12 The Cognitive Neuroscience of Sharing and Understanding Others' Emotions

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For the vast majority of human beings, empathy—understanding and responding to others' internal states—is more than an ability. It is a preoccupation. We exert an enormous amount of energy thinking and talking about other people (Dunbar 2004) and spend much of our free time engulfed in the lives of fictional others presented in novels and films (Mar and Oatley 2008). This preoccupation with others is well advised: without a keen grasp of other people's internal states—including their beliefs, intentions, and emotions—we would have difficulty managing cooperative endeavors ranging from group hunting trips to building suspension bridges, and without a tendency to share other peoples' states, we would be disconnected from the vital bonds of social life. These types of interpersonal difficulties plague individuals with illnesses that include deficits in sharing or understanding other people's internal mental states, such as autism spectrum disorders and psychopathy (Blair 2005). The experiences of these disordered populations drive home the point that the social world may provide the most affectively taxing and cognitively challenging experiences we face, and our skills in this domain are honed to a primarily social environment (Humphrey 1976).

Given the importance of empathy, it is unsurprising that a quickly growing number of cognitive neuroscientists have devoted their energy to exploring the neural mechanisms underlying sharing and understanding others' internal states. Perhaps more surprisingly, these studies have, by and large, been conducted in two different ways and published in two different kinds of papers: one focusing on the neural mechanisms involved in vicariously sharing or taking on the states of others (known as *experience sharing*) and the other focusing on the systems involved in cognitively appraising other people's internal states (known as *mental state attribution*).

Experience sharing and mental state attribution are subcomponents of the multifaceted construct that is empathy. As such, we might imagine that they would be intimately linked. And indeed the relationship between these processes and their joint contribution to empathy in complex social situations has been the focus of several emerging theories (Decety and Jackson 2004; Singer 2006; Keysers and Gazzola 2007; Uddin et al. 2007; Zaki and Ochsner 2009). However, whereas empirical energy

continues to be focused on the valuable work of characterizing subcomponents or "pieces" of empathy such as experience sharing and mental state attribution, fewer data have been gathered on how those pieces actually come together.

This chapter examines the evolution of cognitive neuroscience research on empathy. Toward this end, the chapter is divided into three parts. First, we briefly chronicle research over the last decade that has characterized the separate neural systems underlying experience sharing and mental state attribution using highly controlled—but also highly simplified and nonnaturalistic—social cues. Second, we describe problems inherent to overemphasizing the separability of these systems based on data designed to functionally isolate them. Third, we describe newer research (largely published in the last four years) demonstrating that these systems are not as isolated as they first appeared, and instead coactivate, interact, and jointly support social cognitive behavior. These data highlight empathy as a multicomponent process, where varying situational constraints and requirements determine which components come into play.

A Tale of Two Systems

Although the term "the social brain" was coined only two decades ago (Brothers 1990), the neuroscience of social cognition has grown quickly into a predominant research topic. This topic has been approached in two ways, each with a distinct line of empirical research and theorizing.

The Shared Representation System

The first line of research deals with the mechanisms through which one person comes to vicariously experience, or share, the internal states of another. Work exploring this question borrows conceptually from many sources, ranging from eighteenth century moral philosophy (Smith 1790/2002) to aesthetic theory (Lipps 1903), to contemporary models of motor cognition (Prinz 1997; Dijksterhuis and Bargh 2001). The common thread uniting various proponents of this approach is the idea that when *perceivers* (individuals focusing on another person's internal state) observe *targets* (individuals who are the focus of perceivers' attention) experiencing an internal state, perceivers engage many of the cognitive and somatic processes they would engage while experiencing those states themselves. This link between perception of others and one's own experience has been supported by demonstrations that perceivers automatically adopt the bodily postures (Chartrand and Bargh 1999), facial expressions (Dimberg, Thunberg, and Elmehed 2000), autonomic arousal (Vaughan and Lanzetta 1980), and self-reported emotional states (Neumann and Strack 2000) of targets. These data led to the supposition that various forms of experience-sharing may be subserved by a "perception-action matching" system in which observed bodily states are automatically mapped onto an observer's own sensory, motor, and affective

representations (Preston and de Waal 2002). In many ways this "shared representations" approach borrows from the more general idea of "embodied cognition," which posits that concepts related to physical states (including, presumably, those of other people) are processed through sensory and motor representations (Decety 1996; Kosslyn, Thompson, and Alpert 1997; Niedenthal et al. 2005; Barsalou 2008).

Neuroscience research has identified regions thought to support shared representations that are engaged both when perceivers experience an internal state themselves and when they observe targets experiencing those states, a phenomenon we refer to as *neural resonance*. The localization of neural resonance depends on the type of internal state being shared. For example, when both executing and observing motor acts, perceivers engage the so-called mirror neuron system, encompassing premotor, inferior frontal, and inferior parietal cortex (Rizzolatti and Craighero 2004). When experiencing and observing nonpainful touch, perceivers engage somatosensory cortex (Keysers et al. 2004; Keysers, Kaas, and Gazzola 2010). When experiencing pain and observing targets in pain, perceivers also engage somatosensory cortex (Avenanti et al. 2005), but they additionally recruit activity in regions related to the interoceptive and affective components of pain, including the anterior insula and anterior cingulate cortex (Morrison et al. 2004; Singer et al. 2004; Jackson, Meltzoff, and Decety 2005; Ochsner et al. 2008). Newer data suggest that even the hippocampus and posterior medial frontal cortex exhibit resonant properties during action imitation (Mukamel et al. 2010). Hereafter, we refer to all brain regions demonstrating this property as the *shared representation system*, or SRS, 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, the general property of neural resonance has generated a great deal of excitement for at least two reasons. First, as noted above resonance has been put forward as the likely neural basis of shared representations. Second, resonance often has been nominated as the primary mechanism of empathy, social cognition, and even language (Gallese and Goldman 1998; Gallese, Keysers, and Rizzolatti 2004). The first of these claims is plausible and well supported, but the second is not. Although resonance likely plays a part in social cognition in some situations, it is a much less likely mediator of interpersonal understanding in other situations. This is because targets' "higher level" intentions and beliefs cannot be translated into motor or somatic 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 and Jeannerod 2005). Further, 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 his or her true beliefs/feelings); in these cases, relying on one's own internal states to understand a target can hinder interpersonal understanding. Indeed, overascription of one's internal states (especially

one's own knowledge) to others is a common social cognitive error (Gilovich, Medvec, and Savitsky 2000; Epley et al. 2004), which is especially pronounced in autism spectrum disorders (Baron-Cohen 1994).

The Mental State Attribution System

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

Cognitive neuroscience research on MSA over the last fifteen years has utilized a number of paradigms borrowed 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, for example, 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), temporo-parietal junction (TPJ), posterior cingulate cortex (PCC), and temporal poles. As with the SRS, we refer to this set of regions as the mental state attribution system, or MSAS, understanding that this categorization is loose and functional (for more descriptions of the MSAS and its functions, see Fletcher et al. 1995; Goel et al. 1995; Baron-Cohen et al. 1999; Castelli et al. 2002; Mitchell, Heatherton, and Macrae 2002; Saxe and Kanwisher 2003; Ochsner et al. 2004; Olsson and Ochsner 2008; Peelen, Atkinson, and Vuilleumier 2010). The specific roles of these cortical regions are, of course, not limited to MSA-related computations. For example, the TPJ is likely related to orienting attention based on exogenous cues (Corbetta, Patel, and 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, and Laureys 2006); and the MPFC may be related to the formation of higher-order or conceptual appraisals of internal states based on input from these other regions, including the more general ability to "project" one's self into a hypothetical scenario and make judgments about currently nonobservable stimuli encompassed by distal scenarios or points of view (including the past, future, and uncertain or counterfactual

concepts, as well as targets' nonobservable mental states) (see Buckner, Andrews-Hanna, and Schacter 2008; Mitchell 2009a, 2009b; Spreng, Mar, and Kim 2009). Overall, the MSAS likely instantiates a suite of stimulus-general cognitive processes that need to come together in order for perceivers to form explicit cognitive appraisals of targets' internal states.

Dissociation and Its Discontents

The tale of these two systems—the SRS, involved in sharing others' internal states, and the MSAS, involved in appraising and understanding those states—offers much valuable information about each ability and how it is subserved by the brain. But perhaps the most striking feature of this story is how distant the two systems seem from each other. Indeed, it is a tale of systems divided, not united, and as readers may have noticed, the brain regions making up the SRS and the MSAS are almost completely nonoverlapping. This dissociation holds up under meta-analytic scrutiny: studies engaging one system rarely concurrently engage the other (van Overwalle and Baetens 2009). Further, even within individual studies, these systems can be made to "compete" for control over behavior. For example, perceivers asked to *not* imitate the movements of targets attenuate activity in the mirror neuron system but increase activity in the MPFC and TPJ (Brass, Ruby, and Spengler 2009). In another demonstration of cross-system competition, we asked perceivers to rate target emotion based on the combined presentation of two types of social cues: silent videos of targets talking about emotional events, whose perception is known to engage the SRS, and verbal cues conveying contextual information (sentences ostensibly summarizing the event targets were describing), which are known to engage the MSAS. These cues sometimes presented competing ideas about targets' affect (e.g., a target appeared to be happy based on nonverbal cues, but was ostensibly describing a negative event). As a consequence, perceivers' had to decide how to weigh the importance of these cues, and their subsequent judgments reflected their relative "reliance" on one cue-type or the other. For example, a perceiver who decides that the above-mentioned target is happy based on her positive nonverbal cues and negative contextual cues could be said to have relied predominantly on this nonverbal information. Results indicated that, to the extent that perceivers based their judgments on nonverbal information, they engaged the SRS, including sensorimotor cortex, and showed less activity in the MSAS. However, to the extent that they relied on contextual information, they displayed the opposite pattern (Zaki et al. 2010).

Thus, at first blush, empathy seems to fractionate into two disparate forms of computations—experience sharing and mental state attribution—instantiated in 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 these outcomes? Extant research can only go so far in answering this question because the studies designed to examine each individual system typically are designed in such a way that there is no need or cause for the other system to come into play. For example, studies designed to examine the SRS typically involve passive perception of dynamic stimuli (e.g., videos of targets displaying real social cues); whereas studies of the MSAS typically require explicit ratings of a target's internal states based on static, verbal, or abstract stimuli.

These differences between tasks suggest that the historical division between studies of the SRS and MSAS is both helpful and unhelpful to understanding empathy. On the one hand, it is useful to the extent that a careful (and preferably within-subjects) approach to exploring the specific tasks and contexts in which each system is engaged can provide a more complete model of the functional architecture of empathy, including when and how each system will be engaged by social information and underlie subsequent social behavior. On the other hand, it is unhelpful insofar as focusing on the SRS or MSAS in isolation leads only to overly constrained, theories of social cognition and empathy that only describe the perception of a small subset of social stimuli.

Critically, the social cues perceivers encounter outside the lab are often substantially different than those employed by the lion's share of extant research. Specifically, "real-world" social information typically contains features that would be likely to engage *both* the MSAS and SRS, including dynamic, multimodal target cues and the need to translate those cues into explicit inferences about internal states (Keysers and Gazzola 2007; Zaki and Ochsner 2009). Theories that emphasize the dissociability of the MSAS and SRS run the risk of either missing or glossing over this complexity, and as a consequence, formulating theories of empathy that rest too heavily on a single process. For example, two competing and well-known theories have claimed that interpersonal cognition can be largely localized to *either* the SRS *or* MSAS (Gallese, Keysers, and Rizzolotti 2004; Saxe 2005). The resulting debate, although provocative, is likely fatuous, because each side bases its argument on evidence derived from studies examining highly simplified "pieces" of social information processing rather than the complex social cues we might see in everyday situations.

Putting the Pieces Together

More recent research has begun to move beyond either/or theories of empathy by examining neural responses to complex social cues and by updating methods and tasks to characterize the role of brain activity in social behavior in a more ecologically valid manner. This work has capitalized on previous characterizations of the SRS and MSAS to study how these systems respond when "pieces" of isolated social information

(e.g., dynamic biological movement and linguistic cues about beliefs or emotions) must be put together to form a coherent whole.

This resulting picture differs dramatically from prior depictions of the SRS and MSAS as isolated and dissociable. Instead, an emerging consensus demonstrates that these systems are intimately related in at least three ways: (1) both systems are concurrently engaged by naturalistic, complex social information, although their engagement can be mapped to sometimes dissociable task demands; (2) regions in the MSAS and SRS become functionally connected to regions in the other system when they are responding to complex social cues; and (3) engagement of regions within both of these systems predicts interpersonal outcomes, such as accurate understanding of targets' emotions. We now describe each of these newer findings in turn.

Coactivation

Although early data emphasized separable engagement of the SRS and MSAS, these data were based on perceivers' responses to highly simplified social cues. Outside the lab, 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-perceptive capacities simultaneously and demand that we integrate over many social signs and signals in forming a coherent representation of targets' emotional states.

Consistent with this, several studies that have used multimodal social cues such as videos of social targets, and also required participants to draw inferences about those cues (closely approximating the demands of social interactions), have almost unanimously engaged aspects of both the SRS and MSAS. Two recent illustrative studies (de Lange et al. 2008; Spunt, Satpute, and Lieberman 2010) presented participants with videos of moving targets, and asked perceivers to draw either relatively low- or high-level inferences about targets. For example, while watching a target reading a book, perceivers might have been asked "how" the target accomplished this (e.g., by turning a page) or "why" the target accomplished the task (e.g., to learn more about cognitive neuroscience). In both cases dynamic social cues engaged areas within the SRS (and specifically, regions making up the putative mirror neuron system) regardless of condition. However, drawing high level "why" as opposed to low-level "how" inferences led to additional engagement of regions within the MSAS.

Two other studies have examined perceivers' brain activity while they observe targets in naturalistic social interactions. In one of these experiments (Wolf, Dziobek, and Heekeren 2010) perceivers were instructed to attend either to targets' internal states ("How does Kenneth feel during the following conversation?") or to properties of the physical world ("Was the door open or closed when Tracy arrived?"). The authors found that attending to and judging mental states based on complex, dynamic

stimuli engaged regions within both the MSAS and SRS (and again, specifically regions in the mirror neuron system). Another study involving the viewing of complex social interactions (Iacoboni et al. 2004) found similar engagement of areas within both systems even during passive viewing of social stimuli. These data suggest that—in the absence of an explicit nonsocial judgment—perceivers may "default" to drawing inferences about internal states while observing social interactions (Mitchell 2009a, 2009b).

These findings are not shocking by any means: the mirror neuron system and MSAS have been associated, respectively, with observing dynamic target behaviors and drawing explicit inferences about targets for over ten years across scores of studies. It is only sensible that combining stimulus and task characteristics that engage each individual system would lead to engagement of both systems.

Nonetheless, these data make an important point about how theories of empathy and social cognition should discuss prior data. That is, the fact that the SRS 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 SRS is central to empathy, and toward a "when and how" approach to better discriminating the situations likely to engage one or both of these systems.

Interaction

In addition to being concurrently activated during many social tasks, the MSAS and SRS likely interact with each other during many tasks in a feedback loop that informs social information-processing as it unfolds. For example, perceivers who share the sensorimotor states of social targets could use that sharing to inform their inferences about targets. Similarly, some level of inference about targets' situations and their likely responses to those situations is likely necessary to many types of emotion sharing.

Consistent with this idea, a handful of studies has typically found increased functional connectivity between areas in the SRS and MSAS during social cognitive tasks. For example, we (Zaki et al. 2007) examined connectivity during a standard empathy for pain task in which perceivers either experienced pain themselves or observed targets in pain. Consistent with previous studies, both self- and other pain engaged anterior portions of the insula and cingulate (Ochsner et al. 2008). However, each type of pain caused the AI and ACC to exhibit very different patterns of functional connectivity. On the one hand, when perceivers observed targets in pain—but not when they experienced it themselves—the ACC and AI became functionally connected with the MPFC and STS, two regions involved in mental state attribution.

On the other hand, when perceivers experienced pain themselves, the ACC and AI were functionally coupled with midbrain and posterior insula regions involved in somatosensation and low-level nociception. Thus, during empathy for pain (i.e., when observing others in pain), regions involved in shared representations exhibited unique connectivity with those involved in drawing high-level inferences about internal states.

One study has tested the other side of this equation: examining the connectivity of areas in the MSAS during an explicit social inference task. Lombardo 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 involved in sharing lower-level physical and affective states with targets, including areas within the mirror neuron system, as well the anterior insula. This is consistent with the idea that, when attempting to understand others, perceivers draw on a system of neural regions involved in such tasks, which in turn likely receive information from areas involved in sharing internal states.

Interactions need not be tested only within individuals. In a recent study Schippers et al. (2010) examined the communication of information from the brain of a target to that of a perceiver. Gesturers manually pantomimed simple actions (in a task approximating a game of charades) while being scanned using fMRI, and perceivers were later scanned while they guessed what gesturers were attempting to communicate. The researchers then examined how gesturers' brain activity at a given time point predicted perceivers' brain activity moments after they had observed gesturers, focusing on the connectivity between participants' mirror neuron systems. In line with their predictions, activity in the gesturer's premotor and inferior parietal cortex predicted subsequent activity in the same regions in observers. However, engagement of these regions in gesturers also predicted perceivers' engagement of the MPFC and PCC, areas typically involved in explicit mental state attribution, suggesting that to make sense of the pantomimed actions perceivers both needed to represent those actions in the SRS and then to draw explicit inferences about them using the MSAS.

Functional connectivity studies provide important insights about the neural mechanisms of human empathy. Although observing targets in pain and drawing inferences about targets' preferences engage dissociable neural systems (the SRS and MSAS, respectively), these regions interact with regions in the other system in both cases. Thus, even seemingly isolated psychological processes (sharing another person's visceral and affective states versus drawing "cold" cognitive inferences about those states) are likely more intimately connected than the first wave of data on the neuroscience of empathy suggested.

Relationship to Outcomes

The engagement of brain regions during social tasks provides a window into the potential cognitive mechanisms involved in such tasks, but it could also represent additional processing extraneous to successfully sharing or understanding targets' internal states.

One way to address this problem is through convergent data from studies of lesion patients that offer a partial—but not complete—remedy. For example, demonstrations that MPFC damage produces difficulty inferring the mental states of targets (e.g., Shamay-Tsoory, Aharon-Peretz, and Perry 2009) provide compelling evidence of the necessary role of this region in at least one empathic sub-process. However, some MPFC lesion patients are still able to understand others' internal states (e.g., Bird et al. 2004). Further, lesions can affect the function of intact brain regions that form a functional circuit with the lesioned area.

Another way to gain additional insights about the functional role of specific brain regions in empathy is to directly examine the relation between activity in these regions and subsequent social outcomes. For example, researchers could examine whether perceivers' engagement of a specific region predicts the amount that they share targets' emotions or understand those emotions. This approach is analogous to the well-known "subsequent memory" paradigm, in which memory researchers used brain activity at encoding to predict accurate retrieval of memoranda (Brewer et al. 1998; Wagner et al. 1998; Paller and Wagner 2002).

Several studies have begun to apply this approach to the study of social cognitive outcomes. Some of the earliest work in this area explored the social-reference effect in memory: the fact that encoding trait adjectives using a social, as opposed to non-social, strategy (e.g., "Does the word 'honest' describe you?" or "Does the word 'honest' describe Barack Obama?" as compared to "How many syllables does the word 'honest' contain?") results in better memory performance at retrieval. Three imaging studies demonstrated that this effect may reflect unique neural correlates of encoding social—as opposed to nonsocial—information. Specifically, successful encoding of social information—unlike nonsocial memory performance—is linked to activity (and intersubject correlation) in many areas within the MSAS, including the MPFC and PCC (Macrae et al. 2004; Mitchell, Macrae, and Banaji 2004; Hasson et al. 2008). This likely reflects the fact that successful social encoding of information requires MSA-like computations about the chronic mental and emotional states of targets.

Another approach to this issue has been to study how neural activity predicts the specific impressions we form about others' traits. In a recent imaging study perceivers were scanned while they viewed pictures of targets and read multiple sentences conveying trait-diagnostic information about those targets (e.g., "He stepped on his partner's feet during the dance"). Importantly, perceivers read both positive and negative sentences and later rated their overall impressions of targets, allowing the

experimenters to differentiate between information that perceivers later deemed relevant, as compared to irrelevant, to their subsequent overall judgments. This comparison revealed that PCC activity when perceivers first encountered social cues predicted their later decision that those cues were relevant to overall judgments about perceivers (Schiller et al. 2009).

Thus, ascribing traits to targets—as well as remembering those traits—relies on regions within the MSAS but not the SRS. However, this does not mean that the MSAS alone tracks with subsequent social judgments and behavior. Instead, MSAS involvement here may reflect the largely verbal social cues presented in—and abstracted, general social judgments demanded by—the tasks in these studies. Other social outcomes, especially those related to sharing and judging emotional states, could additionally recruit areas within the SRS. Although there are few data to speak to this issue, a few studies offer provocative evidence that the SRS indeed predicts affect-relevant social outcomes. For example, whereas the relationship between activity in the ACC or AI and self-reported sharing of others' pain and emotion has not been tested, activity in these regions does predict the amount of pain perceivers believe targets to be in (Jackson, Meltzoff, and Decety 2005; Saarela et al. 2007) and how unpleasantly perceivers feel while watching targets in pain (Constantini et al. 2008; Singer et al. 2008).

Our group has taken another approach to measuring brain-behavior relationships in empathy. We have explored brain activity that predicts perceivers' accuracy about targets' emotions over time by adapting an "empathic accuracy" paradigm previously used in behavioral and psychophysiological research (Levenson and Ruef 1992; Ickes 1997; Zaki, Bolger, and Ochsner 2008; Zaki and Ochsner in press). Perceivers watched videos of targets describing emotional autobiographical events, and continuously rate how positive or negative they believed targets felt. Importantly, targets themselves had previously rated their emotions at each moment using the same scale perceivers employed. This allowed us to operationalize accuracy about emotions as the correlation between perceivers' ratings of targets emotions and targets' self-ratings of their emotion and to search for brain activity tracking with perceivers' accuracy on a block-by-block basis. The results of this analysis indicated that accuracy was predicted by activity in regions related to explicit attributions about mental states, including the MPFC and temporal poles, and in regions putatively related to shared sensorimotor states, including premotor and inferior parietal regions (Zaki et al. 2009).

Although studies of brain-behavior relationships in empathy remain rare, their findings are promising. This is primarily because they afford the ability to understand not only the tasks and stimuli that engage neural systems related to social perception but also how this brain activity maps onto the actual goals of social perceivers: demonstrably sharing or understanding targets' emotions in situations approximating the demands of real-world social interaction. Preliminary work taking this approach

suggests that accuracy and retention of certain types of social information (especially about traits) are subserved by areas in the MSAS, whereas accuracy and perception of transient emotional states are additionally related to activity in the SRS.

Conclusions and Future Directions

The study of emotion perception, sharing, and understanding is among the fastest growing domains in social cognitive and affective neuroscience. This reflects both the intuitive importance of social perception in our every day lives and the utility of neuroimaging for characterizing the cognitive and neural processes underlying these complex human abilities.

Given the short history of this field of research, the amount of evolution it has gone through is especially impressive. This evolution can be broadly categorized into two "waves" of research. In the first wave researchers characterized two separable neural systems involved in different empathic subprocesses: the SRS, which is involved in sharing targets' sensorimotor and visceral states, and the MSAS, which is engaged when perceivers draw explicit inferences about targets' internal states. This work was foundational because it characterized the neural bases of basic empathic processes with a high degree of consistency. However, it was also limited in its use of highly simplified, nonnaturalistic stimuli and a lack of data connecting brain activity to behavior. These limitations sometimes—though by no means always—led to theories positing that extremely complex phenomena such as empathy are supported by *either* one neural system *or* the other instead of the more likely possibility that these processes tap multiple neural systems simultaneously.

The second wave of research in the neuroscience study of empathy is complementary to the first in that it has capitalized on characterizations of the MSAS and SRS 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 as remembering and understanding targets' internal states. This work provides an integrative view of the brain bases of sharing and understanding others' emotions, seeing theses abilities as flexibly tapping multiple, functionally connected systems of brain regions to translate complex social cues into inferences about others' internal states.

How might we apply insights gained from the second wave of neuroscience research on empathy to future work? The first, most general point is that either/or theories for understanding the cognitive and neural bases of empathy as based on a single process (such as self/other overlap or theory of mind) are outdated, and a more productive approach would be to emphasize subtler questions about when and how each of these systems is involved in processing social information. For example, viewing a target in pain could engage the SRS, MSAS, or both, depending on the structure of the cues

presented about that pain (visual or auditory, dynamic, or static), the task involved (simply watching the target vs. drawing an inference about how that target is feeling), or other features of the situation. Related to this, other recent work has examined how SRS and MSAS activity are modulated by contextual factors ranging from the attributions made about targets (Singer et al. 2006; Lamm, Batson, and Decety 2007) to the experiences of perceivers (Cheng et al. 2007) to the differences or similarities between targets and perceivers (Mitchell, Macrae, and Banaji 2006; Mobbs et al. 2009; Xu et al. 2009); interested readers can find reviews of this specific set of studies elsewhere (Hein and Singer 2008; Mitchell 2009a, 2009b).

Another important application of second-wave research on empathy will be to expand and refine the study of deficits in illnesses such as autism spectrum disorders (ASD). ASD is centrally characterized by abnormalities in reciprocal social interaction, which have often been tied to more proximate difficulties in processing and responding to social cues. Social cognitive abnormalities in ASD have been broadly categorized as being of two types: (1) failures to imitate movements, which could represent difficulties in forming shared motor representations (Rogers et al. 2003); and (2) failures to correctly ascribe complex mental states to others (Baron-Cohen 1994). Not surprisingly, early imaging studies of ASD linked each of these deficits to abnormal processing (usually hypofunction) in the SRS and MSAS, respectively (Baron-Cohen et al. 1999; Hadjikhani et al. 2004; Dapretto et al. 2006; Wang 2006). These data have been extremely fruitful in characterizing social cognitive deficits in ASD, but—much like the cognitive neuroscience study of empathy in typically developing populations— studies of neural hypofunction in ASD have typically employed simplified tasks designed to engage each type of neural system in isolation. Importantly, the data reviewed here suggest that ASD could involve additional abnormalities in social information processing that cannot be tapped by studying single neural systems such as the MSAS or SRS in isolation. For example, individuals with ASD may have increased difficulties integrating multiple pieces of social information when faced with complex, multimodal social cues; such a deficit could reflect not only on hypo-function *within* single neural systems, but also on hypo-connectivity *between* these systems. This possibility is supported by more recent data characterizing ASD as involving problems in synaptogenesis during development that lead to abnormal patterns of interregional connectivity later in life (e.g., Courchesne and Pierce 2005). Employing second-wave techniques and paradigms in studying ASD could allow researchers to better understand possible difficulties individuals with this illness may have in integrating social information through concurrent engagement of multiple neural systems.

Conclusions

The study of empathy has produced one of the most exciting subfields in neuroscience research. Programmatic work in this field has allowed empathy to be decomposed into

multiple computational "pieces" that rely on separate systems of brain regions to meet separate computational goals. Newer work, however, is also emphasizing the way that these pieces come together to form whole impressions of others' internal states. Future work will help further clarify how disparate types of social cues enable us to share others' emotions, to form insightful, high-level appraisals of what others are experiencing, and to use the abilities in concert.

Acknowledgments

References

Avenanti, A., D. Bueti, G. Galati, and S. M. Aglioti. 2005. Transcranial Magnetic Stimulation Highlights the sensorimotor side of empathy for pain. *Nature Neuroscience* 8 (7): 955–960.

Baron-Cohen, S. 1994. *Mindblindness*. Cambridge, MA: MIT Press.

Baron-Cohen, S., A. M. Leslie, and U. Frith. 1985. Does the autistic child have a "theory of mind"? *Cognition* 21 (1): 37–46.

Baron-Cohen, S., H. A. Ring, S. Wheelwright, E. T. Bullmore, M. J. Brammer, A. Simmons, et al. 1999. Social intelligence in the normal and Autistic Brain: An fMRI study. *European Journal of Neuroscience* 11 (6): 1891–1898.

Barsalou, L. W. 2008. Grounded cognition. *Annual Review of Psychology* 59: 617–645.

Bird, C. M., F. Castelli, O. Malik, U. Frith, and M. Husain. 2004. The impact of extensive medial frontal lobe damage on "theory of mind" and cognition. *Brain* 127 (Pt 4): 914–928.

Blair, R. J. 2005. Responding to the emotions of others: Dissociating forms of empathy through the study of typical and psychiatric populations. *Consciousness and Cognition* 14 (4): 698–718.

Brass, M., P. Ruby, and S. Spengler. 2009. Inhibition of imitative behaviour and social cognition. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364 (1528): 2359–2367.

Brewer, J. B., Z. Zhao, J. E. Desmond, G. H. Glover, and J. D. Gabrieli. 1998. Making memories: Brain Activity that predicts how well visual experience will be remembered. *Science* 281 (5380): 1185–1187.

Brothers, L. (1990). The social brain: A project for integrating primate behavior and neurophysiology in a new domain. *Concepts in Neuroscience* 1: 27–51.

Buckner, R. L., J. R. Andrews-Hanna, and D. L. Schacter. 2008. The brain's default network: Anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences* 1124: 1–38.

*Castelli, F., C. Frith, F. Happe, and U. Frith. 2002. Autism, Asperger syndrome and brain mechanisms for the attribution of mental states to animated shapes. *Brain* 125 (Pt 8): 1839–1849.

Chartrand, T. L., and J. A. Bargh. 1999. The chameleon effect: The perception-behavior link and social interaction. *Journal of Personality and Social Psychology* 76 (6): 893–910.

Cheng, Y., C. P. Lin, H. L. Liu, Y. Y. Hsu, K. E. Lim, D. Hung, et al. 2007. Expertise modulates the perception of pain in others. *Current Biology* 17 (19): 1708–1713.

Constantini, M., G. Gaspare, G. L. Romani, and S. Aglioti. 2008. Empathic neural reactivity to noxious stimuli delivered to body parts and non-corporeal objects. *European Journal of Neuroscience* 28: 1222–1230.

Corbetta, M., G. Patel, and G. L. Shulman. 2008. The reorienting system of the human brain: From environment to theory of mind. *Neuron* 58 (3): 306–324.

Courchesne, E., and K. Pierce. 2005. Why the frontal cortex in autism might be talking only to itself: Local over-connectivity but long-distance disconnection. *Current Opinion in Neurobiology* 15 (2): 225–230.

Dapretto, M., M. S. Davies, J. H. Pfeifer, A. A. Scott, M. Sigman, S. Y. Bookheimer, et al. 2006. Understanding emotions in others: Mirror neuron dysfunction in children with autism spectrum disorders. *Nature Neuroscience* 9 (1): 28–30.

Decety, J. 1996. Do imagined and executed actions share the same neural substrate? *Brain Research. Cognitive Brain Research* 3 (2): 87–93.

Decety, J., and P. L. Jackson. 2004. The functional architecture of human empathy. *Behavioral and Cognitive Neuroscience Reviews* 3 (2): 71–100.

de Lange, F. P., M. Spronk, R. M. Willems, I. Toni, and H. Bekkering. 2008. Complementary systems for understanding action intentions. *Current Biology* 18 (6): 454–57.

Dijksterhuis, A., and J. Bargh. 2001. the perception-behavior expressway: automatic effects of social perception on social behavior. *Advances in Experimental Social Psychology* 33: 1–40.

Dimberg, U., M. Thunberg, and K. Elmehed. 2000. Unconscious facial reactions to emotional facial expressions. *Psychological Science* 11 (1): 86–89.

Dunbar, R. 2004. Gossip in evolutionary perspective. *Review of General Psychology* 8: 80–100.

Epley, N., B. Keysar, L. Van Boven, and T. Gilovich. 2004. Perspective taking as egocentric anchoring and adjustment. *Journal of Personality and Social Psychology* 87 (3): 327–339.

Flavell, J. 1999. Cognitive development: Children's knowledge about other minds. *Annual Review of Psychology* 50: 21–45.

Fletcher, P. C., F. Happe, U. Frith, S. C. Baker, R. J. Dolan, R. S. Frackowiak, et al. 1995. Other minds in the Brain: A functional imaging study of "theory of mind" in story comprehension. *Cognition* 57 (2): 109–128.

Gallese, V., and A. Goldman. 1998. Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences* 2 (12): 493–501.

Gallese, V., C. Keysers, and G. Rizzolatti. 2004. A Unifying View of the basis of social cognition. *Trends in Cognitive Sciences* 8 (9): 396–403.

Gilovich, T., V. H. Medvec, and K. Savitsky. 2000. The spotlight effect in Social Judgment: An egocentric bias in estimates of the salience of one's own actions and appearance. *Journal of Personality and Social Psychology* 78: 211–222.

Goel, V., J. Grafman, N. Sadato, and M. Hallett. 1995. Modeling other minds. *Neuroreport* 6 (13): 1741–1746.

Hadjikhani, N., R. M. Joseph, J. Snyder, C. F. Chabris, J. Clark, S. Steele, et al. 2004. Activation of the fusiform gyrus when individuals with autism spectrum disorder view faces. *NeuroImage* 22 (3): 1141–1150.

Hasson, U., O. Furman, D. Clark, Y. Dudai, and L. Davachi. 2008. Enhanced intersubject correlations during movie viewing correlate with successful episodic encoding. *Neuron* 57 (3): 452–462.

Hein, G., and T. Singer. 2008. I feel how you feel but not always: The empathic brain and its modulation. *Current Opinion in Neurobiology* 18 (2): 153–158.

Humphrey, N. 1976. The social function of intellect. In *Growing Points in Ethology*, edited by P. Bateson and R. Hinde. Cambridge: Cambridge University Press.

Iacoboni, M., M. D. Lieberman, B. J. Knowlton, I. Molnar-Szakacs, M. Moritz, C. J. Throop, et al. 2004. Watching social interactions produces dorsomedial prefrontal and medial parietal bold fMRI signal increases compared to a resting baseline. *NeuroImage* 21 (3): 1167–1173.

Ickes, W. 1997. *Empathic Accuracy*. New York: Guilford Press.

Jackson, P. L., A. N. Meltzoff, and J. Decety. 2005. How do we Perceive the pain of others? A window into the neural processes involved in empathy. *NeuroImage* 24 (3): 771–779.

Jacob, P., and M. Jeannerod. 2005. The motor theory of social cognition: A critique. *Trends in Cognitive Sciences* 9 (1): 21–25.

Keysers, C., and V. Gazzola. 2007. Integrating simulation and theory of mind: From self to social cognition. *Trends in Cognitive Sciences* 11 (5): 194–196.

Keysers, C., J. H. Kaas, and V. Gazzola. 2010. Somatosensation in social perception. *Nature Reviews. Neuroscience* 11 (6): 417–428.

Keysers, C., B. Wicker, V. Gazzola, J. L. Anton, L. Fogassi, and V. Gallese. 2004. A touching sight: SII/PV activation during the observation and experience of touch. *Neuron* 42 (2): 335–346.

Kosslyn, S. M., W. L. Thompson, and N. M. Alpert. 1997. "Neural Systems Shared by Visual Imagery and Visual Perception: A Positron Emission Tomography Study." *NeuroImage* 6 (4): 320–334.

Lamm, C., C. D. Batson, and J. Decety. 2007. "The Neural Substrate of Human Empathy: Effects of Perspective-Taking and Cognitive Appraisal." *Journal of Cognitive Neuroscience* 19 (1): 42–58.

Levenson, R. W., and A. M. Ruef. 1992. "Empathy: A Physiological Substrate." *Journal of Personality and Social Psychology* 63 (2): 234–246.

Lipps, T. 1903. Einfühlung, innere Nachahmung und Organempfindung. *Archiv fur die Gesamte Psychologie* 1: 465–519.

Lombardo, M. V., B. Chakrabarti, E. T. Bullmore, S. J. Wheelwright, S. A. Sadek, J. Suckling, MRC AIMS Consortium, and S. Baron-Cohen. 2010. Shared neural circuits for mentalizing about the self and others. *Journal of Cognitive Neuroscience* 22: 1623–1635.

Macrae, C. N., J. M. Moran, T. F. Heatherton, J. F. Banfield, and W. M. Kelley. 2004. Medial prefrontal activity predicts memory for self. *Cerebral Cortex* 14 (6): 647–654.

Mar, R. A., and K. Oatley. 2008. The function of fiction is the abstraction and simulation of social experience. *Perspectives on Psychological Science* 3: 173–192.

Mitchell, J. P. 2008. Activity in right temporo-parietal junction is not selective for theory-of-mind. *Cerebral Cortex* 18 (2): 262–271.

Mitchell, J. P. 2009a. Inferences about mental states. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364 (1521): 1309–1316.

Mitchell, J. P. 2009b. Social psychology as a natural kind. *Trends in Cognitive Sciences* 13 (6): 246–251.

Mitchell, J. P., T. F. Heatherton, and C. N. Macrae. 2002. Distinct neural systems subserve person and object knowledge. *Proceedings of the National Academy of Sciences of the United States of America* 99 (23): 15238–15243.

Mitchell, J. P., C. N. Macrae, and M. R. Banaji. 2004. Encoding-specific effects of social cognition on the neural correlates of subsequent memory. *Journal of Neuroscience* 24 (21): 4912–4917.

Mitchell, J. P., C. N. Macrae, and M. R. Banaji. 2006. Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. *Neuron* 50: 1–9.

Mobbs, D., R. Yu, M. Meyer, L. Passamonti, B. Seymour, A. J. Calder, et al. 2009. A key role for similarity in vicarious reward. *Science* 324 (5929): 900.

Morrison, I., D. Lloyd, G. di Pellegrino, and N. Roberts. 2004. Vicarious responses to pain in anterior cingulate cortex: Is empathy a multisensory issue? *Cognitive, Affective & Behavioral Neuroscience* 4 (2): 270–278.

Mukamel, R., A. D. Ekstrom, J. Kaplan, M. Iacoboni, and I. Fried. 2010. Single-neuron responses in humans during execution and observation of actions. *Current Biology* 20 (8): 750–756.

Neumann, R., and F. Strack. 2000. "Mood contagion": The automatic transfer of mood between persons. *Journal of Personality and Social Psychology* 79 (2): 211–223.

Niedenthal, P., L. W. Barsalou, F. Ric, and S. Krauth-Gruber. 2005. Embodiment in the acquisition and use of emotion knowledge. In *Emotion and Consciousness*, edited by L. Feldman Barrett, P. Niedenthal, and P. Winkielman, 186–210. New York: Guilford Press.

Ochsner, K. N., K. Knierim, D. H. Ludlow, J. Hanelin, T. Ramachandran, G. Glover, et al. 2004. Reflecting upon feelings: an fMRI study of neural systems supporting the attribution of emotion to self and other. *Journal of Cognitive Neuroscience* 16 (10): 1746–1772.

Ochsner, K. N., J. Zaki, J. Hanelin, D. H. Ludlow, K. Knierim, T. Ramachandran, et al. 2008. Your pain or mine? Common and distinct neural systems supporting the perception of pain in self and others. *Social Cognitive and Affective Neuroscience* 3 (2): 144–160.

Olsson, A., and K. N. Ochsner. 2008. The role of social cognition in emotion. *Trends in Cognitive Sciences* 12 (2): 65–71.

Paller, K. A., and A. D. Wagner. 2002. Observing the transformation of experience into memory. *Trends in Cognitive Sciences* 6 (2): 93–102.

Peelen, M. V., A. P. Atkinson, and P. Vuilleumier. 2010. Supramodal representations of perceived emotions in the human brain. *Journal of Neuroscience* 30 (30): 10127–10134.

Premack, D., and G. Woodruff. 1978. Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences* 1: 515–526.

Preston, S. D., and F. B. de Waal. 2002. Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences* 25 (1): 1–20, discussion 20–71.

Prinz, W. 1997. Perception and action planning. *European Journal of Cognitive Psychology* 9 (2): 129–154.

Rizzolatti, G., and L. Craighero. 2004. The mirror-neuron system. *Annual Review of Neuroscience* 27: 169–192.

Rogers, S. J., S. L. Hepburn, T. Stackhouse, and E. Wehner. 2003. Imitation performance in toddlers with autism and those with other developmental disorders. *Journal of Child Psychology and Psychiatry, and Allied Disciplines* 44 (5): 763–781.

Saarela, M. V., Y. Hlushchuk, A. C. Williams, M. Schurmann, E. Kalso, and R. Hari. 2007. The compassionate brain: Humans detect intensity of pain from another's face. *Cerebral Cortex* 17: 230–237.

Saxe, R. 2005. Against simulation: The argument from error. *Trends in Cognitive Sciences* 9 (4): 174–179.

Saxe, R., and N. Kanwisher. 2003. People thinking about thinking people: The role of the temporo-parietal junction in "theory of mind." *NeuroImage* 19 (4): 1835–1842.

Schiller, D., J. B. Freeman, J. P. Mitchell, J. S. Uleman, and E. A. Phelps. 2009. A neural mechanism of first impressions. *Nature Neuroscience* 12 (4): 508–514.

Schippers, M. B., A. Roebroeck, R. Renken, L. Nanetti, and C. Keysers. 2010. Mapping the information flow from one brain to another during gestural communication. *Proceedings of the National Academy of Sciences of the United States of America* 107 (20): 9388–9393.

Shamay-Tsoory, S. G., J. Aharon-Peretz, and D. Perry. 2009. Two systems for empathy: A double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions. *Brain* 132 (Pt 3): 617–627.

Singer, T. 2006. The neuronal basis and ontogeny of empathy and mind reading: Review of literature and implications for future research. *Neuroscience and Biobehavioral Reviews* 30 (6): 855–863.

Singer, T., B. Seymour, J. O'Doherty, H. Kaube, R. J. Dolan, and C. D. Frith. 2004. Empathy for pain involves the affective but not sensory components of pain. *Science* 303 (5661): 1157–1162.

Singer, T., B. Seymour, J. P. O'Doherty, K. E. Stephan, R. J. Dolan, and C. D. Frith. 2006. Empathic neural responses are modulated by the perceived fairness of others. *Nature* 439 (7075): 466–469.

Singer, T., R. Snozzi, G. Bird, P. Petrovic, G. Silani, M. Heinrichs, et al. 2008. Effects of oxytocin and prosocial behavior on brain responses to direct and Vicariously Experienced Pain. *Emotion (Washington, DC)* 8 (6): 781–791.

Smith, A. [1790] 2002. *The Theory of Moral Sentiments*. Cambridge: Cambridge University Press.

Spreng, R. N., R. A. Mar, and A. S. Kim. 2009. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: A quantitative meta-analysis. *Journal of Cognitive Neuroscience* 21 (3): 489–510.

Spunt, R. P., A. B. Satpute, and M. D. Lieberman. 2010. Identifying the what, why, and how of an observed action: An fMRI study of mentalizing and mechanizing during action observation. *Journal of Cognitive Neuroscience* 23: 63–74.

Uddin, L. Q., M. Iacoboni, C. Lange, and J. P. Keenan. 2007. The self and social cognition: The role of cortical midline Structures and mirror neurons. *Trends in Cognitive Sciences* 11 (4): 153–157.

van Overwalle, F., and K. Baetens. 2009. Understanding others' actions and goals by mirror and mentalizing systems: A meta-analysis. *NeuroImage* 48 (3): 564–584.

Vaughan, K. B., and J. T. Lanzetta. 1980. Vicarious instigation and conditioning of facial expressive and autonomic responses to a Model's Expressive Display of pain. *Journal of Personality and Social Psychology* 38 (6): 909–923.

Vogt, B. A., L. Vogt, and S. Laureys. 2006. Cytology and functionally correlated circuits of human posterior cingulate areas. *NeuroImage* 29 (2): 452–466.

Wagner, A. D., D. L. Schacter, M. Rotte, W. Koutstaal, A. Maril, A. M. Dale, et al. 1998. Building memories: Remembering and forgetting of verbal experiences as predicted by brain activity. *Science* 281 (5380): 1188–1191.

Wang, A. T., S. S. Lee, M. Sigman, and M. Dapretto. 2006. Neural basis of irony comprehension in children with Autism: The Role of prosody and context. *Brain* 129 (Pt 4): 932–943.

Wolf, I., I. Dziobek, and H. R. Heekeren. 2010. Neural correlates of social cognition in naturalistic settings: A model-free analysis approach. *NeuroImage* 49 (1): 894–904.

Xu, X., X. Zuo, X. Wang, and S. Han. 2009. Do you feel my pain? Racial group membership modulates empathic neural responses. *Journal of Neuroscience* 29 (26): 8525–8529.

Zaki, J., N. Bolger, and K. Ochsner. 2008. It takes two: The interpersonal nature of empathic accuracy. *Psychological Science* 19 (4): 399–404.

Zaki, J., K. Hennigan, J. Weber, and K. N. Ochsner. 2010. Social cognitive conflict resolution: Contributions of domain-general and domain-specific neural systems. *Journal of Neuroscience* 30 (25): 8481–8488.

Zaki, J., and K. Ochsner. 2009. The need for a cognitive neuroscience of naturalistic social cognition. *Annals of the New York Academy of Sciences* 1167: 16–30.

Zaki, J., and K. N.. Ochsner. In press. Re-integrating the study of accuracy into social cognition research. *Psychological Inquiry*.

Zaki, J., K. N. Ochsner, J. Hanelin, T. Wager, and S. C. Mackey. 2007. Different circuits for different pain: Patterns of functional connectivity reveal distinct networks for processing pain in self and others. *Social Neuroscience* 2 (3–4): 276–291.

Zaki, J., J. Weber, N. Bolger, and K. Ochsner. 2009. The neural bases of empathic accuracy. *Proceedings of the National Academy of Sciences of the United States of America* 106 (27): 11382–11387.