nature neuroscience

# The neuroscience of empathy: progress, pitfalls and promise

Jamil Zaki[1] & Kevin Ochsner[2]

**The last decade has witnessed enormous growth in the neuroscience of empathy. Here, we survey research in this domain with an eye toward evaluating its strengths and weaknesses. First, we take stock of the notable progress made by early research in characterizing the neural systems supporting two empathic sub-processes: sharing others' internal states and explicitly considering those states. Second, we describe methodological and conceptual pitfalls into which this work has sometimes fallen, which can limit its validity. These include the use of relatively artificial stimuli that differ qualitatively from the social cues people typically encounter and a lack of focus on the relationship between brain activity and social behavior. Finally, we describe current research trends that are overcoming these pitfalls through simple but important adjustments in focus, and the future promise of empathy research if these trends continue and expand.**

Compared to many other animals on the planet, human beings are small, slow and weak. And yet, we have unequivocally won the cross-species competition for global domination. What allowed us, as physical underdogs, to claim this unlikely victory?

Although many answers may be offered to this question, psychologists increasingly believe that it is our interpersonal faculties, especially our ability to cooperate with and understand others, that have supported our species' success[1]. These abilities, in turn, are supported by the multifaceted psychological construct of empathy. Empathy comprises related but distinct processes through which 'perceivers' (individuals focusing on another person's internal states) relate to 'targets' (individuals who are the focus of perceivers' attention). Although the literature on empathy has used a raft of overlapping terms to describe these processes, we find it useful to group them into three broad classes, which are depicted in **Figure 1** alongside some allied terms from the literature. The three include (i) experience sharing: vicariously sharing targets' internal states[2], (ii) mentalizing: explicitly considering (and perhaps understanding) targets' states and their sources[3], and (iii) prosocial concern: expressing motivation to improve targets' experiences (for example, by reducing their suffering)[4].

Over the last two decades, neuroscientists have devoted a large and growing amount of attention to the neural bases of human empathy. Here, we offer a three-part survey of this research area (see ref. 5 for a review of related work on empathy in nonhuman animals). First, we will briefly review its progress in characterizing the neural systems supporting empathy. Work in this domain began with a primary focus on the first two facets of empathy described here: experience sharing and mentalizing. Second, we will point out two methodological and conceptual pitfalls into which extant research has often fallen, and which limit the translational value of neuroscience in this domain. Third, we will outline two simple but important shifts in researchers' approach—which are gaining traction in more recent work—that can maximize the promise of future research to deepen our mechanistic understanding of empathy.

## Progress

By now, hundreds of studies have examined the neural mechanisms underlying human empathy. Historically, the lion's share of this work focused on a detailed characterization of two subprocesses: experience sharing and mentalizing. (A small but growing number of studies are now examining the neural bases of prosocial motivation; we turn to this research trend below.) Early work in this domain, here defined as encompassing roughly 1995–2005, uncovered key insights about each of these processes.

**A tale of two systems.** Given that experience sharing and mentalizing ostensibly represent two paths to the same goal (understanding and responding to another person's internal states), they are subserved by surprisingly disparate neural systems. Experience sharing is often tied to a mechanism known as 'neural resonance': perceivers' tendency to engage overlapping neural systems when they experience a given internal state and when they observe (or know that) targets (are) experiencing that same state (**Fig. 2a**). Neural resonance accompanies the experience and observation of motor intentions[6], sensory experiences[7] and visceral states such as pain and disgust[8]. By contrast, mentalizing—usually examined by asking perceivers to draw explicit inferences about targets' states (**Fig. 2b**)—engages a system of midline and superior temporal structures broadly involved in 'self-projection': the ability to represent states outside of a perceiver's 'here and now' including the future, past, counterfactuals and targets' perspectives[9,10] (see **Fig. 2c** for an outline of brain regions associated with experience sharing and mentalizing).

Until recently, the neural activity accompanying these two processes seemed almost entirely non-overlapping. That is, tasks and social cues that engaged one of these systems typically did not concurrently engage the other system[11]. Further, lesions to areas in each of these neural systems produce dissociable impairments in

---

[1]Department of Psychology, Harvard University, Cambridge, Massachusetts, USA. [2]Department of Psychology, Columbia University, New York, New York, USA. Correspondence should be addressed to J.Z. (zaki@wjh.harvard.edu) or K.O. (ochsner@psych.columbia.edu).

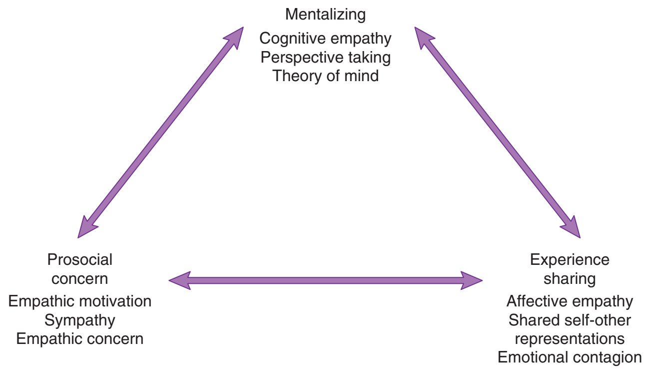

**Figure 1** Three major facets of empathy. For decades, behavioral research has examined each of these processes and developed theories about the nature of and relationships between each one. By contrast, the lion's share of neuroscience research in empathy has focused on two empathic processes: the tendency to take on, resonate with, or 'share' the emotions of others (experience sharing) and the ability to explicitly reason and draw inferences about their mental states (mentalizing). A third facet, the prosocial motivation to help others as a result of using one or both of the other facets to share and/or cognitively understand the emotions they are experiencing (prosocial concern), has begun receiving increasing neuroscientific attention in the last few years. Each of these empathic processes has also been described using other terms, some of which are listed here.

experience sharing and mentalizing[12]. Together, such findings supported the assertion that these two processes are fundamentally dissociable routes to empathy.

**Variance in empathic processes.** Perceivers empathize with targets often, but not always. Some individuals are more likely to deploy experience sharing and mentalizing than others[13], and some situations are more likely to elicit these processes than others. Consistent with this idea, the neural systems supporting empathic subprocesses exhibit both contextual and interindividual variance. For example, individual differences in self-report measures of empathy track with engagement of brain regions associated with mentalizing[14] and experience sharing[15]. Further, social contexts known to affect empathy also modulate activity in these systems: perceivers are less likely to engage neural resonance when viewing dissimilar others experiencing pain[16] and less likely to engage areas associated with mentalizing when encountering socially derogated targets[17].

Abnormal engagement of empathy-related neural systems also characterizes psychiatric conditions involving social deficits. For example, individuals with autism spectrum disorders exhibit reduced engagement of brain areas associated with mentalizing and experience sharing[18], which correlates with deficits in clinical measures of social impairments[19]; similar patterns emerge in other disorders such as schizophrenia[20] and psychopathy[21]. Together, these data bolster the argument that neural systems associated with empathic subprocesses support human social abilities.

## Pitfalls

The early research reviewed above made crucial headway in building a functional architecture of empathy that specifies separable neural systems underlying mentalizing and experience sharing, with variance in these systems tracking contextual and individual differences in empathic processing. That said, this work also has been prone to two recurring conceptual and methodological pitfalls that may limit its ability to connect with other domains of research—most notably, the vast psychological literature on empathy.

**Artificiality.** At first blush, early research on the neuroscience of empathy seemed to make a convincing case that experience sharing and mentalizing are isolated social information processing streams: they engage largely dissociable neural systems (**Fig. 2c**), and tasks that engage one of these system rarely engage the other concurrently. By contrast, psychological models of empathy view these processes—along with prosocial motivation and other phenomena—as deeply interactive.

Given this state of affairs, researchers were left with (at least) three options. First, they could speculate about interactions between mentalizing, experience sharing and other processes that underlie empathy as a whole[22], an option to which we will turn momentarily. Second, they could focus mainly on a single empathic process and remain agnostic about how this process might interact with others. Third, they could build single-process models of empathy that largely excluded other processes; this approach was embodied in a debate about whether human social abilities are predominantly supported by experience sharing or mentalizing[2,23].

Notably, models that focus on single empathic subprocesses while remaining agnostic about the role of others or excluding them altogether run the risk of reflecting historical quirks in the field's choice of methods instead of deeper insights about the structure of empathy. This is because until a few years ago neuroscientific studies of empathy almost always used highly simplified cues and tasks designed to isolate one type of empathic subprocess and its associated neural systems. For example, neuroimaging studies of experience sharing typically presented perceivers with decontextualized pictures of sensorimotor cues (such as a single target facial expression or movement) without requiring perceivers to draw any explicit inferences about target states. By contrast, studies of mentalizing typically asked perceivers to draw just such inferences from either contextual information describing the source of those internal states (for example, vignettes describing scenarios in which targets' form false beliefs) or decontextualized sensorimotor information (for example, static images of targets' eyes or faces). In other words, the first decade of cognitive neuroscience research on empathy homed in on how perceivers process isolated 'pieces' of social information, but left unclear how perceivers put those pieces together when cues combine, as they often do in everyday social interactions[24].

This approach parallels the early study of any complex cognitive process. The use of simple, tractable and artificial cues and tasks has been paramount to building early models of the mechanisms involved in vision, memory, attention and the like. Empathy is no different, and without using the simplest possible experimental systems, neuroscientists could not have gained traction on the way that processes such as mentalizing or experience sharing operate. That said, for at least two reasons, important problems emerge when researchers rely on overly simplified models of any complex psychological phenomenon for too long, especially when they attempt to 'scale up' data gleaned from such models into broader conclusions about how these phenomena work in other contexts.

First and most broadly, complex cognitive phenomena are difficult, if not impossible, to describe through data about their building blocks alone; that is, these phenomena are greater than the sum of their parts. To the extent that laboratory and 'wild-type' stimuli differ qualitatively in the patterns of information processing they produce, data gleaned from simplified models may offer limited insight into how empathy most often operates (see ref. 25 for discussions of this issue in other domains). By analogy, this may be akin to drawing inferences about how the brain processes the sound of an orchestra based on data describing how the

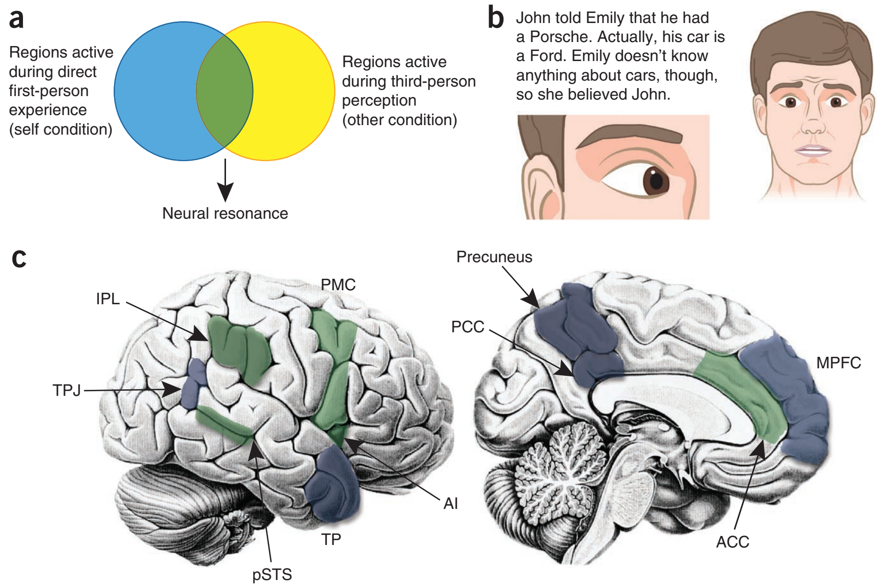

**Figure 2** Neuroscientific approaches to studying experience sharing and mentalizing, and the brain regions that are associated with each. (**a**) The experimental logic underlying studies of experience sharing. The blue circle represents brain regions engaged by direct, first-person experience of an affective response, motor intention or other internal state. The yellow circle represents regions engaged by third-person observation of someone else experiencing the same kind of internal state. To the extent that a region demonstrates neural resonance—common engagement by first- and third-person experience (green overlap)—it is described as supporting a perceiver's vicarious experience of a target's state (regions demonstrating such properties are highlighted in green in **c**). (**b**) Studies of mentalizing typically ask participants to make judgments about targets' beliefs, thoughts, intentions and/or feelings, as depicted in highly stylized social cues, including vignettes (top left), posed facial expressions (right), or even more isolated nonverbal cues, such as target eye gaze (bottom left). Regions engaged by such tasks (blue in **c**) are described as contributing to perceivers' ability to mentalize. (**c**) Brain regions associated with experience sharing and mentalizing. IPL, inferior parietal lobule; TPJ, temporoparietal junction; pSTS, posterior superior temporal sulcus; TP, temporal ole; AI, anterior insula; PMC, premotor cortex; PCC, posterior cingulate cortex; ACC, anterior cingulate cortex; MPFC, medial prefrontal cortex.

brain processes the sound of each individual instrument, agnostic to the types of information (for example, harmonies across instruments) that uniquely characterize the real world stimuli of interest. As we will see (in the Naturalism section below), newer research indeed suggests that complex, as compared to simplified, social cues engage qualitatively different patterns of neural activity, suggesting that empathy cannot be understood fully by deconstructing it into constituent parts.

Theorists have long been sensitive to the likely differences between neuroscientific data about isolated empathic processes on the one hand, and the more complex phenomenon of empathy on the other. As such, several early theories speculated about ways that empathic subprocesses might interact during complex social information processing (for example, most real-world social interactions)[22,26]. However, because early empirical studies of empathy focused almost exclusively on simplified social contexts, the evidence needed to support or refute such models remained scarce.

A second issue is that relying too heavily on highly simplified models can introduce interpretational confounds into existing models of empathy. For example, although studies of experience sharing and mentalizing clearly engage separable neural systems, the fact that these studies tend to rely on different stimulus types (for example, sensorimotor versus contextual social cues) and task sets (for example, passive viewing of, versus active inferences about, targets) renders the psychological meaning of their neural distinction unclear. Dissociations between these neural systems could reflect deep separation between empathic subprocesses, but they could just as easily reflect less interesting variance in the stimuli to which perceivers have access or their motivations to make particular sorts of judgments about targets. In fact, newer work demonstrates that neural systems typically associated with mentalizing and experience sharing also are sensitive to manipulations of these 'lower level' factors[27,28]. Thus, it is difficult, if not impossible, to secure a conceptual hold on the function of these systems in supporting empathy without first decoupling theoretical descriptions of empathic subprocesses from the particular models through which they are studied in neuroscience.

**Imprecision.** A related but distinct pitfall in the neuroscience of empathy arises from the use of psychological terms in the absence of connections to psychological theory and behavioral data. "Empathy" is a term historically fraught with interpretational ambiguity[29]. Neuroscientists have sensibly adopted decades-old concepts used by psychologists to describe empathic processes: affect sharing, self/other overlap and theory of mind are all examples. However, until a few years ago, neuroscientists did not focus on building methodological connections with other research traditions that examine empathy.

Psychological approaches, perhaps not surprisingly, lean heavily on behavior to indicate the operation of empathic processes. For example, perceivers' accuracy in discerning targets' internal states can serve as an indicator of how much perceivers engage mentalizing and experience sharing[30], and their choices to engage in prosocial behavior indicates their concern for targets' well being[4]. By contrast, until the last few years, neuroimaging studies of empathy focused much 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 judging targets' intentions; related brain activity was then interpreted as relevant to the empathic subprocess this task putatively engages. In almost all cases, these experiments did not relate brain activity to behavior, either because they required no responses from perceivers (as in many passive experience-sharing tasks) or used very simple social inference tasks that produce near perfect accuracy (and thus not enough variance in performance to relate to brain activity)[24].

The lack of cross-talk between behavioral and neuroscientific data limited both (i) the confidence with which neuroscientists could describe the function of any brain area or system of brain areas and (ii) the ability of build interdisciplinary models of empathy by amassing converging evidence from across psychology and neuroscience. To illustrate, consider the anterior insula, which is engaged during both the experience and observation of pain[8]. The logic of association holds that overlapping brain activity across two tasks indicates overlapping information processing[31]. In this example, such overlapping neural responses for the first- and third-person perception of pain is taken to mean that perceivers vicariously share targets' affective responses to pain, a conclusion bolstered by the findings that insula activity in response to others' pain is modulated by factors such as perceivers' self-reported tendency to share others' affect[15] and their social closeness to targets[16].

That said, in the absence of brain–behavior relationships, conclusions about the insula's role in experience–sharing tasks requires reverse inference: assumptions about the functional specificity of a given brain region[32]. Such inferences can reliably be drawn about brain regions to the extent that they participate in fewer rather than more processes. The insula is involved in a slew of computations, and as such is dangerous territory for this type of reasoning. Specifically, although overlapping insular activity during experienced and observed pain could indicate sharing of others' affect, it could just as easily reflect other processes, such as a perceiver remembering her own painful experiences or her experience of personal distress self-oriented discomfort at the sight of someone else's suffering. Personal distress, in particular, differs in important ways from other-oriented affect sharing in its phenomenology and the behavior it produces[4], but it is unclear how it can be separated from affect sharing based on neuroimaging data alone. In other words, without incorporating behavior into the neuroscience of empathy, it remains difficult to precisely characterize the meaning of many findings in this field.

## Promise

Although the pitfalls reviewed above are problematic, these types of obstacles naturally arise during the early study of any complicated psychological phenomenon. In the neuroscience of empathy, simplified stimuli and tasks were needed to localize the bases of empathic subprocesses, and such localization may have been needed before researchers could focus on variance in social behavior and more complicated interactions among systems.

Now that this field has built a foundation for understanding empathic subprocesses, by characterizing neural systems associated with experience sharing and mentalizing, we have reached a turning point. As was the case in other domains of psychological research, empathy researchers are now capitalizing on earlier insights and using more nuanced approaches that can better flesh out how empathic subprocesses interact. Here, we describe three simple, but important, shifts in strategy that have begun taking hold over the last few years. These new approaches can largely circumvent the pitfalls we have described above, and in the process produce integrated neuroscientific models of empathy that connect more strongly with psychological data.

**Naturalism.** As noted earlier, the use of artificial and highly controlled stimuli is critical for gaining traction in building a functional architecture of any complex cognitive process and its constituent parts. But one should not assume that the brain's response to such stimuli will translate to typical social experiences[25], because the information processing demands on individuals in laboratory and real-world settings may differ qualitatively.

One way forward is to use naturalistic (ecologically valid) paradigms, which combine many dynamic social cues (for example, both sensorimotor and contextual information) and inferential tasks that parallel perceivers' goals in everyday social interactions[24]. Naturalistic tasks by no means can or should supplant more simplified ones. Instead, naturalistic and simplified approaches are fundamentally complementary, and neither approach, on its own, can support complete models of empathy. Without understanding the operation of single processes in isolation, it would be impossible to interpret the results of more naturalistic experiments, which include complex information processing demands that can be difficult to parse. In essence, knowledge gleaned from simplified models provides a framework for understanding the results of more naturalistic ones, and naturalistic models give researchers a window through which to observe interactions among empathic subprocesses.

Naturalistic social cognitive paradigms are quickly becoming common in neuroscience, and their results have highlighted the limitations of earlier views of empathy that focused on single processes. Rather than being engaged in isolation, this work has shown that the neural systems involved in experience sharing and mentalizing commonly coactivate when perceivers encounter complex social cues, such as videos of targets describing autobiographical events[33] or targets engaging perceivers in live joint attention tasks[34]. Combining naturalistic cues with clever experimental manipulations has further elucidated the task sets and stimulus qualities that are likely to interactively engage one or both of these neural systems. For example, observing sensorimotor cues such as targets' goal-directed actions or emotional expressions engages brain areas supporting perceivers' own motor intentions, but combining these cues with either explicit instructions to infer targets' intentions[27] or cues that draw perceivers' attention toward target goals[35] causes perceivers to concurrently engage brain areas associated with mentalizing. Further, evidence in the past few years demonstrates that the neural systems previously identified as accompanying experience sharing and mentalizing become functionally coupled during complex social tasks[36,37], underscoring the integrated nature of empathic subprocesses during naturalistic social inference. Together, data from naturalistic models have allowed scientists to begin moving past 'either/or' conceptualizations of empathy's processes as distinct, and toward a 'when/how' model, which posits that perceivers flexibly deploy multiple, interactive processes when they are relevant to current social goals and cues.

**Brain–behavior links.** A major issue hampering the neuroscience of empathy has been the sparse connections between the vast literature on brain activity during purportedly empathy-inducing tasks on the one hand, and the even vaster literature on behavioral correlates of empathic processes on the other. To circumvent this issue, researchers have begun directly relating known neural correlates of empathic tasks (for example, coactivation of the insula during both experience and observation of pain) to behavioral indices that have been used for decades as signals that perceivers are engaging empathically with targets. This approach allows researchers to move beyond simply characterizing empathic subprocesses and toward understanding how these processes contribute to important downstream social consequences such as interpersonal rapport and understanding[38]. For example, our own group has demonstrated that activity in neural systems previously associated with both experience sharing and mentalizing tracks with perceivers' accuracy about targets' affective states[39].

A critical contribution afforded by this approach is 'cross-pollination', by which brain–behavior links both clarify the function of given neural systems in supporting empathy and provide converging evidence to address outstanding debates in the behavioral literature. Consider the case of prosocial motivation. This key feature of empathy was relatively ignored by early social neuroscience research, but an increased focus on brain–behavior relationships has allowed researchers to more thoroughly examine neural predictors of individuals' decisions to act prosocially or selfishly.

As it turns out, data from such experiments may contribute to resolving to a classic debate in social psychology, whose opposing arguments map nicely onto neuroscientific data concerning other empathic subprocesses. One line of research suggests that overlapping self-other representations (akin to experience sharing) underlie perceivers' decisions to help targets: I suffer when viewing you in pain, and it is the desire to reduce my vicarious suffering that causes me to help you[40]. Against this view, another line of research suggests that other-oriented perspective taking (akin to mentalizing) drives prosociality[4].

Recently, neuroscience has been used to adjudicate this debate by examining the neural systems that support prosocial decision-making[41]. Do neuroscientific data come down on the side of shared experience or mentalizing as supporting prosociality? As is the case for so many other questions about complex social behaviors, the emerging answer is that it depends on the context in which these processes are deployed. For example, when perceivers passively watch targets experiencing pain[16] or reward[42], their own engagement of neural structures associated with those states (neural resonance) predicts later prosociality. By contrast, when perceivers are asked to explicitly consider targets' internal states, areas associated with mentalizing (especially medial prefrontal cortex) predict later helping[43]. Further, manipulations known to alter both experience sharing and mentalizing, such as a target's group membership, also shift the relationship between brain activity and prosocial choices[16], suggesting nuanced and contextualized relationships between thinking about targets' mental states and motivations to help those targets. Together, these data bolster a model of prosociality as flexibly supported by both mentalizing and experience sharing, and raise questions about whether each of these processes could induce forms of prosociality that are similar on their surface but nonetheless differ in their phenomenology and behavioral characteristics.

**Methodological breadth.** Because we wished to track the history of neuroscientific research on empathy, here we have focused mainly on functional neuroimaging, which has been by far the most common tool used in this domain. This in no way implies that neuroimaging is or should be the only approach commonly used to assess empathy's biological substrates. Indeed, data on empathy are increasingly being produced using genetics[44], pharmacology[45], patient studies[12] and many other techniques. Often, such techniques offer more power than neuroimaging to examine key features of empathic processing. For example, although early neuroimaging studies suggested that experiencing pain oneself and observing others in pain produce common activation in brain regions related to affective components of nociception[15], transcranial magnetic simulation studies demonstrated that, in fact, such shared experience likely also draws on lower level, sensorimotor components of pain[46]. Similarly, although neuroimaging can distinguish the spatial profiles of neural systems associated with experience sharing and mentalizing, electrophysiological techniques are more useful for elucidating the temporal dynamics of these processes. For example, a recent study elegantly used electroencephalographically recorded event-related potentials to demonstrate that brain activity associated with experience sharing come online earlier than mentalizing-related activity[47].

Converging evidence from across these approaches will be vital to building complete models of empathy in the future. That said, the value of such convergence is predicated on first establishing models and approaches that can provide the strongest data from across the methodological spectrum. We believe that part of the promise of strategies such as naturalism and brain–behavior correlation lies in providing researchers with strong starting points for asking the clearest and most productive questions about the functional architecture of empathy.

Finally, the promise of these new approaches is not limited to the study of healthy populations. Indeed, the evolution of basic methodologies also opens new vistas for exploring clinical disorders characterized by empathic deficits. One well known example is autism spectrum disorders (ASD). Researchers have typically examined empathic abnormalities in ASD using simplified social scenarios. Such work has produced theories of ASD as largely affecting either mentalizing or experience sharing[48], and has produced interventions that improve acuity for simplified social cues[49]. Notably, however, such interventions often fail to improve clinical indices of social dysfunction in ASD. More naturalistic approaches are now demonstrating that ASD can be characterized by difficulty integrating multiple social cues, an abnormality related to disrupted long-distance connections between neural systems[50]. This model is just now beginning to take hold in the literature on ASD (see ref. 38 for review) and can support the development of new, more ecologically valid tools for assessing and enhancing empathic abilities in this population.

## Conclusion

The neuroscience of empathy has expanded with amazing speed over the last decade and a half to produce detailed characterizations of neural systems involved in empathic subprocesses. As a 'teenage' field, it has also experienced some growing pains: sometimes assuming that data say more than they actually do about real-world empathy and other times lacking connection with its parent disciplines. Nonetheless, a few simple changes in focus—which are already gaining force among a new generation of empathy studies—will position the field to continue advancing and ever more insightfully describing one of our most vital human abilities.

ACKNOWLEDGMENTS
Writing of this paper was supported by a Templeton Positive Neuroscience Award (to J.Z.) and National Institute on Drug Abuse Grant 1R01DA022541-01 (to K.O.).

COMPETING FINANCIAL INTERESTS
The authors declare no competing financial interests.

1. Tomasello, M. *The Cultural Origin of Human Cognition* (Harvard Univ. Press, Cambridge, Massachusetts, USA, 2000).
2. Gallese, V., Keysers, C. & Rizzolatti, G. A unifying view of the basis of social cognition. *Trends Cogn. Sci.* **8**, 396–403 (2004).
3. Leslie, A.M., Friedman, O. & German, T.P. Core mechanisms in "theory of mind". *Trends Cogn. Sci.* **8**, 528–533 (2004).
4. Batson, C.D. *Altruism in Humans* (Oxford Univ. Press, New York, 2011).
5. de Waal, F.B. Putting the altruism back into altruism: the evolution of empathy. *Annu. Rev. Psychol.* **59**, 279–300 (2008).
6. Rizzolatti, G. & Sinigaglia, C. The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nat. Rev. Neurosci.* **11**, 264–274 (2010).
7. Keysers, C., Kaas, J.H. & Gazzola, V. Somatosensation in social perception. *Nat. Rev. Neurosci.* **11**, 417–428 (2010).
8. Lamm, C. & Singer, T. The role of anterior insular cortex in social emotions. *Brain Struct. Funct.* **214**, 579–591 (2010).
9. Buckner, R.L. & Carroll, D.C. Self-projection and the brain. *Trends Cogn. Sci.* **11**, 49–57 (2007).
10. Spreng, R.N., Mar, R.A. & Kim, A.S. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. *J. Cogn. Neurosci.* **21**, 489–510 (2009).
11. Van Overwalle, F. & Baetens, K. Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. *Neuroimage* **48**, 564–584 (2009).

12. Shamay-Tsoory, S.G., Aharon-Peretz, J. & Perry, D. Two systems for empathy: a double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions. *Brain* **132**, 617–627 (2009).
13. Davis, M. Measuring individual differences in empathy: evidence for a multidimensional approach. *J. Pers. Soc. Psychol.* **44**, 113–126 (1983).
14. Wagner, D.D., Kelley, W.M. & Heatherton, T.F. Individual differences in the spontaneous recruitment of brain regions supporting mental state understanding when viewing natural social scenes. *Cereb. Cortex* (2011).
15. Singer, T. *et al.* Empathy for pain involves the affective but not sensory components of pain. *Science* **303**, 1157–1162 (2004).
16. Hein, G., Silani, G., Preuschoff, K., Batson, C.D. & Singer, T. Neural responses to ingroup and outgroup members' suffering predict individual differences in costly helping. *Neuron* **68**, 149–160 (2010).
17. Harris, L.T. & Fiske, S.T. Dehumanizing the lowest of the low: neuroimaging responses to extreme out-groups. *Psychol. Sci.* **17**, 847–853 (2006).
18. Philip, R.C. *et al.* A systematic review and meta-analysis of the fMRI investigation of autism spectrum disorders. *Neurosci. Biobehav. Rev.* **36**, 901–942 (2012).
19. Dapretto, M. *et al.* Understanding emotions in others: mirror neuron dysfunction in children with autism spectrum disorders. *Nat. Neurosci.* **9**, 28–30 (2006).
20. Harvey, P.O., Zaki, J., Lee, J., Ochsner, K. & Green, M.F. Neural substrates of empathic accuracy in people with schizophrenia. *Schizophr. Bull.* (in the press).
21. Blair, R.J. Responding to the emotions of others: dissociating forms of empathy through the study of typical and psychiatric populations. *Conscious. Cogn.* **14**, 698–718 (2005).
22. Keysers, C. & Gazzola, V. Integrating simulation and theory of mind: from self to social cognition. *Trends Cogn. Sci.* **11**, 194–196 (2007).
23. Saxe, R. Against simulation: the argument from error. *Trends Cogn. Sci.* **9**, 174–179 (2005).
24. Zaki, J. & Ochsner, K. The need for a cognitive neuroscience of naturalistic social cognition. *Ann. NY Acad. Sci.* **1167**, 16–30 (2009).
25. Neisser, U. *Cognition and Reality: Principles and Implications of Cognitive Psychology* (W.H. Freeman, San Francisco, 1976).
26. Preston, S.D. & de Waal, F.B. Empathy: its ultimate and proximate bases. *Behav. Brain Sci.* **25**, 1–20, discussion 20–71 (2002).
27. Spunt, R.P. & Lieberman, M.D. An integrative model of the neural systems supporting the comprehension of observed emotional behavior. *Neuroimage* **59**, 3050–3059 (2012).
28. Zaki, J., Hennigan, K., Weber, J. & Ochsner, K.N. Social cognitive conflict resolution: Contributions of domain-general and domain-specific neural systems. *J. Neurosci.* **30**, 8481–8488 (2010).
29. Wispé, L. The distinction between sympathy and empathy: to call forth a concept, a word is needed. *J. Pers. Soc. Psychol.* **50**, 314–321 (1986).
30. Ickes, W. *Empathic Accuracy* (Guilford Press, New York, 1997).
31. Henson, R. Forward inference using functional neuroimaging: dissociations versus associations. *Trends Cogn. Sci.* **10**, 64–69 (2006).
32. Poldrack, R.A. Can cognitive processes be inferred from neuroimaging data? *Trends Cogn. Sci.* **10**, 59–63 (2006).
33. Wolf, I., Dziobek, I. & Heekeren, H.R. Neural correlates of social cognition in naturalistic settings: a model-free analysis approach. *Neuroimage* **49**, 894–904 (2010).
34. Redcay, E. *et al.* Live face-to-face interaction during fMRI: a new tool for social cognitive neuroscience. *Neuroimage* **50**, 1639–1647 (2010).
35. Wheatley, T., Milleville, S.C. & Martin, A. Understanding animate agents: distinct roles for the social network and mirror system. *Psychol. Sci.* **18**, 469–474 (2007).
36. Zaki, J., Ochsner, K.N., Hanelin, J., Wager, T. & Mackey, S.C. Different circuits for different pain: patterns of functional connectivity reveal distinct networks for processing pain in self and others. *Soc. Neurosci.* **2**, 276–291 (2007).
37. Lombardo, M.V. *et al.* Shared neural circuits for mentalizing about the self and others. *J. Cogn. Neurosci.* **22**, 1623–1635 (2010).
38. Zaki, J. & Ochsner, K. Reintegrating accuracy into the study of social cognition. *Psychol. Inq.* **22**, 159–182 (2011).
39. Zaki, J., Weber, J., Bolger, N. & Ochsner, K. The neural bases of empathic accuracy. *Proc. Natl. Acad. Sci. USA* **106**, 11382–11387 (2009).
40. Cialdini, R.B., Brown, S.L., Lewis, B.P., Luce, C. & Neuberg, S.L. Reinterpreting the empathy-altruism relationship: when one into one equals oneness. *J. Pers. Soc. Psychol.* **73**, 481–494 (1997).
41. Zaki, J. & Mitchell, J. Equitable decision making is associated with neural markers of subjective value. *Proc. Natl. Acad. Sci. USA* **108**, 19761–19766 (2011).
42. Harbaugh, W.T., Mayr, U. & Burghart, D.R. Neural responses to taxation and voluntary giving reveal motives for charitable donations. *Science* **316**, 1622–1625 (2007).
43. Masten, C.L., Morelli, S.A. & Eisenberger, N.I. An fMRI investigation of empathy for 'social pain' and subsequent prosocial behavior. *Neuroimage* **55**, 381–388 (2011).
44. Ebstein, R.P., Israel, S., Chew, S.H., Zhong, S. & Knafo, A. Genetics of human social behavior. *Neuron* **65**, 831–844 (2010).
45. Bartz, J.A., Zaki, J., Bolger, N. & Ochsner, K.N. Social effects of oxytocin in humans: context and person matter. *Trends Cogn. Sci.* **15**, 301–309 (2011).
46. Avenanti, A., Bueti, D., Galati, G. & Aglioti, S.M. Transcranial magnetic stimulation highlights the sensorimotor side of empathy for pain. *Nat. Neurosci.* **8**, 955–960 (2005).
47. Fan, Y. & Han, S. Temporal dynamic of neural mechanisms involved in empathy for pain: an event-related brain potential study. *Neuropsychologia* **46**, 160–173 (2008).
48. Oberman, L.M. & Ramachandran, V.S. The simulating social mind: the role of the mirror neuron system and simulation in the social and communicative deficits of autism spectrum disorders. *Psychol. Bull.* **133**, 310–327 (2007).
49. Golan, O. & Baron-Cohen, S. Systemizing empathy: teaching adults with Asperger syndrome or high-functioning autism to recognize complex emotions using interactive multimedia. *Dev. Psychopathol.* **18**, 591–617 (2006).
50. Courchesne, E. & Pierce, K. Why the frontal cortex in autism might be talking only to itself: local over-connectivity but long-distance disconnection. *Curr. Opin. Neurobiol.* **15**, 225–230 (2005).