to the suggestion that the ESS and MSAS were fundamentally dissociable, but—as mentioned above—this was based on stimuli and paradigms designed to isolate single social cognitive processes. Outside the laboratory, social targets more often than not present us with a barrage of multimodal social cues that unfold over time (e.g. a friend looks uncomfortable, then reveals that she has just lost her job, and then leans forward and begins crying). Such cues tap all of our social capacities simultaneously and demand that we integrate over many social signals in forming a coherent representation of targets' internal states. Intuitively, we might expect that such demands would engage multiple social cognitive processes and neural systems.

Consistent with this, several studies combining complex, dynamic social stimuli with the requirement for explicit inferences about targets' states (requirements often present in typical social interactions) have consistently demonstrated concurrent engagement of both areas within the ESS and MSAS. In many cases, these studies also help to reveal the specific contextual triggers that produce such coactivation. For example, watching videos of targets executing motor acts engages areas within the ESS involved in sharing motor intentions; if these videos are further paired with demands to draw explicit inferences about targets' intentions—or situational cues drawing attention to targets' likely intentions—they also engage areas in the MSAS (de Lange, Spronk, Willems, Toni, & Bekkering, 2008; Spunt, Satpute, & Lieberman, 2010; Wheatley et al., 2007). Similarly, engaging in a joint attention task with a target engages regions within both of these neural systems (Redcay, Dodell-Feder, Pearrow, Mavros, Kleiner, Gabrieli, et al., 2010). Together, these data suggest that areas within the ESS may engaged relatively automatically by dynamic social stimuli (e.g. moving social targets), but that requirements to further digest the internal states implied by targets' movements brings the MSAS online as well (Spunt & Lieberman, 2011).

These patterns of coactivation translate to emotion perception as well. For example, when perceivers view videos of targets expressing emotions, they typically engage both areas within the ESS and MSAS (Wolf, Dziobek, & Heekeren, 2010; Zaki, Weber, Bolger, & Ochsner, 2009). Furthermore, the system that comes online most strongly under such circumstances may depend on perceivers' inferential goals. A recent study elegantly demonstrated this point: when attending to the way targets **express** their emotions (e.g. through laughing), perceivers prominently engaged the ESS—and especially regions involved in sharing motor intentions—whereas attending to the **sources** of target emotions (e.g. hearing a good joke), perceivers most

strongly engaged the MSAS (Spunt & Lieberman, 2013). Such findings not only provide us with a more holistic picture of coactivation in these systems, but also refine our understanding of the specific social sensitivities exhibited by these neural systems.

These data make an important point about how theories of empathy should discuss prior data. That is, the fact that the ESS and MSAS can be dissociated using simplified stimuli and tasks does not necessitate, or even imply, that those systems are dissociable in the majority of social contexts. In fact, studies employing naturalistic methods suggest that the demands of most social situations would engage these systems—and the processes they underlie—simultaneously. This probability motivates a shift away from an "either / or" argument about whether the MSAS or ESS is central to empathy, and towards a "when and how" approach to better discriminating the situations likely to engage one or both systems.

Functional coupling between systems

In addition to being engaged together, a parsimonious account of empathy might posit that processes such as experience sharing and mental state attribution should intricately interact during naturalistic social cognition. For example, understanding the sources behind a target's likely internal states (e.g. that he has just won a gold medal) could cause perceivers to vastly reinterpret that target's sensorimotor cues (e.g. crying). Presumably, this efficient use of multiple pieces of social information could be instantiated through communication between the ESS and MSAS.

Consistent with this approach, a number of studies have documented functional coupling between the ESS and MSAS during social cognitive tasks. For example, classic work on neural resonance demonstrates that areas within the "pain matrix" (especially the anterior insula and anterior cingulate cortex) are engaged both when targets experience pain themselves and when they observe targets in pain (Singer et al., 2004). However, this does not mean that these regions are performing identical computations during both pain perception and experience. On the contrary, the interpretation of a single region's activity depends on the other regions with which that region communicates during a given task. Our own group has examined this idea within the context of empathy for pain. We found that the ACC and AI were engaged during both experience and observation of pain (Ochsner et al., 2008), but that these regions demonstrated very different patterns of connectivity across these tasks: during observation, but not experience, ACC and AI became functionally coupled with areas within the MSAS (Zaki, Ochsner, Hanelin, Wager, & Mackey, 2007). Similar connectivity patterns also apply to the experience and observation of disgust (Jabbi, Bastiaansen, & Keysers, 2008). Together, these data suggest that, during experience sharing tasks, neural resonance— shared activity for self and other experience—may depend on communication with regions involved in mental state attribution.

Other studies have tested the other side of this equation: examining the connectivity of areas in the MSAS during an explicit social inference task. For example, Lombardo, Chakrabarti, Bullmore, Wheelwright, Sadek, Suckling, et al. (2010) asked perceivers to draw inferences about their own preferences and those of targets. Both of these conditions engaged many regions classically making up the MSAS, including the mPFC, PCC, and TPJ. Interestingly, during both types of inference, the mPFC and TPJ were also functionally connected with many regions in the ESS, regardless of whether participants answered questions about themselves or social targets. This suggests that even relatively simple inferences about targets may require communication between regions involved in drawing such inferences and regions involved in sharing of intention and affect with targets.

Connectivity can also be studied *across* perceivers and targets. For example, Schippers, Roebroeck, Renken, Nanetti, & Keysers (2010 asked targets to manually pantomime simple actions (*à la charades*) while being scanned using fMRI; perceivers were later scanned while guessing what gesturers were attempting to

communicate. Using an innovative analysis, the researchers demonstrated that activity in **targets'** motor cortex while they executed a gesture predicted activity in **perceivers'** motor cortex while they perceived those gestures. Interestingly, however, targets' motor activation also predicted activity within perceivers' MSAS—specifically the mPFC—suggesting that perceivers process targets' intentions using both the ESS and MSAS. Further, communication between the mPFC and areas within the ESS are modulated by perceivers' intentions to actively guess what targets are pantomiming vs. passively viewing target actions (Schippers & Keysers, 2011), again suggesting that situational and motivational context critically affect the interplay between empathic sub-processes.

p. 223 Predicting social cognitive outcomes

When mapping the neural architecture of any complex cognitive process, a key concern is that brain activity in a given region does not actually index the computational process a researcher is interested in. Empathy is not excepted from this issue, and based in imaging data alone, it is difficult to know exactly what engagement of, for example, ESS regions during a shared experience task actually means psychologically.

This has been especially problematic because of the distance that has historically separated psychological and neuroscientific approaches to empathy. Social psychological approaches—perhaps not surprisingly— lean heavily on behavior to indicate the operation of empathic processes. For example, perceivers' accuracy for targets' internal states can serve as an indicator of how much perceivers engage both mentalizing and experience sharing (Ickes, 1997; Levenson & Ruef, 1992; Tetlock & Kim, 1987), whereas stereotyping or derogation of targets can index the absence of these processes (Devine, 1989; Harris & Fiske, 2007). Similarly, perceivers' choices to engage in prosocial behavior can serve as an index of their concern for targets' well being (Batson, 2011).

By contrast, neuroimaging studies of empathy—especially during the "first stage"—concentrated far less on behavioral outcomes, and more on relationships between stimuli and brain activity. For example, perceivers might be scanned while observing targets in pain or making guesses about targets' intentions, and related brain activity would be interpreted as relevant to the empathic sub-process that task putatively engages. In almost all cases, these paradigms do not produce variance in behavior, either because they required no responses from perceivers (as in many passive experience sharing tasks) or employed very simple social inference tasks that produce near perfect accuracy.

This precluded neuroimaging studies of empathy from mapping brain activity directly on to behavior, reducing the ability of researchers to draw maximally strong inferences about neuroimaging results. For example, although the ESS is engaged during observation of pain, in the absence of brain-behavior relationships, it is difficult to know whether this activation actually tracks with experience sharing, or instead tracks concurrent, but less interesting, processing step (e.g. remembering one's own painful experiences, desire to escape the discomfort of observing suffering, a perceiver's attempt to distract himself from viewing the unpleasant stimulus). Individual difference correlations (Jabbi, Swart, & Keysers, 2007) and lesion studies (Shamay-Tsoory, Aharon-Peretz, & Perry, 2009) provide a partial remedy to this concern, but cannot replace the utility of brain-behavior links.

Other domains within cognitive neuroscience have fruitfully studied brain-behavior correlations. Notably, memory researchers used the **subsequent memory** paradigm to link encoding-related activation in the medial temporal lobe and inferior frontal cortex to successful retrieval of memoranda (Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Wagner, Schacter, Rotte, Koutstaal, Maril, Dale, et al., 1998). The "second stage" of empathy research has picked up this trend, by relating activity in the MSAS and ESS to subsequent social behaviors, including accuracy for social information and subsequent prosocial behavior.

With respect to accuracy, early work "piggybacked" on the original subsequent memory paradigm to examine whether and how brain activity would predict accurate recall for social—as opposed to non-social—information. A spate of studies demonstrated that MSAS activity when perceivers encounter socially relevant stimuli (e.g. trait adjectives) predicted successful retrieval of this information, but only when perceivers were drawing social inferences about those stimuli (e.g. how much an adjective described a social target, as opposed to how many vowels it contained) (Hasson, Furman, Clark, Dudai, & Davachi, 2008; Macrae, Moran, Heatherton, Banfield, & Kelley, 2004; Mitchell, Macrae, & Banaji, 2004). A later study took this approach into a more naturalistic ↳ context, demonstrating that reliable patterns of activity within both MSAS and ESS areas predicted the accuracy with which perceivers recall targets' descriptions of autobiographical events (Stephens, Silbert, & Hasson, 2010).

Our group has examined brain-behavior correlations in the affective domain, by studying the neural correlates of accurate inferences about targets' emotions based on naturalistic social cues (Ickes, 1997; Levenson & Ruef, 1992; Zaki, Bolger, & Ochsner, 2008; Zaki & Ochsner, 2011). In our studies, perceivers watch videos of targets describing emotional events, and continuously rate how positive or negative they believed targets feel. Importantly, targets themselves had previously rated their emotions at each moment using the same scale perceivers employed. This allows us to quantitatively operationalize interpersonal accuracy as the correlation between perceivers' ratings of targets emotions and targets' self-ratings. Using this approach, we have demonstrated that accuracy is predicted by activity in regions in both the MSAS and ESS (Harvey, Zaki, Lee, Ochsner, & Green, in press; Zaki et al., 2009).

Finally, a small set of studies has examined brain activity related to the use of mental state information during game theoretic decision-making. Although not measuring accuracy *per se*, these tasks offer the attractive possibility of formally modeling the use of mental states in interpersonal strategizing. For example, in both the "work / shirk" and "beauty contest" games, perceivers' must strategically infer what others will think in order to maximize their own gains. In both of these games, perceivers level of social inference (e.g. how much their decisions reflect thinking about others' minds) can be quantified; and, in both cases, activity in the MSAS—and specifically the mPFC—tracks with this measure (Coricelli & Nagel, 2009; Hampton, Bossaerts, & O'Doherty, 2008). This strengthens the inference that the MSAS directly tracks with the insightful, task-related use of others' mental states during social interactions.

A second growing literature has focused on brain-behavior correlations in another domain: using brain activity to predict prosocial behaviors such as sharing resources and helping social targets. The motives behind prosocial behavior have been the topic of a high profile debate among social psychologists. Interestingly, this debate can be recast along the dimensions of experience sharing and mental state attribution: whereas Cialdini and colleagues (Cialdini, Brown, Lewis, Luce, & Neuberg 1997; Cialdini, Schaller, Houlihan, Arps, Fultz, & Beaman, 1987) suggested that prosocial behavior stemmed from a sense of "oneness" or overlapping identity with targets (akin to experience sharing), Batson and colleagues (Bateson, 1991, 2011; Bateson et al., 1991) countered that a specific form of other oriented cognition (akin to mental state attribution) was the stronger driver of prosocial behavior.

Which one of these mechanisms supports prosociality? Neuroscience can provide converging evidence through which this question can be addressed, by examining the extent to which activity in the MSAS and ESS predicts later prosocial acts. Like so many features of second stage neuroscience work on empathy, the emerging answer seems to be that both systems are involved, in a context-dependent manner. For example, ESS activity consistent with perceivers' sharing of targets' pain (Hein, Silani, Preuschoff, Batson, & Singer, 2010; Masten, Morelli, & Eisenberger, 2011) and reward (Harbaugh, Mayr, & Burghart, 2007; Zaki, Lopez, & Mitchell, 2013; Zaki & Mitchell, 2011) predicts perceivers' willingness to make costly decisions that help those targets. In other cases, activity in the MSAS (especially the mPFC) when perceivers consider targets' internal states predicts their later willingness to act prosocially (Morelli, Rameson, & Lieberman, 2012; Waytz, Zaki, & Mitchell, 2012).

The specific contextual factors that determine when activity in the MSAS or ESS will best predict prosocial behavior remain relatively unexplored. Future work should address this issue, and examine whether prosocial behavior prompted by experience sharing and mental state attribution, ↳ respectively, differ in their subjective or behavioral features. Nonetheless, the small, but growing literature on this topic clearly provides evidence consistent with both sides of the psychological debate: under at least some conditions, it seems that both of these processes can drive prosocial motivations.

Conclusions and future directions

For all of our impressive mental firepower, most humans (including both authors of this chapter) would not last a week alone in the wild. But put us together in a group, and we can survive just about anything. Why? In simple terms, it is because we are built for other people, in more ways than one. Behaviorally, our species has thrived on coordinated interpersonal actions. Psychologically, we are equipped with myriad affective and cognitive mechanisms perfectly suited to understanding and relating to other minds. Empathy and all of its components are foundational to who we are and why we succeed as a species.

Although empathy has been a perennial topic among philosophers, the neuroscience of empathy is in its teenage years. Given its immaturity, the rapid evolution of this domain of research is especially impressive. Here we have chronicled two of these evolutionary "stages." In the first stage, researchers characterized the neural systems supporting two major empathic sub-processes: the ESS, which is involved in sharing targets' sensorimotor and visceral states, and the MSAS, which is involved in perceivers' explicit inferences about targets' states.

This work was hugely important in building a functional architecture of empathy. However, it was also hamstrung by two important problems. First, in mapping the neural bases of empathic sub-processes, researchers necessarily began by using highly simplified non-naturalistic social cues, and this sometimes led to overly constrained models of empathy as comprising a number of "pieces" that operated in relative isolation. Secondly, first stage empathy research in neuroscience rarely related brain activity to observable social behaviors, making it difficult to draw direct conclusions about the functional role of the ESS and MSAS.

The "second stage" of this program has begun to remedy these issues. Critically, however, it has not overwritten the first stage, but rather built on the important insights of earlier work. Specifically, it has capitalized on first-stage descriptions of the ESS and MSAS to further demonstrate (1) that these systems are concurrently engaged by naturalistic, multimodal social cues, (2) that they interact with each other when processing such stimuli, and (3) that their engagement can predict subsequent social-behavioral outcomes such understanding targets' internal states and motivations to help targets. This work provides an integrative view of empathy as tapping multiple, functionally connected sets of brain regions to translate complex social cues into inferences about others' internal states. Further, second stage research has highlighted the context-dependent nature of empathy: depending on situational features, the same social cues can engage very different patterns of activity across the ESS and MSAS, and the activity of these systems can differentially predict subsequent social behaviors (cf. Hein & Singer, 2008). Overall, the second stage of empathy research has refined and integrated models of isolated empathic sub-processes into more holistic accounts of an integrated "system" of processes that perceivers deploy flexibly based on current social goals and information.

This summary begs the question of what a "third stage" of neuroscience research on empathy might bring. Although this is difficult (if not impossible) to predict, the insights garnered by the first two stages of work suggest some exciting possibilities, two of which we will mention here. First, extant work has yet to capture —in any meaningful way—a central feature of social encounters: the fact that perceivers themselves are

also usually targets, and visa-versa. Unless they are ↳ watching television, perceivers rarely observe targets without themselves being observed. As such, much of perceivers' ongoing social cognitive labor entails iteratively sampling their effect on targets (wondering, e.g. "Does she know I'm paying attention? How is what I'm saying now affecting him?"), and adjusting their behavior accordingly (Neisser, 1980; Schilbach, 2010). Future work should examine whether these unique features of social interactions are subserved by the same networks of brain regions that are involved in observing non-interactive targets, or whether extant work may have yet to chart the neural bases of some critical features of everyday empathy.

A second exciting avenue for suture work lies in the use of quantitative models to formally describe the role of neural systems in producing social behavior. First and second stage research on empathy have equipped us with reliable insights about the neural signatures of processes such as mental state attribution, and we can now use these signatures to directly model the relationship between these processes and "downstream" inferences, decisions, and behaviors. This type of advance also has the potential to increase our understanding of potential parallels between social cognition and other domains, such as perceptual decision-making (Freeman, Schiller, Rule, & Ambady, 2010; Zaki, in press and reinforcement learning (Behrens, Hunt, Woolrich, & Rushworth, 2008; Jones, Somerville, Li, Ruberry, Libby, Glover, et al., 2011).

The neuroscience of empathy has evolved fruitfully by consistently building on prior work to refine and improve the questions and models this field produces. So long as this trajectory continues, this field will continue growing at an amazing pace, and producing fundamental insights about the nature of our critical social abilities.

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