Chapter 5

Social Cognitive Neuroscience

MATTHEW D. LIEBERMAN

Who we are as humans has a lot to do with what happens between our ears. What happens between our ears has a lot to do with the social world we traverse, engage, and react to. The former has been the province of neuroscience and the latter the province of social psychology for nearly a century. Recently, scientists have begun to study the social mind by literally looking between the ears using the tools of neuroscience. *Social cognitive neuroscience* uses the tools of neuroscience to study the mental mechanisms that create, frame, regulate, and respond to our experience of the social world. On its worst days, social cognitive neuroscience is phrenological, cataloguing countless brain regions involved in the vast array of social processes. On its best days, social cognitive neuroscience enhances our understanding of the social mind as well as any other method.

The goals of this handbook chapter are to give an overview of the human history of this research area (Section I), to summarize the techniques common to this approach (Section II), to survey the functional neuroanatomy of social cognition (Section III), and to discuss how brain research can make specific contributions to the social psychological enterprise (Section IV). A special note to social psychologists with little intrinsic interest in the brain trying to determine whether social cognitive neuroscience is worth getting acquainted with: Go straight to Section IV.

I. HISTORY

The *Oxford Dictionary of Psychology* (Colman, 2006) identifies a 2001 conference, held at the University of California, Los Angeles, as a starting point for social cognitive neuroscience. This was the first formal meeting on social cognitive neuroscience, and many of the attendees have become leaders in the field, despite few having published social cognitive neuroscience findings at that point. There were introductory talks on social cognition and cognitive neuroscience by Neil Macrae and Jonathan Cohen, respectively, along with symposia on stereotyping (William Cunningham, Jennifer Eberhardt, Matthew Lieberman, and Wendy Mendes), self-control (Todd Heatherton, Kevin Ochsner, and Cary Savage), emotion (Ralph Adolphs, Turhan Canli, Elizabeth Phelps, and Stephanie Preston), imitation and social relations (Alan Fiske, Marco Iacoboni, David Perrett, and Andrew Whiten), and theory of mind (Chris Ashwin, Josep Call, Vittorio Gallese, and Kevin McCabe). If this meeting represented the first time that all of the ingredients of social cognitive neuroscience were mixed together in a single pot, the water was already boiling when the ingredients were tossed in. To appreciate how the pot got this way, several historical strands must be highlighted.

In the early 1990s, John Cacioppo used the term “social neuroscience” (Cacioppo, 1994) to characterize how the social world affects the nervous system. Work in this area was mostly health relevant (Berntson, Sarter, & Cacioppo, 1998; Kiecolt-Glaser & Glaser, 1989; Segerstrom, Taylor, Kemeny, & Fahey, 1998) or animal research (Carter, 1998; Insel & Winslow, 1998; Panksepp, 1998) examining the impact of social factors on the autonomic, neuroendocrine, and immune systems (Blascovich & Mendes, this volume). In other words, early social neuroscience primarily focused on how the social world affects the peripheral nervous system and other bodily systems. Although neurocognitive mechanisms clearly fall under the umbrella of social neuroscience, there were few investigations linking social processes with brain processes during the 1990s. Social cognitive neuroscience represented a new arm of social neuroscience that primarily focused on the neurocognitive mechanisms of

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I would like to thank Naomi Eisenberger and members of the UCLA Social Cognitive Neuroscience Laboratory for various discussions about the contents of this chapter.

everyday social cognition. Subsequently, the terms "social cognitive neuroscience" and "social neuroscience" have largely become synonymous because the domains and methods of study have merged.

Although social cognitive neuroscience reached its boiling point around 2001, with numerous scientists beginning to use neuroscience methods to study social cognition, there were isolated programs of research focusing on social cognitive neuroscience in the 1990s. Antonio and Hannah Damasio's work on the socioemotional changes in individuals with ventromedial prefrontal cortex (PFC; see Table 5.1 for a list of acronyms and neuroscience terms used in this chapter) (Bechara, Damasio, Damasio, & Anderson, 1994) sparked great interest in social cognitive neuroscience, affective neuroscience (Panksepp, 1998), and neuroeconomics (Camerer, Loewenstein, & Prelec, 2005). Chris and Uta Frith began an extremely fruitful line of research on the neural bases of theory of mind in the mid-1990s (Fletcher et al., 1995), a topic that is foundational within social cognitive neuroscience. Stan Klein and John Kihlstrom examined self-knowledge by examining a patient with temporary amnesia, providing the best early example of how neuroscience could provide constraints on social psychological theories (Klein, Loftus, & Kihlstrom, 1996). Research on the neural bases of face and biological motion processing were relatively advanced in this period (McCarthy, Puce, Gore, & Allison, 1997), but not yet in a way that resonated with traditional social psychological questions. Finally, Cacioppo, Crites, and Gardner (1996) examined the neural bases of attitudes and evaluative processing using event-related potentials (ERPs) and demonstrated important dissociations between social cognitive processes that were seemingly similar. These lines of research are the precursors of social cognitive neuroscience and served as inspiration for many who would go on to work in this area.

Table 5.1 Acronyms and Jargon in Social Cognitive Neuroscience

PFC	Prefrontal Cortex
STS	Superior Temporal Sulcus
TPJ	Tempoparietal Junction
FFA	Fusiform "Face" Area
ACC	Anterior Cingulate Cortex
Anterior	Towards the front of the brain
Posterior	Towards the back of the brain
Rostral	Towards the front of the brain
Caudal	Towards the back of the brain
Dorsal	Towards the top of the brain
Ventral	Towards the bottom of the brain
Superior	Towards the top of the brain
Inferior	Towards the bottom of the brain
Lateral	Away from the middle of the brain
Medial	Towards the middle of the brain

Finally, a great deal of human capital was spent bringing social cognitive neuroscience into existence. Influential scientists already doing social neuroscience, such as John Cacioppo and Ralph Adolphs, helped promote funding for and publication of social cognitive neuroscience research. Established top-notch social psychologists including Todd Heatherton, Mahzarin Banaji, Neil Macrae, and Susan Fiske began conducting social cognitive neuroscience research and lent much-needed credibility to the fledgling area of research. Finally, Steve Breckler and Carolyn Morf, program officers at the National Science Foundation (NSF) and National Institute of Mental Health (NIMH), respectively, had the vision to fund young scientists in this area, before the area even existed.

Stir all these ingredients together and drop in a generous helping of motivated graduate students and, voilà: social cognitive neuroscience. In 2000, the term "social cognitive neuroscience" first appeared in two papers (Lieberman, 2000; Ochsner & Schachter, 2000), and the first functional magnetic resonance imaging (fMRI) study examining a traditional social psychology topic was published (Phelps et al., 2000). In 2001, the first review of social cognitive neuroscience was published (Ochsner & Lieberman, 2001), although, in truth, the paucity of published research at that time made this review as much a promissory note as a progress report.

In the decade since, social cognitive neuroscience has gone through an explosion. In 2001, a Google search for "social cognitive neuroscience" returned 6 hits. In 2009, the same search returned over 52,000 hits (see Figure 5.1). Similarly, the number of empirical social cognitive neuroscience articles published each year has steadily increased from 2000 through 2008 (see Figure 5.1). There have been numerous literature reviews of social cognitive neuroscience (Adolphs, 2001; Amodio & Frith, 2006; Bechara, 2002; Blakemore, Winston, & Frith, 2004; Lieberman, 2007a; Ochsner, 2004, 2007), not to mention a few critiques (Cacioppo et al., 2003; Kihlstrom, 2006; Vul, Harris, Winkielman, & Pashler, 2009; Willingham & Dunn, 2003). There have been special issues on social cognitive neuroscience in several journals, including *Journal of Personality and Social Psychology* (2003), *Neuropsychologia* (2003), *Journal of Cognitive Neuroscience* (2004), *Neuroimage* (2005), *Brain Research* (2006), *New York Academy of Sciences* (2007), *Group Processes and Intergroup Relations* (2008), and *Child Development* (2009). Two new journals were founded in 2006 to focus on this area of study: *Social Cognitive and Affective Neuroscience* (SCAN) and

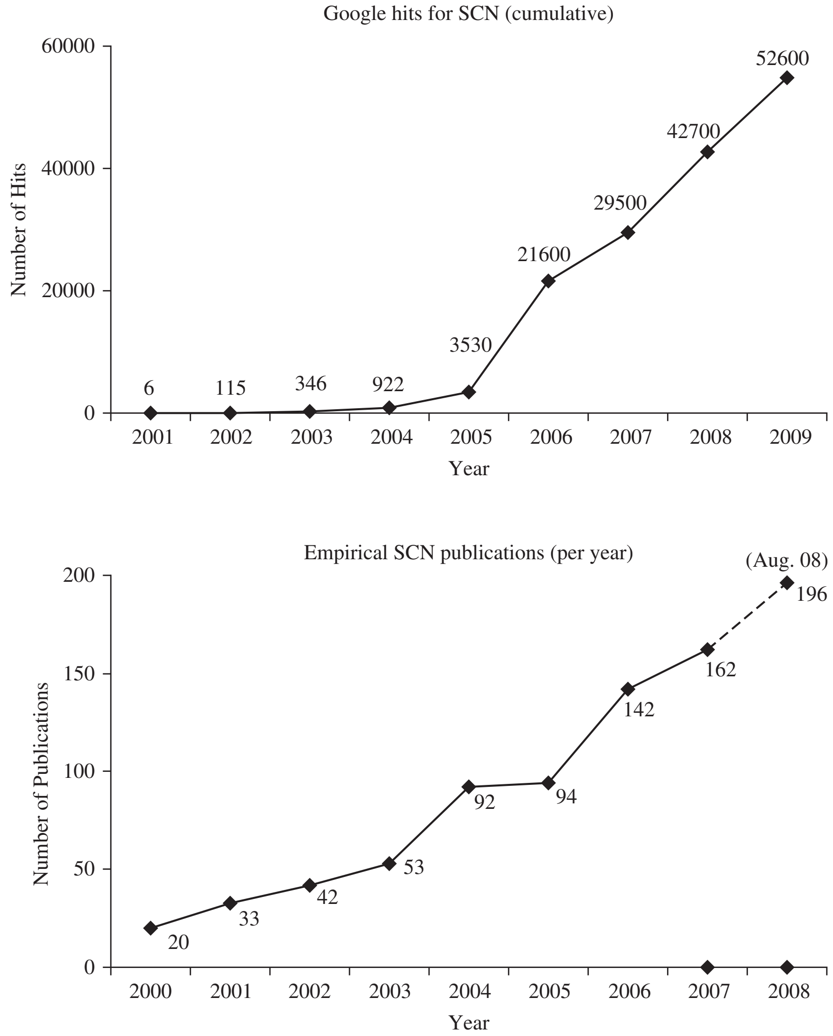

Figure 5.1 Growth of social cognitive neuroscience. The top panel displays the number of hits returned from a Google search of "social cognitive neuroscience" on January 1 of each year from 2001–2009. The bottom panel displays the number of social cognitive neuroscience empirical articles published each year from 2000–2009. Note that the 196 articles indicated for 2008 were from January through August.

Social Neuroscience. Several funding agencies have had special funding initiatives for social cognitive neuroscience; these agencies include the National Institute of Mental Health, National Institute of Drug Addiction, National Institute of Aging, and the National Institute of Alcohol Abuse and Alcoholism. Finally, there have been a series of social cognitive neuroscience preconferences and small meetings, and now a yearly Social and Affective Neuroscience (SAN) conference. In this decade, social cognitive neuroscience has gone from virtually nonexistent to having an increasingly firm foundation and the other accoutrements of a scientific discipline.

II. METHODS AND ANALYSIS

Social Cognitive Neuroscience Methods

Before jumping into a review of what has been learned with the tools of social cognitive neuroscience it is important to understand the tools themselves (this section) and the techniques (next section) used to draw inferences about social psychological processes in the brain. The primary tools used are neuroimaging techniques (fMRI, PET, ERP) and lesion studies.

Positron Emission Tomography

The earliest neuroimaging that focused on functional brain localization was PET. In PET, the subject is either injected with or inhales radioactive tracers that attach to biologically active molecules. Gamma rays from these tracers can then be detected with PET, allowing for the identification of where the tracers are traveling in the brain during different kinds of mental activity. Typically, PET scans have a temporal resolution of about a minute (i.e., one aggregate data point per minute) and a spatial resolution of about a cubic centimeter. Apart from being the first form of functional neuroimaging of the whole brain, PET's greatest advantage is that different kinds of molecules can be tagged by tracers, thereby allowing studies to examine not just blood flow in the brain but also the distribution of neurochemical processes.

Functional Magnetic Resonance Imaging

Functional magnetic resonance imaging (fMRI) is a noninvasive neuroimaging technique that has replaced PET as the dominant mode of functional neuroimaging largely because of its better temporal resolution (1 to 2 seconds) and spatial resolution (approximately $3\,mm^3$). Most fMRI studies use blood oxygen level–dependent (BOLD) fMRI to determine which brain regions are more or less active during any psychological task. BOLD fMRI works on the principle that the blood flowing to an active region is more oxygenated than blood elsewhere, and oxygenated blood has different magnetic properties than deoxygenated blood: fMRI can detect the spatial location of these different magnetic properties and reconstruct where blood was flowing to. A limitation of fMRI is that each condition of interest must typically be represented by several trials, which can lead to habituation and contamination effects. Also, nearly all fMRI analyses are comparisons between experimental conditions within a subject, typically aggregated across subjects. Between-group analyses are the exception, not the norm, and even these are between-group comparisons of within-subject comparisons. Various social psychological findings become difficult to replicate with fMRI if subjects are exposed to all task conditions.

Event-Related Potentials

Event-related potentials (ERPs) are derived from an electroencephalograph (EEG), which measures the summated electrical activity from neurons firing in the outer layers of the cortex. ERPs are the reliable responses that occur time-locked to a stimulus or response, averaged over several trials. The two primary advantages of the ERPs are that they directly measure the brain's electrical activity and have millisecond temporal resolution, allowing for exquisite measurement of time course. Two weaknesses of ERPs are that only the outer cortex can be reliably assessed and the spatial resolution of ERPs is quite poor.

Lesions

By examining individuals with damage to different brain regions and observing the ensuing psychological deficits, one can determine the contributions of the damaged regions to psychological function. The great advantage of lesion studies over neuroimaging methods is that neuroimaging only identifies regions active during psychological processes but cannot establish their causal relevance, whereas lesion studies yield causal inferences. The main limitation of lesion studies is that damage is rarely limited to one brain region and thus it is difficult to make inferences to a specific region.

Transcranial Magnetic Stimulation

Transcranial magnetic stimulation (TMS) allows for the creation of temporary lesions to a particular region of cortex and thereby overcomes some of the limitations of lesion studies. TMS relies on electromagnetic pulses, which stimulate the neurons in a small area of cortex. This is typically done to excite the neurons until they stop operating efficiently. Functionally speaking, this repetitive TMS will take a brain region offline for several minutes, allowing researchers to determine which temporary lesions produce performance deficits on tasks of interest.

Neuroimaging Analyses

Most published social cognitive neuroscience research has used fMRI, and thus it is worth describing in more detail how analyses are conducted with fMRI data (also see Lazar, 2008). This section is provided with an eye toward the social psychologist who may want to know a bit more about the steps involved in inferring that "region X is more active during task A than during task B," without having to mire through too much jargon.

Preprocessing

fMRI data are typically preprocessed before analyses are conducted. What this means is that various things are done to the raw data that are obtained during scanning to make the information suitable for analysis. One can think of it a bit like statistically normalizing scales before combining them or applying log transformations to make a distribution more normal. In fMRI studies, realignment, normalization, and smoothing are the standard components to preprocessing. It should be noted that each of these steps introduces some noise to the signal while improving the signal in other ways. Assumptions go into how each of these steps is performed, and the practical implementation of these assumptions is never perfect.

Realignment is a process that corrects the brain images to account for the motion of a subject's head while in the scanner. Small movements of a few millimeters in any direction can alter whether the signal appears to be coming from one brain structure or another. Realignment uses structural features of the brain to determine how the brain has moved and then "puts the brain back" in the same space as the brain was in during a reference scan. When successful, realignment ensures that the amygdala, for instance, shows up in the same place in the acquired brain images throughout the entire data collection.

Whereas realignment tries to ensure that an individual's brain maintains its own constant "coordinate space," the goal of normalization is to put all of the different subjects' realigned brain scans into a single coordinate space so that the brain structures line up across subjects. Brains come in all shapes and sizes, and normalization essentially morphs different brains into a common space. Different programs do this in different ways, and no method does this perfectly.

Spatial smoothing is the last key step in preprocessing. Smoothing involves averaging over adjacent "voxels" (i.e., three-dimensional [3D] pixels) in the brain images. This provides a number of benefits in terms of enhancing the detection of certain kinds of signals, but this is done at the expense of diminishing the likelihood of detecting other kinds of signals. Usually this is a desirable trade-off, but it again demonstrates that the data analyzed in fMRI studies are far from their raw state and represent a series of decisions and transformations that render the data more analyzable, while sometimes introducing problems when the data do not conform to the assumptions behind the transformations. In many ways this differs little from the assumptions that are made in statistical analyses but are often untested in our behavioral studies (heteroscedasticity anyone?).

Whole-Brain Analyses

The great majority of analyses reported in fMRI research are whole-brain analyses comparing brain activations under two task conditions across all of the voxels in the brain. For instance, imagine a study in which the subject spends alternating 30-second periods looking at pictures of ingroup members and then outgroup members, for a total of 3 minutes. Say we want to know which brain regions are differentially activated under these two conditions. The MRI scanner may collect a full brain volume (i.e., a set of images taken at roughly the same time that, stacked together, cover the entire brain) every 3 seconds, and thus there are a total of 60 volumes takes over the 3-minute scan. Each of the 60 volumes represents a time point; thus, at each voxel in the brain there is a 60-point time series reflecting the relative activation of each voxel. The statistical tools convolve a hypothetical BOLD response (i.e., a model of how the blood oxygenation typically rises and falls over time in an active area) with the experimental design to create a hypothetical time series of what a brain region's activity would look like if it were differentially sensitive to the two conditions of the experiment. This hypothesized time series is then regressed against the actual time series at every voxel in the brain to see which voxels in the brain show a pattern of activation consistent with the hypothesized pattern. When several contiguous voxels from a brain region all show the hypothesized pattern across time, it is generally inferred that this region of the brain is more active under one condition than another. The brain images in published articles that show yellow and orange "blobs" typically represent the regions that cross some threshold (e.g., 10 contiguous voxels all with regression values of $p < .001$) for consistency with the experimental regressor.

These analyses yield the brain regions for a single subject that are sensitive to task demands. Our interest is usually in generalizing to the population at large, so we combine single-subject whole-brain analyses across subjects to determine which brain regions are reliably active across subjects. This is done by computing one sample *t*-test at each voxel, using the parameter estimates (i.e., regression coefficients) from each subject at the same voxel. If the average parameter estimate from each subject in a particular region is large enough, it will emerge as significant in this random effects analysis.

Region of Interest Analyses

Neuroimaging studies commonly report the results of region of interest (ROI) analyses. Such analyses reflect the search within a specific region of the brain for significant activations. ROI analyses can serve several different purposes in a study. One benefit of searching within a smaller region of the brain is that it reduces the number of simultaneous statistical tests and thus reduces the burden of correcting for multiple comparisons. It also allows for a priori hypothesis testing by intentionally searching within brain regions thought to be relevant to the comparison. In some ways, this is analogous to performing one-tailed rather than two-tailed *t*-tests where a more lenient test can be performed because a precise hypothesis is specified. One unfortunate side effect of papers that rely solely on the ROI approach is that they can give the inadvertent impression that only the examined regions are involved in a process of interest.

Whatever the purpose of an ROI analysis, it is important to know exactly what kind of ROI analysis is being reported. There are at least two kinds of distinctions to be drawn between different ROI analyses. First, an ROI can be either functionally or anatomically defined. An anatomically defined ROI involves trying to find the true borders of a brain structure on the brain images. Functional ROIs ignore anatomical boundaries and instead use some existing pattern of activation to identify the ROI. For instance, one might run a "localizer scan" (Saxe, Brett, & Kanwisher, 2006) to define an ROI using a task well known to activate a particular brain structure and then examine what that ROI does in some new experimental condition.

The second kind of distinction among ROI analyses concerns whether the ROI is treated as a "supervoxel" or a "search space." Some ROI analyses treat the ROI as a space within which significant clusters of activation can be detected. Other ROI analyses treat the ROI as a single entity that is either significant as a whole or not.

Each kind of ROI analysis described here is valid, and there are more kinds that were not described. Nevertheless, it is critical to know which kind of ROI is being used because each supports different kinds of inferences and has different limitations.

Connectivity Analyses

Researchers are increasingly interested in the relationships between brain regions, rather than focusing on what each brain region is doing independently. Connectivity analyses provide an estimate of the extent to which brain regions are showing coordinated activity under particular task conditions. Inverse connectivity is also of interest within social cognitive neuroscience because this indicates that two brain regions show a pattern consistent with one region regulating the other. These analyses do not establish causality, as they are entirely correlational; however, the correlations do point to the regions that are good candidates to have causal effects.

There are two main kinds of connectivity analyses that correspond roughly to between-subjects and within-subjects analyses. Between-subjects connectivity analyses are much easier to conduct, but they are less likely to be able to provide strong evidence that brain regions are actually working together or at odds with one another. Such analyses involve correlating a single estimate of activity for each subject in one brain region with a single estimate of activity for each subject in another brain region. What such analyses reveal is whether the extent to which a person activates brain region X more during task A than task B is associated with the activity in brain region Y during the same comparison of task A and B. For instance, is the magnitude of activity in a region of prefrontal cortex for each subject during attempts at self-control, compared with a baseline task, inversely associated with the magnitude of amygdala activity across subjects as well. The limitation of this procedure is that a single average estimate of activity during the task is used (i.e., how much did a subject activate the prefrontal region averaged across all self-control trials of the task?) and thus it says nothing about the temporal dynamics of the brain regions.

The second type of connectivity, functional connectivity, addresses this issue by examining the extent to which the time series of activation in two regions are correlated with one another. Specifically, functional connectivity assesses whether the time series of activation between brain regions X and Y are more strongly correlated under task A than under task B. This analysis must be carried out on each subject individually and then aggregated across subjects. The conceptual limitation of these analyses is that they typically assess only how brain regions are correlated at the same moment in time. One can easily imagine that the true dynamics between some regions involve time lags of up to a few seconds (e.g., 2 seconds of prefrontal effort toward self-control might be needed before downstream reductions in amygdala area are observed). A between-subjects connectivity analysis might still capture this effect because it does not make assumptions about the temporal dynamics, but a functional connectivity analysis would probably miss the effect. Solutions to these problems, allowing for hypothesis-driven time lags, are being worked on (Formisano et al., 2002).

Regression Analyses

Because social psychologists are interested in how social and personality factors interact to affect task behavior, social cognitive neuroscience commonly uses regression analyses in fMRI. Regression analyses are straightforward to run in most fMRI statistical packages. Here, a vector of regressor values, one value per subject, is entered into a whole-brain comparison of two task conditions. The output will look like any whole-brain analysis with p-values for each voxel, indicating the reliability for the correlation, and brain maps displaying clusters of activation. For discussion of the characterization of such analyses as “voodoo,” see papers by Vul et al. (2009) and Lieberman, Berkman, and Wager (2009).

With use of this technique, any trait-level or self-report variable can be used to examine whether it is associated with the pattern of activity across subjects. Socioeconomic status, neuroticism, and rejection sensitivity are just a few of the trait variables whose relation to neural responses have been examined. One can also assess behavior that occurs after the scanning procedures to examine the relation of that behavior to neural responses during a relevant task in the scanner. For instance, one could examine whether individual differences in automatic mimicry in a laboratory setting are associated with individual differences in the magnitude of imitation-related brain activity in an fMRI scanning session. The between-subjects connectivity analyses described earlier are actually just a special application of this kind of regression analysis.

One can also use physiological, behavioral, or self-report responses obtained during the scanning session itself as a regressor at the single-subject level. Here, as with functional connectivity, the regressor of interest is correlated with the time series of activity to determine whether the two are related. For instance, a study might involve the presentation of 50 works of art and obtain the subject’s rating of desirability for each. These ratings can then be entered as a regressor unfolding over time to determine, within a subject, which brain regions have activity that rises and falls with this psychological response.

Reverse Inference

Reverse inference refers to a particular difficulty in drawing psychological inferences from neuroimaging data (Poldrack, 2006). Ideally, neural activations could serve as markers that a particular psychological process has occurred. If we could confidently assert that every time the amygdala is activated some form of fear processing has occurred, this would be a boon to social psychologists for whom the limitations of self-report and introspection are well-known (Nisbett & Wilson, 1977). Unfortunately, the amygdala is activated under numerous task conditions, including, for instance, getting a reward. Without a one-to-one correspondence between function and structure, reverse inferences become far less reliable (Ochsner, 2007).

In truth, reverse inference is a part of almost every study and will continue to be. It is only slightly different outside of fMRI research. For instance, reaction times can vary for any number of reasons, and thus it is problematic to assume that it necessarily reflects the number of underlying operations or the difficulty of each operation. Realistically, reverse inference will always be a potential inferential problem, but several steps can be taken to minimize the problem.

First, a focus on networks of brain regions rather than a single brain region can help dramatically. For instance, the dorsomedial PFC, posterior superior temporal sulcus (STS), and temporal poles are commonly coactivated when subjects perform theory of mind or mentalizing tasks (i.e., thinking about the psychological states and characteristics of another; Frith & Frith, 2003). Although the temporal poles may be activated under various task conditions (e.g., semantic processing), there is little evidence that all three regions are coactivated under conditions that do not involve mentalizing (Cabeza & Nyberg, 2000). Thus, the presence of any one of the three regions may not be a valid marker for mentalizing, but the three together may constitute a marker. Connectivity analyses can also suggest that these regions are working in concert with each other during a particular task, strengthening the inference further. Localizer scans can help as well. If each subject performs an explicit mentalizing task prior to a second task where we would like to surreptitiously assess whether mentalizing is occurring, functionally defined ROIs can be created for each subject in the particular regions used for mentalizing. It is then possible to determine whether those same ROIs are activated during the subsequent task.

Eye Movement Confounds

Another consideration before leaving this section concerns how eye movement may dramatically alter our interpretation of neuroimaging (and for that matter, behavioral) data. It has been observed that autistic individuals, compared with healthy matched control subjects, show less amygdala activity when presented with emotional faces (Baron-Cohen et al., 1999; Pelphrey, Morris, McCarthy, & LaBar, 2007). The initial inference drawn was that the amygdalae of autistic persons were less sensitive to faces or the emotional content of faces. However, autistic individuals also spend less time looking at the eyes of a face than do healthy individuals, and the eyes are extremely important for identifying emotional expressions (Adolphs et al., 2005). When eye gaze differences were accounted for, using eye-tracking equipment in the scanner, there were no remaining differences in amygdala responses of autistic versus control subjects (Dalton et al., 2005). Similarly, when a patient with amygdala damage who was impaired at recognizing fear expressions (Adolphs, Tranel, Damasio, & Damasio, 1994) was retested with instructions to attend to the eyes of the target faces, the patient performed at normal levels (Adolphs et al., 2005). These results change the interpretation of the original findings, suggesting that the amygdala directs eye gaze to important cues in the environment and that autistic individuals and those with amygdala damage are less likely to spontaneously do this. Another possibility is the amygdalae of autistic persons are hypersensitive, rather than hyposensitive, to distressing social information and therefore look less at these stimuli. It is natural to think that the extent to which a region of the brain responds to a stimulus presented in the scanner reflects that brain region's sensitivity to that class of stimuli. Knowing where the subjects are looking, what they are attending to, or what they are thinking about while processing the stimulus can lead to very different interpretations.

III. FUNCTIONAL NEUROANATOMY

Welcome to the "lite-brite" portion of the chapter. This section reviews the known neural bases of social cognition, self-processes, and processes specific to social interactions. "Lite-brite" is a pejorative term, based on a toy from the 1960s, for studies that examine social psychological processes in the scanner and see what lights up. This is also referred to as brain mapping and has gotten something of a bad rap. Social psychologists have rightly pointed out that knowing where a process occurs in the brain does not in itself add one iota to psychological theories. But sometimes, such studies lead to other studies that do add an iota or two to our theories. Sometimes, several brain mapping studies considered together can suggest new divisions and commonalities between processes that might not have been obvious from other behavioral and self-report methods (see Section IV).

Social Perception

Humans and other primates are sensitive to a wide array of nonverbal cues of social significance. We may not always reflect on the meaning of these cues, but ongoing social perception invariably influences our thoughts, feelings, and behaviors. Basic capacities of social perception are taken for granted in many models of social cognition, yet it is these basic capacities that received the most attention in the early days of social cognitive neuroscience. Cognitive neuroscientists have extensively studied the neural bases of face and body perception, biological motion, action observation, and emotion recognition. Each of these social perception processes is reviewed in this section (see Figure 5.2).

Face and Body Perception

Face perception research has been a major topic for neuroimaging research since the mid-1990s. The primary question has been whether there are regions of the brain that are tuned specifically for the processing of faces or whether faces are one of many entities decoded through a common set of perception processes. A number of neuroimaging studies have converged on a region of the fusiform gyrus, which links the occipital and temporal cortices, that is selectively and maximally activated by facial stimuli (Kanwisher, McDermott, & Chun, 1997; McCarthy et al., 1997). This region has been dubbed the fusiform face area (FFA) by Kanwisher and colleagues (1997). A second, more posterior region that also shows face selectivity has been called the occipital face area (OFA; Hoffman & Haxby, 2000).

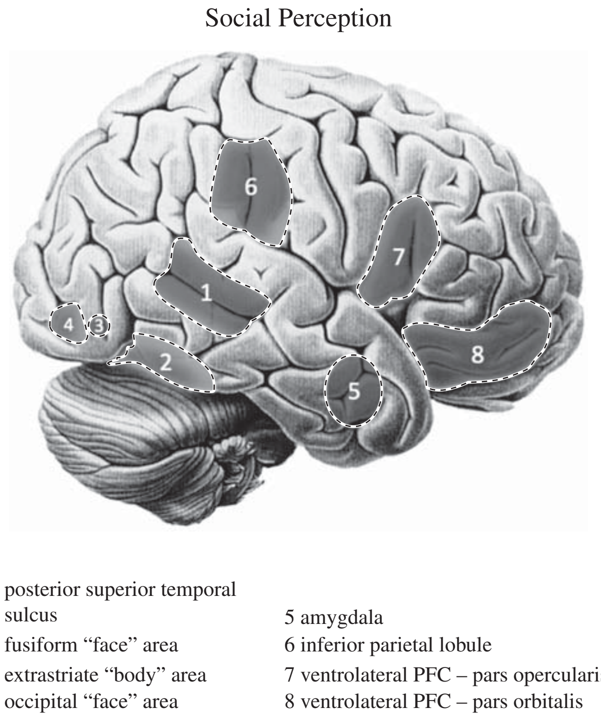

Figure 5.2 The brain regions involved in social perception (face and body perception [2–4], biological motion perception [1], action observation [6, 7], and emotion recognition [5, 8]). Numbers in brackets correspond to the regions in the figure reliably associated with a particular aspect of social perception.

A significant challenge to the equating of the FFA and OFA with face processing came from Gauthier, Skudlarski, Gore, and Anderson (2000). Gauthier argued that the FFA is specialized for expert visual processing and that face processing is just one obvious application of this region's computations. Gauthier created fictional animals ("greebles") and found that increased perceptual experience with greebles led to increases in FFA activity. Similarly, car and bird experts show significant activity in the FFA and OFA to cars and birds, respectively (Gauthier et al., 2000). Kanwisher notes that across these studies, the FFA still shows the greatest activation to faces (Grill-Spector, Knouf, & Kanwisher, 2004).

Another approach (Haxby et al., 2001) suggests that although the FFA may be most attuned to faces, whereas other regions of occipitotemporal cortex are more responsive to nonface objects, this is not the only metric that matters. Regardless of what class of object each of these regions is most responsive to, the activity in each of these regions still discriminates between the presence and absence of numerous kinds of stimuli. Thus, the FFA may be most relevant to processing faces and yet still participate, along with other regions in a distributed network, in the processing of various nonface stimuli.

Just as the FFA is particularly responsive to the presence of faces, another region in occipital cortex, referred to as the extrastriate body area (EBA), is more active when subjects are presented with bodies than when shown faces or other stimuli (Downing, Yuhong, Shuman, & Kanwisher, 2001). Interestingly, the response of the EBA is greater when the head is occluded than when the head is visible (Morris, Pelphrey, & McCarthy, 2006). The EBA is also more active when subjects view bodies from a distance, allocentrically, rather than from an egocentric perspective typically associated with viewing one's own body directly (Chan, Peelen, & Downing, 2004).

Biological Motion

The fact that even infants have the ability to discriminate between biological motion (i.e., movements consistent with the biomechanics of biological organisms) and nonbiological motion (Fox & McDaniel, 1982) suggests that the brain may have dedicated support for processing biological motion. Like many aspects of nonverbal decoding, biological motion simply appears to us in perception as qualitatively different from nonbiological motion.

Biological motion is detectable from "point light walkers" (Johansson, 1973) in which only a handful of points identifying a target's joint locations are shown as the target moves. Several fMRI studies have shown that the posterior STS (see Figure 5.2) is more active during the presentation of point light walkers than various control stimuli (Grèzes et al., 2001; Grossman & Blake, 2002; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001). Additionally, increased posterior STS activity to point light walker stimuli over a period of training is associated with improvements in behavioral performance (Grossman, Blake, & Kim, 2004). Even sounds of people walking activate the posterior STS (Bidet-Caulet, Voisin, Bertrand, & Fonlupt, 2005; Saarela & Hari, 2008). Finally, lesions to this region produce deficits in processing point light walkers (Saygin, 2007). Together, these findings suggest a strong link between this form of biological motion detection and the posterior STS (cf. Noguchi, Kancoke, Kakigi, Tanabe, & Sadato, 2005). The inferior parietal lobule (IPL) and FFA have also been implicated in a subset of point light walker studies (Grèzes et al., 2001; Grossman & Blake, 2002; Grossman et al., 2004; Vaina et al., 2001).

Processing the gaze direction of others has also reliably activated the posterior STS, particularly in the right hemisphere (Cloutier, Turk, & Macrae, 2008; Hoffman & Haxby, 2000; Hooker et al., 2003; Mosconi, Mack, McCarthy, & Pelphrey, 2005; Pelphrey, Morris, & McCarthy, 2005; Pelphrey, Singerman, Allison, & McCarthy, 2003; Pelphrey, Viola, & McCarthy, 2004; Wicker, Perrett, Baron-Cohen, & Decety, 2003). Young children show this effect (Mosconi et al., 2005), whereas individuals with lesions to the superior temporal region have gaze-processing deficits (Akiyama, Kato, Muramatsu, Saito, Nakachi, et al., 2006; Akiyama, Kato, Muramatsu, Saito, Umeda, et al., 2006). Hoffman and Haxby (2000) observed that the presentation of faces showing different gaze cues could modulate FFA or posterior STS activity depending on whether subjects were instructed to attend to the targets' identity or gaze, respectively. Similar to the observation of walking, gaze perception also modulates activity in the IPL (Hoffman & Haxby, 2000; Pelphrey et al., 2003).

Action Observation

Action observation involves the perception of biological motion that implies a specific action is being enacted intentionally. Most action observation studies have examined the neural responses to "reaching to grasp" actions or other hand actions. These studies have commonly observed increased activity in the left IPL and left posterior ventrolateral PFC (bleeding into the contiguous region of ventral premotor cortex) during action observation compared with control stimuli (Chong, Williams, Cunnington, & Mattingley, 2008; Decety et al., 1997; Johnson-Frey et al., 2003; Lamm, Batson, & Decety, 2007; Lotze et al., 2006; Molnar-Szakacs, Kaplan, Greenfield, & Iacoboni, 2006; Pierno et al., 2009). One study examining the effects of cognitive load on action observation found that IPL and posterior STS activity were unaffected by load but that ventrolateral PFC responses to action were absent during load (Chong et al., 2008). In addition, the posterior STS and temporoparietal junction (TPJ) have been observed in some of these studies as well (Chong et al., 2008; Lamm, Batson, et al., 2007; Liljeström et al., 2008).

Emotion Recognition

Recognizing the emotional displays of other people is one of the most frequent and important forms of nonverbal decoding performed by humans. Such displays provide relatively automatic, prereflective access into the psychological state of others, although it should be noted that the bare perception of these displays does not necessarily imply that those psychological states are being explicitly represented or processed.

A number of brain regions have been implicated in the processing of emotional facial expressions; however, the vast majority of studies have focused on the amygdala. The amygdala has been a central focus of study in affective neuroscience more generally, in part because of its clear causal role in fear conditioning in rodents (LeDoux, Iwata, Cicchetti, & Reis, 1988) and its frequent activation in neuroimaging studies of fearful faces (Morris et al., 1996). Since these early studies, it has become clear that the amygdala can respond to both positively and negatively valenced stimuli (Hamann, Ely, Hoffman, & Kilts, 2002), as long as they are high in arousal (Anderson, Christoff, Panitz, De Rosa, & Gabrieli, 2003; Cunningham, Raye, & Johnson, 2004), as well as various facial expressions (Fitzgerald, Angstadt, Jelsone, Nathan, & Luan Phan, 2006; van der Gaag, Minderaa, & Keysers, 2007). An increasingly common view is that the amygdala serves as a detector of potential emotional significance of things in the environment. Consistent with this view, the amygdala is responsive to novelty, regardless of valence or arousal, as new things may provide as yet unidentified reward or threat (Schwartz et al., 2003).

If the amygdala is part of the brain's advance scout team determining what is important to focus on and react to, one would expect this region to operate very efficiently. There is now converging evidence to suggest that the amygdala processes the emotional significance of perceptual stimuli automatically. First, the amygdala responds to threat stimuli presented subliminally (Morris, Öhman, & Dolan, 1998; Whalen et al., 1998) or in binocular rivalry paradigms (Pasley, Mayes, & Schultz, 2004; Williams, Morris, McGlone, Abbott, & Mattingley, 2004). Second, individuals who have damage to visual pathways still produce activation of the amygdala to emotional stimuli (Anders et al., 2004; Hamm et al., 2003; Vuilleumier et al., 2002). Third, intracranial recordings of amygdala activity suggest that it responds to emotional stimuli within 200 ms of their presentation (Krolak-Salmon, Hénaff, Vighetto, Bertrand, & Mauguière, 2004). Finally, amygdala activity to emotional stimuli is preserved under some forms of cognitive load (Anderson et al., 2003; Vuilleumier, Armony, Driver, & Dolan, 2001), although not always (Pessoa, McKenna, Gutierrez, & Ungerleider, 2002).

With respect to facial expressions, the role of the amygdala has been most clearly established in lesion studies by Adolphs, Tranel, Damasio, and Damasio (1995) demonstrating that damage to the amygdala produces deficits in identifying emotional expressions, particularly fear. Lesions to the insula (Calder, Keane, Manes, Antoun, & Young, 2000), basal ganglia (Calder, Keane, Lawrence, & Manes, 2004), and ventromedial PFC (Heberlein, Padon, Gillihan, Farah, & Fellows, 2008) have also been shown to impair identification of one or more facial expressions.

The FFA is also modulated by emotional expressions compared with neutral faces; however, a series of studies by Vuilleumier and colleagues have demonstrated that this response is likely due to feedback from the amygdala after the amygdala has already processed the facial expression. First, the pattern of activity in amygdala and FFA under dual-task conditions is more consistent with the amygdala's influence over FFA than visa versa (Vuilleumier et al., 2001; Vuilleumier, Mohr, Valenza, Wetzel, & Landis, 2003). Second, patients with amygdala lesions do not show greater FFA activity to emotional than nonemotional faces (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004).

The right ventrolateral PFC is another region that is commonly activated during emotion recognition. This activity may be specifically related to explicitly identifying an emotional expression (Lieberman et al., 2007; Nomura et al., 2004), as this region is less often observed during passive viewing of emotional faces and is typically absent if attention is directed toward nonemotional aspects of emotional faces. This parallels the finding of decreased activity in the ventrolateral PFC during action observation under cognitive load, described earlier, and other similar findings in the domains of visual self-recognition (Sugiura et al., 2000) and imitation (Lee, Josephs, Dolan, & Critchley, 2006), described later.

Although the lion's share of emotion recognition has focused on facial expressions, some studies have examined emotional prosody (i.e., tone of voice) as well as body position and movements as indicators of emotional state. Passive presentations of emotional compared with nonemotional prosody have been shown to activate the right superior temporal gyrus or STS in a region anterior to the region commonly observed in studies of biological motion (Beaucousin et al., 2007; Wiethoff et al., 2007). When the emotional tone heard is explicitly labeled, there is still STS activity along with activity in right or bilateral ventrolateral PFC (Bach et al., 2008; Ethofer et al., 2006; Wildgruber, Pihan, Ackermann, Erb, & Grodd, 2002; Wildgruber et al., 2005). Identifying emotion from bodies has been shown to activate the right posterior STS, right TPJ, EBA, amygdala, and bilateral temporal pole each in one of three studies (de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Grèzes, Pichon, & de Gelder, 2007; Peelen, Atkinson, Andersson, & Vuilleumier, 2007), with only the bilateral ventrolateral PFC appearing in multiple studies. Finally, one study has used a standardized test of nonverbal decoding ability, the Profile of Nonverbal Sensitivity (Rosenthal, Hall, DiMatteo, Rogers, & Archer, 1979), and observed posterior STS, left IPL, left TPJ, and bilateral ventrolateral PFC activity while labeling the emotional state of the targets. Additionally, those self-reporting greater social skills produced larger increases in right ventrolateral PFC, dorsomedial PFC, and basal ganglia.

Social Inference

Social inference has been at the heart of social cognition for more than three decades. Social inference encompasses a variety of processes invoked as we form representations of the psychological states, traits, and preferences of others. These inferences can be made using inferential algebra (Jones & Harris, 1967), covariation analyses (Kelley, 1973), stereotype-based inferences (Ames, 2004; Fiske & Neuberg, 1990), or by projecting oneself onto the target (Ross, Greene, & House, 1977). Some of these processes occur automatically, whereas others occur slowly guided by specific inferential intentions that require cognitive resources and effort (Gilbert, Pelham, & Krull, 1988).

Despite social psychology's focus on a deficit in the ability of humans to make sense of other minds (Gilbert & Malone, 1995), the vast majority of social cognitive neuroscience studies of social inference have been inspired by the study of children developing the ability to make sense of other minds (i.e., "mentalizing"). Wimmer and Perner (1983) first used false-belief tests to determine when children begin to show basic mentalizing competence. These tasks are usually of the following form: Person A knows that X is true (e.g., Sally knows her marble is in the box on the left); while Person A is absent, things are changed such that X is no longer true (e.g., while Sally is out of the room, Anne moves the marble to the box on the right). The subject is then asked what Person A now believes about X. The subject knows that X is no longer true, but Person A does not and therefore the subject should indicate that Person A believes X is true. Good performance is thought to indicate that the child has a theory of other minds (i.e., theory of mind; Premack & Woodruff, 1978) and that other minds can represent the world differently from our own. Most children master this basic mentalizing skill by age three or four.

Mentalizing

To isolate the neural correlates of mentalizing, several researchers have used verbal stimulus materials, including variants of the false-belief paradigm described earlier (Gobbini, Koralek, Bryan, Montgomery, & Haxby, 2007; Grèzes, Berthoz, & Passingham, 2006; Grèzes, Frith, & Passingham, 2004; Mitchell, 2008; Perner & Aichhorn, 2006; Saxe & Kanwisher, 2003; Saxe, Moran, Scholz, & Gabrieli, 2006; Saxe, Schulz, & Jiang, 2006). Other verbal tasks have used short stories that require mentalizing to explain a target's behavior, but do not specifically depend on a false belief (Fletcher et al., 1995; Gallagher et al., 2000; Happé et al., 1996; Hynes, Baird, & Grafton, 2006; Saxe & Kanwisher, 2003; Völlm et al., 2005). Also, some verbal tasks are used to assess the ability to infer other individual's feelings, rather than thoughts (Hynes et al., 2006; Shamay-Tsoory, Tibi-Elhanany, & Aharon-Peretz, 2006; Shamay-Tsoory & Aharon-Peretz, 2007; Vollm et al., 2006).

Other tasks induce mentalizing nonverbally. Several studies have used animations of geometric shapes inspired by the classic Heider and Simmel (1944) fighting triangles video (Castelli, Frith, Happé, & Frith, 2002; Gobbini et al., 2007; Moriguchi et al., 2006; Ohnishi et al., 2004; Schultz, Imamizu, Kawato, & Frith, 2004), which promote anthropomorphism and mental state attributions to the shapes. Some nonverbal tasks require inferences to be drawn about mental states from a target's eyes (Baron-Cohen et al., 1999; Platek, Keenan, Gallup, & Mohamed, 2004) or use nonverbal cartoons in which subjects choose a final panel based on their understanding of the target's mental state from the earlier panels (Brunet, Sarfati, Hardy-Baylé, & Decety, 2000; Gallagher et al., 2000).

A third type of mentalizing study examines judgments of enduring psychological characteristics of others via impression formation, for example, by asking what characteristics the person has (Harris, Todorov, & Fiske, 2005; Heberlein & Saxe, 2005; Mitchell, Banaji, & Macrae, 2005a, 2005b; Mitchell, Cloutier, Banaji, & Macrae, 2006), and via conceptual perspective-taking, for example, by asking how the person would judge topic X (Ruby & Decety, 2003, 2004). Inferences about momentary intentions have also been examined in paradigms that require subjects to infer the intentions of others (Ciaramidaro et al., 2007; German, Niehaus, Roarty, Giesbrecht, & Miller, 2004; Kampe, Frith, & Frith, 2003; Walter et al., 2004) or to determine what one's own intention would be in particular situations (Blakemore, den Ouden, Choudhury, & Frith, 2007; den Ouden, Frith, & Blakemore, 2005).

A final set of mentalizing studies has examined online mentalizing as it occurs in the context of interaction with other people (although not face-to-face). In three studies, subjects played strategy games (e.g., prisoner's dilemma) against a person or computer, under the assumption that mentalizing should occur only when playing against a person (Fukui, Murai, Shinozaki, 2006; Gallagher, Jack, Roepstorff, & Frith, 2002; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004). In a fourth study, subjects believed they were either collaborating on a task with the experimenter or working alone (Gilbert et al., 2007). In a fifth study, professional taxi drivers drove a simulated taxi in a virtual reality environment in which they interacted with numerous other characters whose mental states were relevant (Spiers & Maguire, 2006).

In addition to these different methods for studying mentalizing, there have been a handful of studies that have reported on the neural bases of irony and idiom comprehension (Lauro, Tettamanti, Cappa, & Papagano, 2008; Wakusawa et al., 2007; Wang, Lee, Sigman, & Dapretto, 2006a, 2006b). Comprehension of irony and idiom involves understanding of communicative intent and requires distinguishing literal from contextually suggested meanings. Therefore, these tasks probably require similar, if not identical, processes as those used for mentalizing.

Across 45 tasks/studies,[1] three regions were present in more than half of the studies (see Table 5.2 and Figure 5.3). The dorsomedial PFC (Brodmann areas [BA] 8/9) was reported in 91% of mentalizing tasks, whereas the TPJ and temporal pole were reported in 59% and 52%, respectively. The posterior STS and precuneus were each observed in 39% of studies, and the medial PFC (BA 10) was observed in 33%. In approximately half of the studies reporting temporal pole, posterior STS, and TPJ activations, these activations were bilateral. In those studies in which these regions were reported in only one hemisphere, only the posterior STS was reliably lateralized, appearing in the right hemisphere in 88% of these nonbilateral studies.

Table 5.2 also breaks down the activations by mentalizing induction type for any method that has been used at least four times (false belief, story, animation, impression formation, intention inference, online mentalizing, and irony and idiom comprehension). There are three notable conclusions. First, the dorsomedial PFC is the only region that is reliably

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[1] Studies including runs of more than one method are counted separately for each method's results.

Table 5.2 Activations from 45 Mentalizing Studies

	DMPFC	TPJ	Temporal Pole	pSTS	Precuneus	MPFC	IFG	VMPFC	Fusiform Gyrus
False belief (n=8)	88%	88%	25%	25%	63%	25%	25%	0%	0%
Verbal stories (n=6)	83%	100%	67%	17%	33%	17%	17%	17%	0%
Animations (n=5)	100%	0%	100%	100%	20%	20%	40%	20%	80%
Impression formation (n=6)	100%	66%	33%	33%	66%	33%	33%	50%	0%
Intention inference (n=6)	100%	67%	67%	67%	67%	67%	33%	17%	17%
Online mentalizing (n=5)	100%	40%	40%	20%	20%	40%	0%	0%	0%
Irony & idioms (n=4)	75%	25%	75%	75%	0%	50%	25%	50%	0%
Total (n=45)	**91%**	**59%**	**52%**	**39%**	**39%**	**33%**	**24%**	**15%**	**13%**

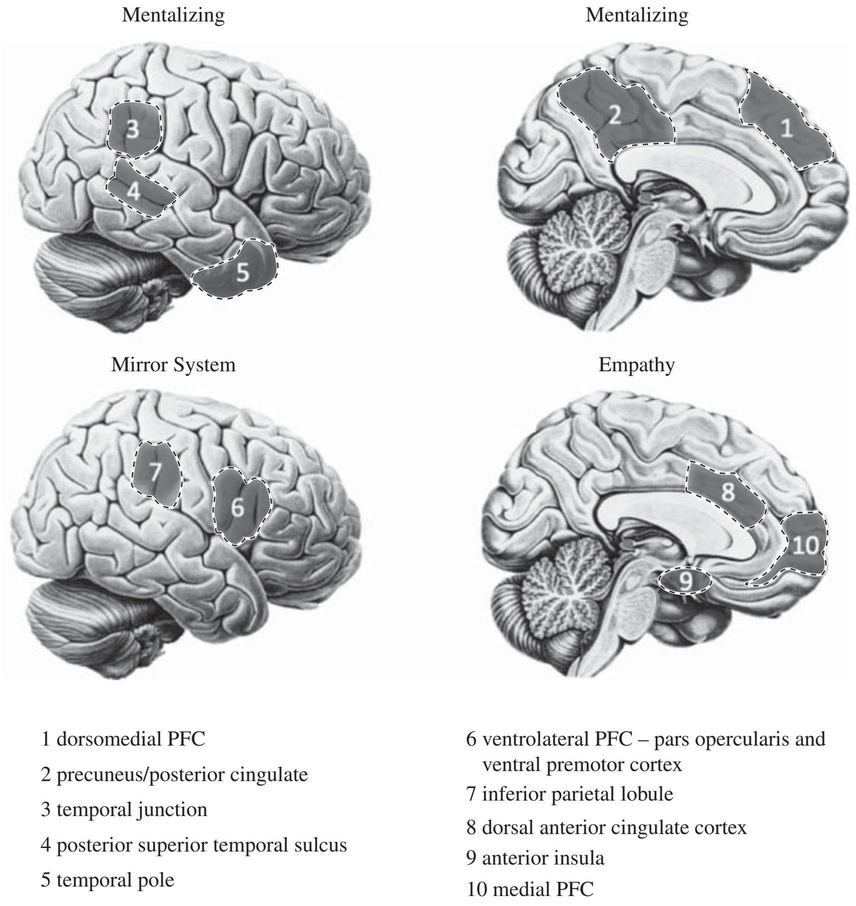

Figure 5.3 The brain regions involved in social inference. The top row of images displays the regions commonly activated in mentalizing and theory of mind tasks. The bottom left image displays the mirror system. The bottom right image displays brain regions identified in studies of empathy.

Note: Anterior insula is displayed on the medial wall for presentation purposes, but is actually between the medial and lateral walls of the cortex.

activated by each mentalizing paradigm. Second, animation-induced mentalizing consistently recruits the temporal pole and posterior STS, but not the TPJ; verbally induced mentalizing via false belief and other verbal stories consistently recruits the TPJ, but not the temporal pole and posterior STS. This is consistent with the notion that the STS and TP are involved in nonreflective social cognition, whereas the TPJ, as part of lateral parietal cortex, is involved in more reflective aspects of social cognition (Satpute & Lieberman, 2006; Liberman, 2009b). Finally, although fusiform gyrus was observed in 13% of the studies overall, it was present in 80% of the animation-based studies.

These results suggest that the dorsomedial PFC may play a central role in mentalizing in general, with other subsets of regions being recruited for particular kinds of materials or task demands. There is at least some evidence to suggest that dorsomedial PFC activation is modulated by an explicit mentalizing goal and can be taken offline by cognitive load in dual-task paradigms. Conversely, the posterior STS and temporal pole can be activated to mentalizing-relevant materials in the absence of a mentalizing goal and are still activated to the same degree with and without cognitive load (den Ouden, U. Frith, C. Frith, & Blakemore, 2005; Mason, Banfield, & Macrae, 2004;

Mitchell, Macrae, & Banaji, 2004; van Duynslaeger, van Overwalle, & Verstraeten, 2007).

A number of lesion studies have also helped to identify the regions that causally contribute to mentalizing. These studies can be subdivided into those that focus on the prefrontal cortex, TPJ, or amygdala. Several lesion studies have demonstrated prefrontal involvement in mentalizing; however, these studies do not provide much anatomical specificity (Channon & Crawford, 2000; Stone, Baron-Cohen, & Knight, 1998; Stuss, Gallup, & Alexander, 2001). One study did find that left ventrolateral PFC was associated with impairments in making personality judgments (Heberlein, Adolphs, Tranel, & Damasio, 2004).

Bird, Castelli, Malik, and Husain (2004) reported a case study of a patient with focal dorsomedial PFC and medial PFC damage. Despite the strong links in the fMRI literature between the dorsomedial PFC and mentalizing, this patient demonstrated no mentalizing impairments. It is worth noting that developmental mentalizing studies have consistently reported decreasing dorsomedial PFC activity with age, suggesting that it may play a greater causal role in adolescence than in adulthood (Blakemore et al., 2007; Wang et al., 2006a; see also Pfeifer, Lieberman, & Dapretto, 2007). This would be consistent with the dorsomedial PFC playing a controlled processing role in mentalizing that may be less needed as elements of mentalizing are increasingly automated.

In another case study, a patient with focal right ventrolateral PFC damage experienced mentalizing deficits under specific circumstances (Samson, Apperly, Kathirgamanathan, & Humphreys, 2005). The patient was capable of reasoning about a target's false belief if the story was crafted to indicate that the target had a false belief without revealing what the true state of affairs was. In contrast, if the patient knew the true state of affairs, he consistently projected this knowledge onto the target. Samson and colleagues interpreted these findings as indicating an impaired ability to inhibit one's own perspective and knowledge, rather than a deficit in belief reasoning per se (see also Lamm, Nusbaum, Meltzoff, & Decety, 2007). This interpretation is supported by developmental findings that mentalizing abilities in children are correlated with inhibitory skill as well (Carlson & Moses, 2001). Three studies examining left TPJ lesions (Apperly, Samson, Chiavaino, & Humphreys, 2004; Heberlein et al., 2004; Samson, Apperly, Chiavarino, & Humphreys, 2004) also demonstrated significant mentalizing impairments associated with this region (cf. Shamay-Tsoory et al., 2006).

Finally, there has been an ongoing debate about the role of the amygdala in mentalizing. The amygdala figured prominently in early theories of mentalizing (Baron-Cohen et al., 2000), but it was reported in only 2 of the 45 neuroimaging studies of mentalizing reviewed. Although the results of studies looking at mentalizing in individuals with amygdala lesions is mixed (Han, Jiang, Humphreys, Zhou, & Cai, 2005; Shaw et al., 2007; Stone, Baron-Cohen, Calder, Keane, & Young, 2003), a study by Shaw et al. (2004) may help explain the amygdala's role in mentalizing and why it does not appear in most neuroimaging studies. Shaw et al. (2004) compared 15 subjects with congenital amygdala damage from birth or early childhood to 11 subjects with amygdala lesions that developed in adulthood. Early damage was associated with a variety of mentalizing deficits, whereas late damage was not. Moreover, the subject's age at the time the lesion developed was strongly correlated with overall mentalizing performance. This suggests that the amygdala may play a critical role in bridging between early and mature forms of mentalizing. More sophisticated forms of mentalizing may not specifically depend on the amygdala; however, they may develop in the first place only if simpler amygdala-based mentalizing skills are in place to be built upon (see Machado, Snyder, Cherry, Lavenex, & Amaral, 2008).

Attempts are being made to determine the functional contributions of particular brain regions to mentalizing, but most of the results are quite tentative at this point (Decety & Lamm, 2007; Gallagher & Frith, 2003; Saxe & Wexler, 2005). The posterior STS responds to biological motion cues (e.g., gaze shifts, lip movements) that are likely to provide raw perceptual material for drawing inferences about the mental states of others. Temporal poles are commonly activated when seeing the faces or names of familiar people (Sugiura et al., 2006), and some have suggested that this region represents semantic information in the social domain (Lambon Ralph, Pobric, & Jefferies, 2009). Saxe and colleagues have suggested that the TPJ is specifically responsible for belief-related cognition (Saxe & Kanwisher, 2003; Saxe & Wexler, 2005); however, others have suggested that the TPJ is responsible for directing attention to salient cues in the environment (Decety & Lamm, 2007; Mitchell, 2008) rather than having a specific role in mentalizing.

Although the dorsomedial PFC is by far the most commonly activated region during mentalizing, there is not yet an agreed-upon account of its function (Amodio & Frith, 2006; Saxe & Powell, 2006). One relatively unexplored idea suggests an analogy to working memory processes where the dorsolateral PFC is thought to orchestrate working memory using various "slave" systems in the lateral parietal cortex (Baddeley, 2002) and elsewhere (Postle, 2006). In the context of mentalizing, the dorsomedial PFC would orchestrate cognition about mental states with the help of more simplistic slave systems in the TPJ, posterior STS, and temporal poles. Such a model would be relatively straightforward to test with modified working memory paradigms.

Mentalizing About Similar Others

Even if the exact role of the dorsomedial PFC is not yet specified, a recent series of studies have helped clarify how the dorsomedial and medial PFCs differentially contribute to mentalizing. Mitchell and colleagues (Mitchell et al., 2005b; Mitchell, Macrae, & Banaji, 2006) have demonstrated that the subjective similarity between a target and oneself determines which PFC region is most strongly associated with mentalizing. In most mentalizing studies, there is little basis for even evaluating the similarity of targets to oneself, and these studies reliably recruit the dorsomedial PFC. In Mitchell's studies, to the extent that targets are rated as dissimilar to the self, the dorsomedial PFC is again the region most activated by mentalizing. However, to the extent that targets are rated as similar to oneself, a more ventral region in the medial PFC is increasingly activated. Mitchell has suggested that for similar targets, subjects are projecting themselves onto the other person to answer questions about the target. Self-referential processing is strongly associated with medial PFC activity (Lieberman, 2007), and thus this account makes intuitive sense.

Other qualitative distinctions might contribute to a split between the contributions of the dorsomedial PFC and medial PFC in mentalizing. Mentalizing is typically equated with theory of mind processes in a broad fashion. Yet people have a theory of "minds in general" as well as theories of "specific minds." It could be the case that the dorsomedial PFC supports the general theory of mind, including rules for understanding how the average person is likely to experience and respond to different situations and events. In contrast, the medial PFC might support idiosyncratic theories of specific minds, including our own mind and those close to us. To this end, van Overwalle (2009) published a meta-analysis suggesting that mentalizing about close others does reliably recruit the medial PFC (cf. Heatherton et al., 2006). From this perspective, the similarity findings from Mitchell and colleagues (2005b) may be a special case of applying a specific theory of mind (i.e., one's specific theory of one's own mind) to a similar other.

Imitation and the Mirror Neuron System

In the early 1990s, Rizzolatti and colleagues (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) discovered a set of neurons in the ventral premotor cortex in monkeys that was active both when the monkey performed a goal-directed action (e.g., grabbing a raisin) and when the monkey watched someone else perform the same goal-directed action. Later researchers observed similar effects in the anterior section of the IPL (Gallese, Fogassi, Fadiga, & Rizzolatti, 2002). Together, the ventral premotor cortex and anterior IPL form, in monkeys, what has been called the mirror neuron system (Rizzolatti & Craighero, 2004).

Although no human research has identified single neurons in these regions that respond both when observing and when performing an action, there is compelling fMRI data to suggest that a homologous *mirror system* exists in humans. Iacoboni and colleagues (1999) provided the first evidence by having subjects observe and imitate finger tapping while in a scanner. They found three brain regions that were active during both observation and imitation: left posterior ventrolateral PFC,[2] right anterior IPL, and right anterior intraparietal sulcus. The bilateral posterior ventrolateral PFC and bilateral anterior IPL have been identified as the regions central to the mirror system (Chaminade & Decety, 2002; Hamilton, Wolpert, Frith, & Grafton, 2006; Heiser, Iacoboni, Maeda, Marcus, & Mazziotta, 2003; Urgesi, Moro, Candid, & Aglioti, 2006). One critical difference between the human and monkey mirror systems is that in monkeys, only hand actions that are observed in the presence of the object to be manipulated produce activity in the mirror neurons (Gallese et al., 1996). In contrast, for humans a variety of hand actions that do not involve an object or involve an occluded object still produce mirror system activity (Liu et al., 2008; Montgomery, Isenberg, & Haxby, 2007). Also, the human mirror system is active when observing goal-directed actions performed by robots whose action paths differ from human actions (Engel, Burke, Fiehler, Bien, & Rösler, in press; Engel, Burke, Fiehler, Bien, & Rösler, 2008; Gazzola, Rizzolatti, & Keysers, 2008; cf. Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004).

Beyond the original studies of hand–object actions, there have been a number of extensions regarding the classes of actions that activate the mirror system in humans. Communicative hand gestures and mimed actions both activate this system (Liu et al., 2008; Montgomery et al., 2007). Hearing actions activate the ventral premotor cortex (Kohler et al., 2002). In addition, being touched or watching another person being touched produces mirror-like effects in the IPL (Keysers et al., 2004). A series of studies have also determined that the mirror system is activated during observation and imitation of facial expressions (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Hennenlotter et al., 2005;

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[2] For the remainder of this chapter, "posterior ventrolateral PFC" is used to refer to the pars opercularis region of the inferior frontal gyrus and the neighboring ventral premotor region commonly found in imitation studies. "Ventrolateral PFC" is used to refer to mid-ventrolateral and anterior ventrolateral areas, including the pars triangularis, pars orbitalis, and lateral BA 10.

Lee et al., 2006; Leslie, Johnson-Frey, & Grafton, 2004; Pfeifer, Iacoboni, Mazziotta, & Dapretto, 2008). Hennenlotter et al. (2009) found that amygdala activity in response to angry faces was reduced in subjects after Botox injections into their foreheads; they also observed that the reduction in amygdala activity correlated with the reduction in "frown muscle" activity. These results suggest that spontaneous imitation of the observed facial expressions contributes to the strength of one's own limbic responses. Finally, somewhat counter to the notion that the same representation for action is activated both when seeing and when performing an action, performing actions that complement an observed action activate the mirror system more than actually imitating the action (Newmann-Norlund, van Schie, van Zuijilen, & Bekkering, 2007).

The discovery of mirror neurons in primates and the homologous mirror system in humans has produced enormous excitement within the scientific community and beyond. This system is proposed to be at the root of our language abilities, the ability to learn through imitation, a basis for social ingratiation through unconscious mimicking, and a mechanism critical to automatic nonverbal encoding and decoding, mental state inference, and empathy. Faith in the significance of the mirror system has led some to "predict that mirror neurons will do for psychology what DNA did for biology. . . . They will provide a unifying framework and help explain a host of mental abilities that have hitherto remained mysterious" (Motluck, 2001). In contrast, Gopnik (2007) has argued that much like the left-brain/right-brain notions that took root in popular culture in the 1970s and still retain a myth-like status, the mirror neuron mania is promising much more than it has delivered. Publications of articles in the mainstream media with titles such as "Cells That Read Minds" (Blakeslee, 2006) oversimplify the findings and give an inaccurate characterization of what these neurons are known to be doing.

Beyond responding both when an action is observed and performed, what are the functional properties of the mirror system? One open question is whether this is a system that supports vicarious learning of new behaviors or is tuned to respond to actions that are already well established in one's behavioral repertoire. Supporting the latter interpretation, professional pianists show greater mirror system activity when listening to music than do nonmusicians (Bangert et al., 2006) and professional dancers show greater mirror system activity when watching a dance performance in their own style of dance than a performance from another tradition (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005). In contrast, two studies have found that observation of unknown guitar chords, for which no motor representation already exists, produced mirror system activity (Buccino et al., 2004; Vogt et al., 2007), with one of these finding greater mirror system activity for unknown than for known chords (Vogt et al., 2007). One resolution to these conflicting findings centers on the observer's goal. In the studies in which only known actions activated the mirror system, subjects did not have the goal of subsequently performing these unknown actions. In the studies in which unknown actions produced robust mirror system activity, subjects were required to subsequently perform these actions. Thus, having the explicit goal of learning to perform an action can bring the mirror system online even, or perhaps especially, while observing unknown actions.

A final study relevant to the role of the mirror system in known and unknown actions scanned dancers before and after 5 days of training on particular dance routines (Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009). Subjects were scanned while watching several dance routines—some that would be learned and others that would not. For both kinds of dances, the mirror system was at its most active before the training period. Those that were then practiced for 5 days retained nearly the same level of activation in the mirror system, whereas the untrained dances produced far less mirror system activity at the posttest. These data suggest that having a preexisting action representation contributes less to mirror system activity than the motivational relevance of the actions to oneself. The fact that food-grasping behavior produces more mirror system activity in hungry subjects than in satiated subjects is consistent with this motivational account (Chen, Meltzoff, & Decety, 2007).

Is Mirroring Automatic?

It is generally assumed that the mirror neuron system operates automatically, converting third-person observations of actions into embodied first-person experiences, and therefore into an understanding of the mental states (intentions, thoughts, feelings, desires) of others. Taking the automaticity claim first (with the second claim addressed in the next section), the best evidence for this comes from a study in which some subjects were instructed to explicitly focus on an actor's actions and intentions and other subjects were instructed simply to watch the video clips (Iacoboni et al., 2005). Similar levels of mirror system activity were found in both sets of subjects, leading to the conclusion that mirror system activity is automatic. The difficulty with this interpretation is that the subjects not receiving action observation instructions (1) were free to explicitly focus on the intentions and actions in the clips and (2) viewed clips in which there was little else to attend to but the actions. Stronger tests of automaticity have thus far come down on the side of the mirror system being relatively intentional and controlled. For instance, Lee and colleagues asked subjects to look at emotionally expressive faces and to imitate the emotional expressions in one set of trials and to make gender discriminations in the other set of trials (Lee et al., 2006). In both types of trials, subjects were attending to the faces, but only the imitate trials produced mirror system activity. If the mirror system responds automatically, there should have been activity in both conditions. Another study found that when simulated biological motion was viewed along with a task to determine whether the motion was biologically plausible, there was more mirror system activity than if the same motion was observed with an instruction to focus on the colors of the moving elements (Engel et al., 2008). A third study used a working memory paradigm to examine neural responses when one, two, or three actions had to be held in memory for several seconds; mirror system activity in this study was found to increase linearly with the number of actions to be remembered (Engel et al., in press). This suggests that the mirror system may operate as a working memory system for action, which is consistent with a controlled processing account. Given the paucity of studies examining whether the mirror system functions automatically, the answer is not yet clear, but the evidence thus far does suggest that the mirror system may not function automatically.

Mentalizing Versus Mirroring

Most studies examining individuals' ability to infer the contents of another's mind (i.e., mental state inference) have typically come from the theory of mind tradition (Wimmer & Perner, 1983). The mirror system is thought to represent a neural substrate for a second way of understanding the mental states of others characterized by *simulation theory* (Goldman, 1989). According to simulation theory, "we understand others' thoughts by pretending to be in their 'mental shoes' and by using our own mind/body as a model of the minds of others" (Gallese, Ferrari, & Umiltà, 2002, p. 36). In terms of the mirror system, this suggests that we understand the mental states that lead a person to perform a certain action because seeing this action activates the motor representations we possess for performing the same action. This then allows us to use our own activated mental states to understand the other individual's mind.

This is an appealing account of understanding others in an embodied way. The open question is whether the mirror system contributes to understanding others, and if so, in what ways? Despite the claim that mirror neurons provide a unifying "basis of social cognition" (Gallese, Keysers, & Rizzolatti, 2004), studies of the mirror system almost never assess the social understanding supposedly obtained as a result of mirror system activity, and studies that examine social cognition overtly (i.e., mentalizing studies) rarely report activity in the mirror system.

The limitation of previous studies to address this issue is that mentalizing and mirroring studies each leave out a critical element that would lead the "other team" to cry foul. On one hand, imitation studies that successfully recruit the mirror system do not ask subjects to draw inferences about the mental states of the observed target or check whether they have. On the other hand, mentalizing studies, which almost always have an abstract detached quality to them, do not lend themselves to mirror system involvement. Reading vignettes or watching abstract shapes move around are not the kinds of real-life experiences that simulation theory focuses on.

Two studies have attempted to address these multiple concerns in a single study. In a 2 × 2 study design by Wheatley, Milleville, and Martin (2007), subjects were shown object animations. The researchers varied whether the animations looked like animate or inanimate entities and whether subjects were watching or imagining the movements. The mirror system was activated, and to a similar degree, during all four trial types. In contrast, the brain regions that selectively responded to animacy were almost all mentalizing regions and none were mirror system regions, except for the posterior STS, which is the one region that sometimes appears in both networks. Judging animacy is not the same as mental state inference, but it is certainly a step in that direction.

In another study, Spunt, Satpute, and Lieberman (in press) presented subjects with video clips of an actor performing simple everyday goal-directed behaviors (e.g., brushing his teeth) but manipulated the subject's inferential goal along an action identification hierarchy (Vallacher & Wegner, 1987). On different trials, subjects were asked to think about what the target was doing (medium action identification level; "brushing his teeth"), how the target was performing the behavior (low action identification level; "moving his arm"), or why the target was performing the behavior (high action identification level; "maintaining oral hygiene"). Critically higher levels of action identification require a greater focus on the internal mental states of the actor, and lower levels shift attention away from mental states and focus more on the external mechanics of the behavior. Similar to the results of the study by Wheatley et al. (2007), performing each of the identification tasks activated the mirror system to the same degree, suggesting that differential needs for mental state inference did not differentially engage the mirror system. In contrast, multiple regions in the mentalizing network produced parametric increases in activity that tracked increases in action identification level. Given that these were everyday kinds of behaviors that could or could not be used to draw inferences about the mental states of the actor, depending on the subject's goals, it is difficult to raise the abstraction argument that applies to previous mentalizing tasks.

At this point, it appears that the mirror system is primarily involved in understanding observed behaviors externally *as behaviors* (i.e., behavior identification) but may not be involved in consciously understanding or representing the mental states of others. In contrast, the mentalizing network thus far appears to be more central to mental state inference. Interestingly, at rest the mentalizing and mirror system networks are negatively correlated with one another (Fox et al., 2005).

Empathy

Empathy has quickly become a major area of study within social cognitive neuroscience. One of the first studies in this area involved subjects being scanned while alternately receiving painful stimulation and observing their romantic partner receiving painful stimulation (Singer et al., 2004). Analogous to the mirror system's common response to performing and observing an action, Singer and colleagues found that the pain distress regions of the brain, the dorsal anterior cingulate cortex (ACC) and the anterior insula, were activated while receiving and observing another receive painful stimulation. Eight studies have now almost all shown the dorsal ACC and anterior insula to be active in studies of empathy for physical pain (Botvinick et al., 2005; Morrison, Peelen, & Downing, 2007; Ochsner et al., 2008; Singer et al., 2004, 2006), distressing loud noises (Lamm, Batson, et al., 2007), and disgusting odors (Jabbi, Swart, & Keysers, 2007; Wicker, Keysers et al., 2003) in which subjects were both observers and receivers of the distressing experience.

Although this is an extremely robust set of findings, it is unclear how they relate to the broader concept(s) of empathy. More than any other domain in social cognitive neuroscience, there seems to be little agreement about what empathy is and what psychological processes it involves. Lamm, Batson, et al. (2007) recently defined empathy in terms of three components: "(1) an affective response to another person, which some believe entails sharing that person's emotional state; (2) a cognitive capacity to take the perspective of the other person; and (3) some monitoring mechanisms that keep track of the origins (self vs. other) of the experienced feelings" (p. 42). This definition gives a seat at the table to each of several different existing approaches to empathy.

Another way to arrive at the same definition is to consider three things that empathy is not. Empathy is not a mere cognitive understanding of the emotional state of another without having any emotional reaction of one's own. For instance, one could see a picture of Hitler wincing in pain and be able to accurately indicate his level of pain without necessarily feeling a similar emotional response of one's own (Singer et al., 2006). We would not want to label this as an empathic response. Similarly, empathy is not merely being in the same emotional state as another person. If one were to see another in pain and become so distressed that one began to ruminate on one's own distress and how such painful episodes could be avoided by oneself in the future, this also would not be an empathic response (Batson, 1991). Along similar lines, having a positive emotional response to the sight of one's favorite food being served to someone who despises that dish does not seem empathetic either. Here, one would be focused on one's own response rather than the other person's.

Thus, there are open questions as to what common brain activations during the observation and experience of painful stimulation means with respect to empathy. Because self-reported empathic feelings have not been correlated with neural responses in the more than four dozen fMRI studies of empathy, it is difficult to know whether subjects' distress is related to feeling bad for the observed target or if subjects are experiencing a self-focused type of distress. One study has found that dorsal ACC and anterior insula activity is modulated by whether the target receiving painful stimulation has previously been observed treating others unfairly or not (Singer et al., 2006). If pain observation were only leading to self-focused distress, the moral assessment of the pain recipient would probably be of little consequence. Thus, this study provides some evidence that the mirrored pain response may reflect empathic responses rather than self-focused responses.

Another issue is whether the dorsal ACC and anterior insula activations reported during visual observation of pain and distress generalizes to other kinds of empathy inductions (e.g., linguistic) and empathy inductions focused on different domains of experience (e.g., sharing in another's success). Humans are capable of empathizing with an endless variety of experiences, but thus far pain has been the primary experience examined. It is plausible that dorsal ACC and anterior insula activity is a consequence of already feeling empathic toward a person who now happens to be in pain and that other brain regions would be activated if one watched an empathized-with person win the lottery.

Although a number of studies have begun to address these issues, few conclusions have emerged, because there has been little consensus across different studies. For instance, when subjects are exposed to stories or scenarios meant to induce empathic responses (Decety & Chaminade, 2003; Farrow et al., 2001; Shamay-Tsoory, Tomer, Berger, Goldsher, & Aharon-Peretz, 2005), the dorsal ACC and anterior insula are not commonly activated. Instead, mentalizing regions such as the dorsomedial PFC and temporal pole tend to be activated along with amygdala. As mentioned, no study has obtained self-reported empathy to presented stimuli that can be used to correlate with neural responses; however, several studies have assessed trait empathy and correlated this with neural responses. Here, the brain region most commonly associated with trait empathy is the medial PFC (BA 10; Ranklin et al., 2006; Shamay-Tsoory, Tomer, Berger, & Aharon-Peretz, 2003; Shamay-Tsoory, Lester et al., 2005; Singer et al., 2004). Other regions, including the dorsal ACC, anterior insula, ventrolateral PFC (both mirror system and non–mirror system areas), dorsomedial PFC, and ventral striatum, have each been identified in at least two studies using trait empathy measures (Chakrabarti, Bullmore, & Baron-Cohen, 2006; Kaplan & Iacoboni, 2006; Pfeifer et al., 2008; Ranklin et al., 2006; Schulte-Rüther, Markowitsch, Fink, & Piefke, 2007; Singer et al., 2004; Shamay-Tsoory, Lester et al., 2005).

Perhaps most clarifying in light of the tripartite empathy definition given previously are the two studies by Lamm and colleagues (Lamm, Batson, et al., 2007; Lamm, Nussbaum, et al., 2007) that assessed trait emotional contagion, the tendency to mirror what others are feeling. These studies both found that activity in the dorsal ACC, anterior insula, and mirror system was related to trait emotional contagion, suggesting that these regions may be specifically involved in the bottom-up emotion matching that often occurs with empathy, rather than the top-down components of empathy (i.e., perspective taking and keeping focus on the other rather than on the self).

One of these studies in particular helps bolster this interpretation. Lamm, Nussbaum et al. (2007) had subjects view two sets of pictures that depicted needles going through the skin of a person's hand; however, for one set, subjects were informed that the "hand had already been numbed for a biopsy." The bottom-up visual inputs from both sets of images appear painful, but top-down cognitive appraisal should drive very different empathy responses to the two stimuli. Pain regions including the dorsal ACC, anterior insula, and somatosensory cortex were strongly activated by both sets of pictures. In contrast, regions involved in mentalizing (the medial PFC, dorsomedial PFC, ventromedial PFC, and precuneus) and self-control (the right ventrolateral PFC) were differentially activated to the different sets of pictures. These regions may play a role in contextualizing empathic responses to take account of what the experience of the other is likely to be, based on knowledge of their situation (e.g., numbed hand) or personality (e.g., masochist?).

A number of studies have now examined what differs in the brain as one considers another's distress rather than one's own. These studies are an important complement to those that reveal the commonalities. Some of the studies that reported commonalities also reported what was greater during experiencing or observing something distressing (Ochsner et al., 2008; Singer et al., 2004; Wicker, Keysers, et al., 2003). Other studies manipulated the subjects' perspective to focus on a target's experience or their own experience (Jackson, Brunet, Meltzoff, & Decety 2006; Preston et al., 2007; Schulte-Rüther et al., 2007). Although no brain region was observed as being active in a majority of these studies, some regions were more involved in self- or other-focused attention. Specifically, the dorsal ACC, anterior insula, and posterior ventrolateral PFC were more active only during self-focused or personal experience conditions. In contrast, the ventromedial PFC, precuneus, posterior STS, TPJ, IPL, and amygdala tended to be more active during other-focused or target observation conditions. In a connectivity analysis, Zaki, Ochsner, Hanelin, Wager, and Mackey (2007) observed stronger connectivity between the dorsal ACC and medial PFC, posterior STS, precuneus, and IPL during the observation, relative to the experience, of pain. This suggests a role for the mentalizing network in empathy.

Thus, the tentative conclusion that may be drawn at this point is that the dorsal ACC and anterior insula are activated both when a person is observing and experiencing painful stimulation, potentially supporting an internal mirroring of another's affective response. In contrast, self and social cognition regions, including the medial PFC, dorsomedial PFC, ventromedial PFC, and precuneus, may support processes supporting focusing on and making sense of another's experience as it would feel for them.

Attributions of Morality and Trustworthiness

Although most neuroimaging studies examining the processes whereby the psychological states and traits of others are inferred have focused on this process generically, there has been some work focusing on domain-specific attributions. Two commonly studied domain-specific attributions are for morality and trustworthiness.

The most significant finding in the domain of morality judgments is that personal, relative to impersonal, moral decisions recruit more regions associated with mentalizing and self-referential processing, including the medial PFC, precuneus, and TPJ (Greene, Sommerville, Nystrom, Darley, & Cohen, 2001). Moral reasoning in general also invokes elements of the mentalizing and self-reference network, including the medial PFC, ventromedial PFC, TPJ, and posterior STS (Moll, de Oliveira-Souza, Bramati, & Grafman, 2002; Moll, de Oliveira-Souza, Eslinger et al., 2002). Several studies have now shown modulation of these regions as factors related to moral attributions are manipulated, including the actor's intentions (Berthoz, Armony, Blair, & Dolan, 2002; Borg, Hynes, Horn, Grafton, & Sinnott-Armstrong, 2006) and beliefs about the consequences of the action (Young, Cushman, Hauser, & Saxe, 2007), actual consequences (Borg et al., 2006; Young et al., 2007), and whether an audience is present to the actions (Finger, Marsh, Kamel, Mitchell, & Blair, 2006). Additionally, damage to the ventromedial and medial PFCs has been associated with impaired ability to make personal, but not impersonal, moral judgments (Ciaramelli, Muccioli, Ladavas, & di Pellegrino, 2007; Mendez, Anderson, & Shapira, 2005).

In contrast, judgments of trustworthiness have been almost exclusively linked to amygdala activity across studies. Adolphs, Tranel, and Damasio (1998) observed that patients with bilateral amygdala damage, relative to controls, were heavily biased to rate faces as more trustworthy. Similarly, an early fMRI study found that the amygdala was more active when the subject was presented with untrustworthy faces than with trustworthy faces (Winston, Strange, O'Doherty, & Dolan, 2002). Interestingly, Engell, Haxby, and Todorov (2007) observed that amygdala responses more closely tracked consensus judgments of trustworthiness for different faces than the subjects' own ratings for those faces.

Self-Processes

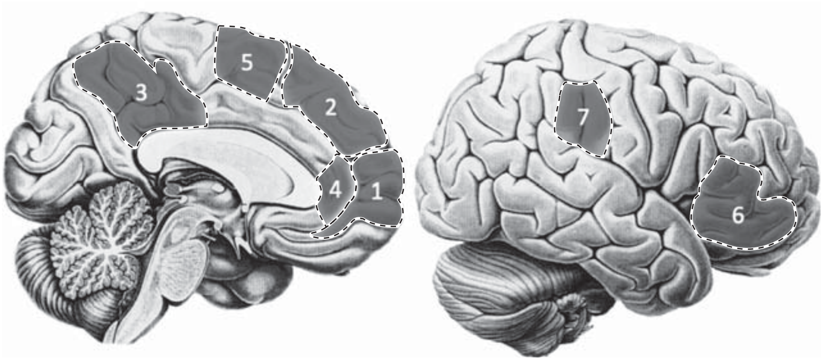
The self has been a central topic within social psychology for decades, because many theories regarding the development, maintenance, and regulation of the self suggest that these are profoundly social processes and because self-processes continuously influence our social cognition and behavior. It is little surprise then that the self has been one of the most actively researched topics within social cognitive neuroscience. In the following sections, I discuss in turn the functional neuroanatomy of agency, self-recognition, self-reflection and self-knowledge, and self-control (see Figure 5.4).

Agency

Agency refers to the sense that one was causally responsible for a particular behavior and forms one of the phenomenological cores of selfhood. The neural correlates of agency have been examined in two different ways. First, a number of studies have compared the neural bases of freely chosen self-initiated actions to externally triggered actions. Although these studies do not assess the experience of agency, they operate under the assumption that freely chosen actions are associated with a sense of agency and free will. Perhaps the most famous of these studies is Libet's, which has been referred to time and again to argue that free will is an illusion (Libet, Wright, & Gleason, 1982).

In Libet's study, subjects freely chose when to make a response and were asked to watch a clock and remember the precise time when they formed the intention to respond. Intriguingly, Libet observed a neural response, the *readiness potential* thought to emanate from the supplementary motor area, a few hundred milliseconds *prior* to when subjects claimed to have formed an intention. Libet argued that the neural responses that would ultimately trigger a behavior were causing an intention to be formed rather than an intention setting the motor response in motion (see also Fried et al., 1991). The neuroimaging studies that have followed have commonly observed supplementary motor area activity, along with the dorsal ACC, lateral PFC, medial PFC, and precuneus (Babiloni et al., 2008; Brass, Derrfuss, & von Cramon, 2005; Brass, Zysset, & von Cramon, 2001; C. Frith, Friston, Liddle, & Frackowiak, 1991; Hunter et al., 2003; Lau, Rogers, Haggard, & Passingham, 2004; Lau, Rogers, Ramnani, & Passingham, 2004). One study observed that supplementary motor area activity that occurs just prior to intention formation predicts the timing of self-reported intention formation, whereas activity in the medial

Self-Processes



1 medial PFC
2 dorsomedial PFC
3 precuneus/posterior cingulate
4 rostral ACC
5 supplementry motor area
6 ventrolateral PFC
7 inferior parietal lobule

Figure 5.4 The brain regions involved in self-processes (agency processing [1, 3, 5, 7], self-recognition [6, 7], self-reflection [1–3], and self-control [4, 5, 6]). Numbers in brackets correspond to the regions in the figure reliably associated with a particular self process.

PFC and precuneus up to 10 seconds prior to intention formation predicts the timing of self-reported intention formation (Soon, Brass, Heinze, & Haynes, 2008).

These studies are not without limitations. Waiting for an extended time until one has an intention to press a button is an artificial task that may well involve processes distinct from those involved in intention–action connections in more naturalistic settings. These studies do not merely examine intention formation but rather intention formation while in the mind-set of reflecting on and detecting one's own intention formation. This would seem to have all of the usual issues with introspection (Nisbett & Wilson, 1977). One can imagine monitoring one's own intention formation, particularly in such an artificial task, to be more of a signal detection task than a direct read-off of one's own psychological states. When attending to one's own thoughts, a variety of fleeting thoughts are likely to occur, and the individual must decide which rise to the level of full-blown intentions and which do not. In the study by Soon et al. (2008), it is not hard to imagine that a partially formed and vaguely conscious intention to press a button occurs at one point but does not meet one's threshold for declaring that an intention has occurred. Nevertheless, this subthreshold intention may set in motion a series of psychological events that trigger the full-blown intention several seconds later. If the subthreshold intention is not reported, its neural correlates would appear to predict the subsequent above-threshold intention, thus subverting the apparent order of events. Consequently, it is unclear at this point whether neural events causally precede all intentions or just those intentions that we reflectively recognize as intentions.

The second approach to the study of agency involves creating discrepancies between one's behavior and the visual presentations of one's behavior. Typically, these studies manipulate visual feedback such that one's arm movements appear to move in a different trajectory than intended, or a delay is used such that one's hand movements are seen a few hundred milliseconds after they are produced. Across these studies, the most common finding is that the IPL, in the area of the TPJ, increases in activity as the mismatch between produced and observed behavior increases (Blakemore, Oakley, & Frith, 2003; Farrer, et al., 2003; Farrer et al., 2008; Leube et al., 2003; Shimada, Hiraki, & Oda, 2005). Studies have used TMS applied to this area to disrupt agency judgments (Preston & Newport, 2008; Tsakiris, Costantini, & Haggard, 2008). Bilateral activity in this region has also been observed when hearing delayed playback of one's own voice (Hashimoto & Sakai, 2003).

Similar to these findings, schizophrenic patients and those with related experiences of external control of one's actions tend to produce greater right IPL activity during normal behavior than do control subjects, with the effect increasing with symptom strength (Franck, O'Leary, Flaum, Hichwa, & Andreasen, 2002; Ganesan, Hunter, & Spence, 2005; Spence, Brooks, Hirsch, Liddle, & Grasby, 1997). Lastly, lesion-induced out-of-body experiences have been localized to the IPL–TPJ region (Blanke, Landis, Spinelli, & Seeck, 2004), with intracranial stimulation and TMS to this region producing out-of-body–like experiences (Blanke, Ortigue, Landis, & Seeck, 2002; Blanke et al., 2005). Together, these results suggest that this region may code for the mismatch between intention and action, with quiescence in this region resulting during normal personal agency.

Overall, these two experimental approaches suggest that forming an intention to act and assigning agency to an observed behavior may depend on different neural systems. Forming an intention appears to rely largely on structures on the medial walls of the cortex, whereas evaluating whether the behavior that results is one's own involves a lateral region of parietal cortex.

Self-Recognition

The canonical test for whether an animal or human baby has self-awareness is the mirror self-recognition test (Gallup, 1970). In this test, colored ink or powder is applied to the subject's forehead while the subject is asleep. Once awake, the subject is placed in front of a mirror. If upon noticing the colored patch in the mirror, the subject proceeds to touch its own forehead where the color is, the subject is then said to have passed the mirror self-recognition test.

A number of neuroimaging studies have now established the network of brain regions involved in recognizing oneself from pictures. Nine of ten neuroimaging studies using "pictures of the self" observed increased right ventrolateral PFC activity (Devue et al., 2007; Hodzic, Muckli, Singer, & Stirn, 2009; Kaplan, Aziz-Zadeh, Uddin, & Iacoboni, 2008; Morita et al., 2008; Platek et al., 2004, 2006; Suguira et al., 2000, 2005, 2008). About half of these also reported increased right IPL activity (cf. Morita et al., 2008). One of these studies (Kaplan et al., 2008) found that identifying the self from pictures or voice recordings activated the same region of right ventrolateral PFC. Additionally, TMS applied to right IPL was found to reduce subjects' sensitivity to self–other distinctions (Uddin, Molnar-Szakacs, Zaidel, & Iacoboni, 2006). One study of note (Suguira et al., 2000) compared active and passive responses to self-images. In the conjunction of these two tasks, right IPL activity was observed, whereas right ventrolateral PFC activity was observed only in the comparison of the two tasks such that it was more active when subjects were explicitly identifying their own faces. Thus, right IPL activity may be involved in lower-level visual processing of the self, whereas right ventrolateral PFC activity may be more involved in intentional self-recognition. Interestingly, in East Asian subjects, right ventrolateral PFC activity is more active for one's own face relative to a coworker's face, if they are primed with an independent self-construal (Sui & Han, 2007), whereas an interdependent self-construal produces similarly strong activations for both faces in this region.

Self-Reflection and Self-Knowledge

The ability to reflect on one's current and past experiences, preferences, traits, and abilities is one of the signature achievements of the human brain. Although some other species have shown evidence of rudimentary self-awareness, perhaps as evidenced by the mirror self-recognition test, no other species has such an overdeveloped self-awareness as to need aisle after aisle of self-help books. A few dozen neuroimaging and lesion studies have now examined the processes by which we focus our attention internally on ourselves.

Free-form reflection on the self has been found to produce activity in the medial PFC and the contiguous regions of the precuneus and posterior cingulate cortex (jointly referred to in this section as precuneus$_{PCC}$) relative to control tasks; in addition, there is more activity in the medial PFC (BA 10) relative to free-form reflection on another individual (D'Argembeau et al., 2005; Farb et al., 2007; Johnson et al., 2006; Kjaer, Nowak, & Lou, 2002). The involvement of the medial PFC is of particular interest given that this is the only region of the prefrontal cortex known definitively to be disproportionately larger in humans than in other primate species (Semendeferi, Schleicher, Zilles, Armstrong, & Van Hoesen, 2001). Trait self-consciousness has also been specifically associated with medial PFC activity (Eisenberger, Lieberman, & Satpute, 2005). Similarly, explicitly attending to one's preferences, relative to a non–self-reflective control task, has reliably been associated with medial PFC and dorsomedial PFC activity (Goldberg, Harel, & Malach, 2006; Gusnard, Akbudak, Shulman, & Raichle, 2001; Johnson et al., 2005; Lane, Fink, Chau, & Dolan, 1997; Ochsner, Knierim, et al., 2004). Interestingly, mindfulness meditation training that attempts to shift self-processing from linguistic self-evaluation to a more experiential basic awareness has been shown to diminish this medial PFC activity (Farb et al., 2007). Another study (Johnson et al., 2006) found that reflecting on the self with a promotion or prevention focus (Higgins, 1998) was associated with either increased medial PFC or precuneus$_{PCC}$ activity, respectively.

Additionally, the medial and ventromedial PFCs have both been associated with self-insight processes. For instance, patients with damage to these regions were less aware of whether their behavior constituted social transgressions compared with patients with damage to the lateral PFC (Beer, John, & Knight, 2006; see also Beer, Heerey, Keltner, Scabini, & Knight, 2003). Similarly, activity in the medial and ventromedial PFCs was greater when subjects successfully predicted whether they would be able to retrieve particular words from memory (Schnyer, Nicholls, & Verfaellie, 2005). Although there have been only a few neuroscience investigations of self-insight, these studies are particularly important because they link neural processes to adaptive outcomes of self-reflection. It is one thing to identify the medial PFC's involvement when people try to reflect on themselves, but it is quite another to determine that activating the medial PFC during these attempts is associated with something useful and accurate about oneself.

The great majority of self-reflection studies have focused on trait self-knowledge. In these studies, subjects are typically asked to indicate whether trait words or phrases are descriptive of themselves, are descriptive of another person, or have some textual or semantic feature (Craik et al., 1999; D'Argembeau, Xue, Lu, Van der Linden, & Bechara, 2008; Fossati et al., 2003, 2004; Gutchess, Kensinger, & Schacter, 2007; Heatherton et al., 2006; Johnson et al., 2002; Kelley et al., 2002; Kircher et al., 2002; Lou et al., 2004; Macrae, Moran, Heatherton, Banfield, & Kelley, 2004; Moran, Macrae, Heatherton, Wyland, & Kelley, 2006; Pfeifer et al., 2007; Saxe, Moran, et al., 2006; Schmitz & Johnson, 2006; Schmitz, Kawahara-Baccus, & Johnson, 2004; Seger, Stone, & Keenan, 2004; Turner, Simons, Gilbert, Frith, & Burgess, 2008; Vanderwal, Hunyadi, Grupe, Connors, & Schultz, 2008; Zhang et al., 2006; Zhu, Zhang, Fan, & Han, 2007). All but one of these studies has shown increased medial PFC activity during self-judgments relative to either other-judgments or control judgments, with precuneus$_{PCC}$ and dorsomedial PFC activations also present in several studies. Two studies have found that the medial PFC is more active while judging positive self-traits than negative self-traits (Fossati et al., 2003, 2004), and a third found that the medial PFC was not sensitive to this distinction and that the subgenual ACC was activated by positive self-traits relative to negative self-traits (Moran et al., 2006). Multiple studies have also linked the medial PFC to subsequent memory for self-relevant traits (Fossati et al., 2004; Macrae et al., 2004), which is consistent with the association of the medial PFC with autobiographical memory relative to episodic memory more generally (Gilboa, 2004).

Given that self-knowledge and self-concepts change over time, it is important to determine the neural processes involved in the developmental and experience-driven changes in these processes. One developmental fMRI study (Pfeifer et al., 2007) found that the medial PFC was significantly more active in 9-year-old children than in adults when making trait self-judgments. In contrast, the levels of medial PFC activity in young adults and older adults were similar when making trait self-judgments (Gutchess et al., 2007). A study on self-schemas compared trait self-judgments in domains for which subjects were or were not self-schematic (i.e., had substantial experience) (Lieberman, Jarcho, & Satpute, 2004). Judgments made in the self-schematic domain produced greater activity in the ventromedial PFC, ventral striatum, amygdala, lateral temporal cortex, and precuneus$_{\text{PCC}}$ than judgments from the nonschematic domain. In contrast, nonschematic judgments produced greater activity in the dorsomedial PFC and medial temporal lobe. These results suggest that schematics may recruit more automatic affective processes than nonschematics in making these judgments.

Change over time has also been examined by asking subjects to take different temporal perspectives on the self. Studies comparing the present perspective of the self to future (Ersner-Hershfield, Wimmer, & Knutson, in press) and past (D'Argembeau et al., 2008) perspectives of the self have both observed greater medial PFC activity when individuals focus on the self as it is currently constituted rather than on the self at other time points. These data are consistent with the notions that there is a greater identification with the current self and that future and past selves may be treated in some ways as if they are altogether different individuals from oneself (Libby, Eibach, & Gilovich, 2005).

Other open questions include whether the medial PFC is similarly active for self- and other-judgments and whether the medial and dorsomedial PFCs are each involved in both self and social cognition. As to the first question, some studies have reported greater medial PFC activity for self-judgments relative to other-judgments (Kelley et al., 2002; Lou et al., 2004), although some have not (Schmitz et al., 2004; Seger et al., 2004). One criticism of those that have shown a difference is that in these studies the self is a far better known target than nonself targets (e.g., the queen of Denmark or the president of the United States). One study (Heatherton et al., 2006) specifically compared self-judgments to judgments of a close friend and still found significantly greater medial PFC activity for self-versus other-judgments; however, others have found similar medial PFC activity for self-judgments and judgments of a significant other or mother (Ochsner et al., 2005; Schmitz et al., 2004; Vanderwal et al., 2008).

With respect to the relative involvement of the medial PFC, dorsomedial PFC, and precuneus$_{\text{PCC}}$, across all of the self-reflection and self-knowledge studies, medial PFC activations were present in 94% of the studies, whereas dorsomedial PFC and precuneus$_{\text{PCC}}$ activations were present in 53% and 63% of studies, respectively. Thus, activations of the dorsomedial PFC and precuneus$_{\text{PCC}}$ are common; however, these activations are not as reliably invoked by self-reflection processes as is medial PFC activity. This is almost the mirror image of the pattern from mentalizing studies in which dorsomedial PFC activations were present in 91% of studies and medial PFC and precuneus$_{\text{PCC}}$ activations were present in 33% and 39% of studies, respectively.

Finally, classic theories of self-knowledge have proposed that self-concepts develop when individuals take the perspective of others on themselves (Cooley, 1902; Mead, 1934). Reflected appraisals constitute one person's assessment of what another person thinks of him or her. Three studies of adults have now examined the neural correlates of reflected appraisals of the self ("what I think you think of me") compared with direct appraisals of the self ("what I think of me"), and each have found similar levels of medial PFC and dorsomedial PFC activity in the two forms of appraisals (D'Argembeau et al., 2007; Ochsner et al., 2005; Pfeifer et al., 2009). One of these studies (Pfeifer et al., 2009) focused primarily on adolescents, because this is a critical period of self-concept development. The TPJ, a region that commonly appears in mentalizing tasks, was strongly activated during reflected appraisals in adolescents and adults. Given that reflected appraisals involve mentalizing about the belief another person holds toward oneself, this is not a surprising result. Perhaps more surprising was the strong activation of the TPJ during direct appraisals in adolescents, but not in adults. This suggests the possibility that adolescents, but not adults, are spontaneously drawing upon social sources of information when asked to generate direct appraisals. Consistent with this notion, a number of regions involved in mentalizing about others were more active during direct appraisals in adolescents than in adults, including the dorsomedial PFC, posterior STS, and precuneus$_{\text{PCC}}$.

Self-Control

Self-control, or the ability to regulate, manipulate, or control one's prepotent thoughts, feelings, and behaviors, has been extensively examined using various tools of neuroscience. Explicit attempts at self-control across various domains commonly recruit a network of brain regions, including the lateral PFC and the contiguous regions of the dorsal ACC, presupplementary motor area (BA 6), and posterior dorsomedial PFC (BA 8). It should be noted that the dorsal ACC is typically thought to serve a conflict detection function indicating the need for self-control, whereas the lateral PFC is thought to be more involved in implementing control or inhibiting prepotent responses (MacDonald, Cohen, Stenger, & Carter, 2000). Lesion data support the latter claim regarding the lateral PFC (Aron, Robbins, & Poldrack, 2004), but they are less supportive of the former claim regarding the dorsal ACC (Fellows & Farah, 2005).

Most relevant to social psychology are the more than 30 neuroimaging studies of affect and emotion regulation (Ochsner & Gross, 2005; for relevant cognitive studies, see Goel & Dolan, 2003; Mitchell et al., 2007). These studies can be divided according to whether emotion regulation is the explicit goal of the task or whether emotion regulation occurs incidentally as a consequence of another process not intended to produce emotion regulation effects. Explicit emotion regulation tasks include reappraisal (Banks, Eddy, Angstadt, Nathan, & Luan Phan, 2007; Beauregard, Levesque, & Bourgouin, 2001; Eippert et al., 2007; Goldin, McRae, Ramel, & Gross, 2007; Harenski & Hamann, 2006; Herwig et al., 2007; Kim & Hamann, 2007; Luan Phan et al., 2005; McRae, Ochsner, Mauss, Gabrieli, & Gross, 2008; Ochsner, Bunge, Gross, & Gabrieli, 2002; Ochsner, Ray, et al., 2004; Schaefer et al., 2003; Urry et al., 2006; Wager, Davidson, Hughes, Lindquist, & Ochsner, 2008), suppression (Goldin et al., 2007; Lee, Dolan, & Critchley, 2008; Ohira et al., 2006), detachment (Kalisch et al., 2005; Levesque et al., 2003), and self-distraction (Kalisch, Wiech, Herrmann, & Dolan, 2006).

Across 19 neuroimaging studies, task conditions that invoked explicit emotion regulation efforts were commonly associated with activations in right ventrolateral PFC (63% of studies), left ventrolateral PFC (63% of studies), the contiguous regions of the presupplementary motor area and posterior dorsomedial PFC (47%), and left dorsolateral PFC (32% of studies). Approximately half of these studies also reported on frontal regions whose activity was associated with regulatory success either in terms of self-reported affect or limbic activity. Although there is not an entirely consistent pattern among these analyses, right and left ventrolateral PFCs do appear more often than other regions.

Most of these studies have examined the regulation of negative affect. Although a few studies have looked at regulation during the presentation of positively valenced images (Kim & Hamann, 2007; Ohira et al., 2006), it is unclear whether such images produce a similarly intense emotional response to the negative images typically used. A study by Delgado, Gillis, and Phelps (2008) examined reappraisal in the context of financial reward and observed increased left ventrolateral and left dorsolateral PFC activity along with diminished ventral striatum activity during reappraisal.

More than a dozen studies have examined incidental emotion regulation using affect-based conflict resolution, placebo, and affect labeling paradigms. In placebo studies, subjects are led to believe that their pain or anxiety will be alleviated by a pill or cream that is in fact pharmacologically inert. Although there is no instruction to intentionally regulate one's pain or anxiety, subjects often report less distress in placebo conditions. In the five neuroimaging studies (Kong et al., 2006; Lieberman, Jarcho, Berman et al., 2004; Petrovic et al., 2005; Wager et al., 2004, studies 1 and 2) that have related neural responses to placebo-related distress reductions, four have reported right ventrolateral PFC activity and two have reported activity in left ventrolateral PFC, right dorsolateral PFC, and rostral ACC. Five studies employed conflict resolution tasks in which emotional cues must be ignored to successfully perform the task (Enger, Etkins, Gale, & Hirsch, 2008; Etkin, Enger, Peraza, Kandel, & Hirsch, 2006; Felmingham et al., 2007; Most, Chun, Johnson, & Kiehl, 2006; Ochsner, Hughes, Robertson, Cooper, & Gabrieli, in press). Here, the regulation of emotional responses is secondary to the main task of making a fast categorical judgment about another stimulus; thus, regulation is secondary to the main task. In all five of these studies, the rostral ACC was associated with successful regulation of the emotional distracter. Lastly, four fMRI studies (Altshuler et al., 2005; Hariri, Bookheimer, & Mazziotta, 2000; Lieberman, Hariri, Jarcho, Eisenberger, & Bookheimer, 2005; Lieberman et al., 2007) have examined the neural basis of why putting feelings into words can dampen emotional responses (Pennebaker & Beall, 1986). In these studies, subjects chose affective labels to characterize the negative emotional images. In each of these studies, right ventrolateral PFC was the primary brain region active during "affect labeling," relative to control conditions. In addition, in each of these studies, right ventrolateral PFC activity was associated with diminished amygdala responses to the negative stimuli. During these studies, emotion regulation was incidental; subjects were not trying to regulate their emotional responses. Across all of the incidental emotion regulation studies, right ventrolateral PFC and rostral ACC activations were present in 57% and 50% of these studies, respectively. Across both intentional and incidental emotion regulation studies, right ventrolateral PFC activity was reported most often (59%), followed by left ventrolateral PFC activity (41%). Although right ventrolateral PFC activity was equally likely to be present in intentional and incidental emotion regulation studies (63% vs. 57%), left ventrolateral PFC activity was far more likely to be present in intentional than in incidental regulation studies (63% vs. 14%), as was the case for the contiguous regions of the presupplementary motor area and posterior dorsomedial PFC (47% vs. 0%). In contrast, the rostral ACC was much more likely to be invoked during incidental regulation studies (50%) than in intentional regulation studies (5%).

Social Interaction

Trust, Cooperation, and Fairness

Building relationships of any kind and effectively working with others depends on mutual trust, a willingness to cooperate, and a sense that rewards and responsibilities are being distributed fairly. Using paradigms created by behavioral economists, social cognitive neuroscientists and neuroeconomists have been examining these different social adhesives (see Figure 5.5).

Several fMRI studies have used variants of the "trust game" (Berg, Dickhaut, & McCabe, 1995) to examine the neural processes invoked when deciding whether to trust a stranger. In the trust game, there are two players: decision maker 1 (DM$_1$) and decision maker 2 (DM$_2$). DM$_1$, also called the investor, is given a sum of money (e.g., $10). This money can be kept or invested. If invested, the money is moved to DM$_2$, also called the trustee. Any money received by the trustee is increased by a known and predetermined factor (e.g., multiplied by 4). DM$_2$ then decides how much money to transfer back to DM$_1$. In the case of mutual trust and repeated games with the same individual, it would be in both players' interest for DM$_1$ to invest the entire sum and for DM$_2$ to return half of the proceeds. However, if DM$_1$ does not trust DM$_2$ to return a fair share, DM$_1$ is less likely to invest as much of the initial endowment. Additionally, in a one-shot game where each player will make only a single decision with the other player, it is considered irrational for DM$_2$ to return any money to DM$_1$.

To examine the neural correlates of trusting another person in a one-shot trust game (McCabe, Houser, Ryan, Smith, & Trouard, 2001), in contrast to mere investing phenomena, subjects played some rounds with a human DM$_2$ and some with a computer DM$_2$. The researchers observed that the medial PFC was more active for DM$_1$ when DM$_1$ decided to transfer the funds over to DM$_2$. It is possible that the medial PFC represents the DM$_1$'s feeling of similarity to DM$_2$ (Mitchell, Macrae, & Banaji, 2006) and thus DM$_1$'s willingness to cooperate. In another type of cooperative game, Decety and colleagues also found the medial and ventromedial PFCs to be more active when a person was being cooperative (Decety, Jackson, Sommerville, Chaminade, & Meltzoff, 2004). In their trust game study, Delgado, Frank, and Phelps (2005) observed greater ventral striatum and left TPJ activity in DM$_1$ when that person chose to trust. King-Casas and colleagues (2005) examined multiple games played between the same DM$_1$ and DM$_2$ and found that when a DM$_1$ responded to DM$_2$'s untrustworthy behavior by investing even more on the next round of the game, rather than less, activity in the caudate in the dorsal striatum of DM$_1$ increased. Finally, Krueger and colleagues (2007) observed greater dorsomedial PFC, ventral striatum, and septal activity in DM$_1$ when that person chose to trust. Thus, although there is substantial variability across studies,

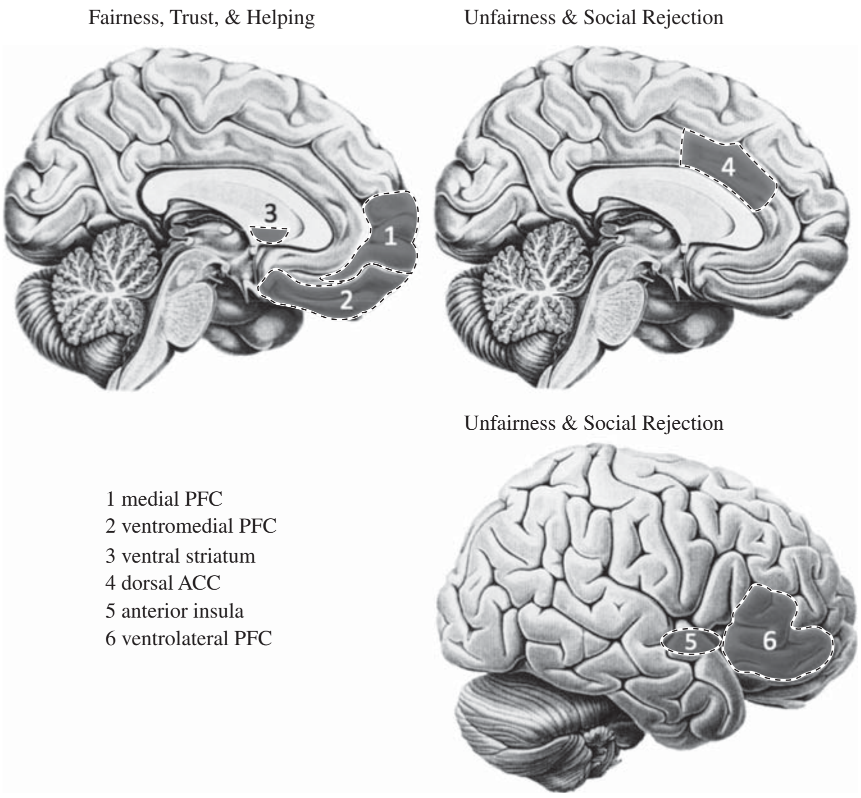


Figure 5.5 The brain regions involved in social interactions. The top left image displays brain regions activated in studies of fairness, trust, and helping. The top right and bottom right images display brain regions activated in studies of unfairness and social rejection.

Note: Anterior insula is displayed on the lateral wall for presentation purposes, but is actually between the medial and lateral walls of the cortex.

these findings do suggest that different regions on the medial prefrontal wall (the dorsomedial PFC, medial PFC, and ventromedial PFC) and in the striatum (dorsal and ventral) are more active during the decision to trust.

Brain-based oxytocin levels are also associated with DM_1's trust behavior in the trust game. In the first study to examine this, a DM_1 receiving an intranasal dose of oxytocin transferred more money to DM_2 than those who had received a placebo (Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005). In another study (Baumgartner, Heinrichs, Vonlanthen, Fischbacher, & Fehr, 2008), a dozen one-shot trust games were played after an oxytocin or placebo induction; however, subjects received feedback about game dynamics after the first six games had been played. At this point, subjects who were in the role of DM_1 were informed that in 50% of the prior games, DM_2 had not transferred money back to them. Knowing that future betrayals were likely, placebo DM_1 subjects reduced their later transfers to DM_2. In contrast, DM_1's who had received oxytocin actually increased their transfers to DM_2 after receiving the feedback. These oxytocin findings make sense in light of the known role of oxytocin in social attachment and pair bonding in animals (Insel & Shapiro, 1992).

Two studies have examined the neural correlates associated with finding out that another person has failed to reciprocate one's own trusting behavior. One study (Rilling, Dagenais, Goldsmith, Glenn, & Pagnoni, 2008) used the "prisoner's dilemma" game in which DM_1's and DM_2's financial outcomes are each dependent on both their own and the other player's decision. If both DM_1 and DM_2 choose to cooperate, they receive equitable outcomes that maximize their joint reward total. However, for each decision maker, given a particular decision by the other player, defecting will produce a greater personal reward than cooperating. Rilling found that if DM_1's cooperation was unreciprocated by DM_2, DM_1 produced greater insula and reduced ventral striatum activity. Similarly, in a trust game, Delgado and colleagues (2005) found that DM_2's choice not to transfer funds back to DM_1 led to reduced ventral striatum activity in DM_1. This might have been due to the diminished financial reward associated with this outcome; however, Delgado also showed that this effect was absent when DM_2 was believed by DM_1 to be of high moral character. This suggests that the diminished ventral striatum activity was at least in part due to social factors.

Finally, multiple studies have examined the decision to punish those who exhibit unfair behavior. A trust game study using PET (de Quervain et al., 2004) found that if DM_1 was given the opportunity to punish DM_2 when DM_2 did not transfer money back, DM_1 showed increased activity in the dorsal striatum, and the magnitude of this activity was correlated with the size of the punishment delivered.

Other studies have used the "ultimatum game" (Fehr & Schmidt, 1999) to examine punishment for unfair treatment. In this game, DM_1 is given an endowment (e.g., $10) and makes a proposal for how DM_1 and DM_2 should split the endowment (e.g., DM_1 will keep $7 and DM_2 will receive $3). If DM_2 accepts the proposal, both players receive what DM_1 has proposed. If DM_2 rejects the proposal, both players get nothing. At one time, economists supposedly argued that DM_2 should accept any nonzero offer, being better than zero, and thus DM_1 should always offer one penny and DM_2 should accept. In actual play, DM_1 usually offers 30% to 50% and DM_2 will reject many of the offers lower than 30%. Sanfey and colleagues published the first neuroimaging study of the ultimatum game and found that subjects in the DM_2 role showed greater anterior insula activity to unfair offers ($1 or $2 out of $10) than to fair offers, but only if DM_1 was a person, not a computer (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). Additionally, the magnitude of anterior insula activity was associated with the tendency to reject the offer. Given that anterior insula activity has been associated with feelings of disgust, Sanfey suggested that this activity may represent the sense of insult or injustice associated with an unfair offer. A second fMRI study of the ultimatum game (Tabibnia, Satpute, & Lieberman, 2008) equated the material payoff of fair and unfair offers, comparing, for instance, a fair offer of $5 out of $10 to an unfair offer of $5 out of $23. As in the study by Sanfey and colleagues, anterior insula activity was associated with the tendency to reject unfair offers.

The study by Tabibnia et al. (2008) also examined the psychological struggle that can occur when an offer is simultaneously unfair and financially desirable (e.g., $5 out of $23). Subjects who more frequently accepted these unfair but desirable offers showed increased activity in right ventrolateral PFC, a region that's been associated with emotion regulation and self-control more generally, and also showed a correlated decrease in anterior insula activity. In contrast, two studies (Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006; van't Wout, Khan, Sanfey, & Aleman, 2005) observed less frequent rejection of unfair offers when TMS was applied to right dorsolateral PFC, presumably reducing the contribution of this region to decision processes during this task.

Two other studies using the ultimatum game have identified causal neural mechanisms contributing to an enhanced tendency to reject unfair offers. In one of these studies (Koenigs & Tranel, 2007), patients with damage to the ventromedial PFC and right ventrolateral PFC were more likely to reject unfair offers. In the second study (Crockett, Clark, Tabibnia, Lieberman, & Robbins, 2008), pharmacological reduction of serotonin levels also led to more frequent rejection of unfair offers. Reduced serotonin levels have been shown to diminish ventrolateral PFC activity during a motor inhibition task (Evers et al., 2005), and thus it is plausible that regulation of one's sense of insult is less effective due to serotonergic depletion effects on the ventrolateral PFC.

Social Rewards and Helping

An interesting finding that has emerged from fMRI studies of two-person economic games described in the previous section is that people show evidence of reward activation when they participate in good interactions involving trusting and fair behavior, even when this treatment confers no additional financial benefit to them or even leads to a loss. In a prisoner's dilemma study (Rilling et al., 2002), subjects showed greater ventral striatum activity during mutual cooperation than during any other combination of responses. This is striking in light of the fact that mutual cooperation is not the most financially rewarding outcome possible. This suggests that against their own financial interest, there is a hedonic benefit to participating in a reciprocated trusting behavior. Similarly, Tabibnia et al. (2008) observed that fair offers produced greater activity in the ventral striatum and ventromedial PFC than unfair offers that would yield the same material benefit.

A number of behavioral studies have yielded results consistent with those of the fMRI studies, suggesting that being treated fairly is rewarding above and beyond the material benefits that fair treatment often brings (De Cremer & Alberts, 2004; Tyler, 1991). It has been suggested that this makes sense evolutionarily because fair treatment can be considered a proxy for whether one is valued by others in a group. From an evolutionary perspective, continued inclusion in social groups has been critical to receiving a share of needed resources and even to survival; thus, any cue that one has met this inclusion criterion is likely to be rewarding.

Indeed, simple signs of social acceptance have been associated with ventral striatum activity in a number of recent studies. Izuma, Saito, and Sadato (2008) found that a person's ventral striatum was similarly activated by financial rewards and by being informed that others view that person in a positive light. In a developmental social neuroscience study (Scott, Dapretto, Ghahremani, Poldrack, & Bookheimer, under review), children's good performance on each trial of a task was rewarded by either financial reward or a smiling female face with the words "that's correct" next to it. Similar increases in ventral striatum activity were observed whether the reward was financial or social.

Another set of studies has shown that helping behavior in the form of charitable giving also generates reward activity. Moll and colleagues (2006) asked people to accept or reject each of a series of propositions that would yield positive, neutral, or negative financial outcomes for oneself and/or for different charities (money really went to these charities in this study). Trials in which subjects could gain money for themselves with no negative consequence for the charity unsurprisingly led to increased ventral striatum activity. What was surprising is that trials in which the charity would gain while the subject would lose money (i.e., a donation) led to a higher level of ventral striatum activity than receiving money oneself. Additionally, the magnitude of ventral striatum activity during donation decisions was associated with the tendency to accept donation propositions during the task. All of these studies taken together suggest that enacting or being the recipient of prosocial behavior activates the ventral striatum, a region that has been commonly associated with reward responses to primary reinforcers and to nonsocial secondary reinforcers such as money, drug cues for addicts, and erotic images (Lieberman & Eisenberber, 2009).

Social Rejection

The study of social rejection and ostracism has been a major area of social psychological research in the past decade (Williams, 2007). Being excluded or rejected represents some of the most distressing experiences that people have, and fear of rejection is a powerful motivator that may help explain a wide array of classic findings of conformity and obedience to authority (Williams, Bernieri, Faulkner, Grahe, & Gada-Jain, 2000). Based initially on animal studies (Panksepp, Herman, Conner, Bishop, & Scott, 1978), it has been suggested that there may be an overlap in the way that the brain represents experiences of physical pain and social pain (i.e., the pain of social rejection, exclusion, or isolation) (Eisenberger & Lieberman, 2004; MacDonald & Leary, 2005).

In humans, the neural components of the physical "pain matrix" are fairly well understood, including the dorsal ACC, anterior insula, somatosensory cortex, and periaqueductal gray (Price, 2000). Of these regions, the dorsal ACC has been most reliably associated with the distress of physical pain (Rainville, Duncan, Price, Carrier, & Bushnell, 1998), in contrast to the somatosensory cortex, which has been primarily associated with the sensory aspects of physical pain (e.g., identifying where on the body the pain is felt). For instance, after surgical lesioning of the dorsal ACC for chronic pain, patients typically report that they can identify the location of a painful stimulus on their body and how intense the stimulus is, but they also report that the pain no longer bothers them (Foltz & White, 1968). Finally, as described earlier, right ventrolateral PFC and rostral ACC have both been associated with the regulation of physical pain distress.

Eisenberger and colleagues have conducted a series of neuroimaging studies that suggest that social pain processes largely rely on this same physical pain network (Eisenberger, Gable, & Lieberman, 2007; Eisenberger, Lieberman, & Williams, 2003; Masten, Telzer, & Eisenberger, under review; Way, Taylor, & Eisenberger, 2009). In these studies, subjects believe they are playing a simulated ball-tossing game on the Internet while they and two other subjects are all in MRI scanners. Once in the scanner, the subjects actually play against computer players programmed to include the subject for a certain amount of time and then stop throwing the ball to the subject for the remainder of the scan. Self-reported social distress during this exclusion episode is associated with greater dorsal ACC activity, whereas lower distress reports are associated with increased right ventrolateral PFC activity (Eisenberger et al., 2003; Eisenberger, Way, Taylor, Welch, & Lieberman, 2007). Other studies have also observed increased dorsal ACC activity in response to rejection-themed images (Kross, Egner, Ochsner, Hirsch, & Downey, 2007) and video clips of disapproving facial movements (Burklund, Eisenberger, & Lieberman, 2007). Additionally, dorsal ACC activity during exclusion in the scanner correlates with daily experiences of social disconnection outside the scanner (Eisenberger, Gable et al., 2007). Thus, the distress of social pain in the dorsal ACC and the regulation of social pain in right ventrolateral PFC closely parallel the findings from the physical pain literature. The animal literature supports these findings as well, having shown that electrical stimulation of the dorsal ACC increases and surgical lesions of ACC decrease distress vocalizations associated with social isolation in nonhuman mammals (MacLean & Newman, 1988; Smith, 1945).

One criticism of these findings (Sommerville, Heatherton, & Kelley, 2006) focuses on the common view that the dorsal ACC is responsible for cognitive processes, whereas the rostral ACC is responsible for corresponding affective processes. This viewpoint suggests that the social rejection findings may reflect a violation of cognitive expectations of inclusion and that the dorsal ACC is therefore activated because of cognitive conflict monitoring. However, this perspective does not account for the activity correlating with the self-reported distress of the experience (Eisenberger et al., 2003). Furthermore, it does not account for the increased dorsal ACC activity in rejection-sensitive individuals to cues of rejection (Burklund et al., 2007), because these individuals expect rejection more and yet show more dorsal ACC activity in response to it. Finally, the strong linkage between an opioid polymorphism and the dorsal ACC response to rejection is hard to square with a purely cognitive account (Way et al., 2009).

It is worth considering where this critique comes from historically. The belief that the dorsal and rostral ACCs are involved in cognitive and affective processes, respectively, is largely a consequence of an influential review paper (Bush, Luu, & Posner, 2000). In this study the researchers reviewed dozens of cognitive conflict studies and found that these tended to activate the dorsal ACC, whereas a study of emotional conflict detection in an emotional Stroop paradigm and other clinical symptom provocation studies produced rostral ACC activity. First, it is important to note that this literature review included no studies of physical pain. Even though the dorsal ACC has been repeatedly associated with the emotional distress of physical pain, this finding was not accounted for in their analysis. Second, subsequent emotional conflict monitoring has found activity in the dorsal ACC (Davis et al., 2005; Ochsner, Hughes, Robertson, Cooper, & Gabrieli, 2009). Third, numerous neuroimaging studies have shown dorsal ACC activity associated with anxiety and other affective processes (Ehrsson, Weich, Weiskopf, Dolan, & Passingham, 2007; McRae, Reiman, Fort, Chen, & Lane, 2008; Simmons et al., 2008; Straube, Mentzel, & Miltner, 2007). Fourth, neuropsychological lesion data are more supportive of the dorsal ACC's role in pain distress than cognitive conflict monitoring, because dorsal ACC lesions are commonly found to diminish pain distress (Foltz & White, 1968), whereas cognitive conflict monitoring is often spared (Baird et al., 2006; Fellows & Farah, 2005; Stuss, Floden, Alexander, Levine, & Katz, 2001).

One way to reconcile these notions of dorsal ACC function is to think of it functioning like an alarm (Eisenberger & Lieberman, 2004). Consider the typical smoke alarm. To work successfully, it must fuse two functions together. On one hand, it must have a mechanism capable of detecting when a critical threshold for smoke particles has been met—a mechanism conceptually analogous to cognitive conflict monitoring. On the other hand, in order to notify people that there's a fire, it must have a mechanism that can sound an audible alarm after the first mechanism has detected the smoke. This latter process resembles the function that pain distress plays in our lives, experientially notifying us that some harm may come to us. From this perspective, determining the function of the dorsal ACC may not be an either/or decision. Rather conflict monitoring and pain distress may reflect coordinated cognitive and experiential components of a single alarm mechanism.

Attachment and Close Relationships

A number of imaging studies have begun to examine how the brain responds to the people we love (spouse, partner, child, parent). Across these studies, most have observed limbic activations (e.g., amygdala, striatum, dorsal ACC, insula), although some report widespread activity in the mentalizing network (Leibenluft, Gobbini, Harrison, & Haxby, 2004; Seifritz et al., 2003). Hearing a child crying has been associated with dorsal ACC activity (Lorberbaum et al., 2002; Seifritz et al., 2003), whereas seeing pictures of one's own child or infant tends to activate the amygdala, dorsal ACC, anterior insula, and bilateral lateral PFCs (Bartels & Zeki, 2004; Leibenluft et al., 2004; Minagawa-Kawai et al., 2008; Ranote et al., 2004). One study of mothers viewing pictures of their infant has shown ventral striatum activity (Strathearn, Li, Fonagy, & Montague, 2008), but this result has not yet been replicated. Only one study has examined the interaction of viewing one's own infant or another's, either in distress or not; this study revealed strong dorsal ACC and dorsomedial PFC activity when mothers viewed their own infant in distress relative to the other conditions (Noriuchi, Kikuchi, & Senoo, 2008). A recent study using near-infrared spectroscopy (Minagawa-Kawai et al., 2008) has examined infants' neural responses to their mother's face and observed greater medial PFC activity in response to their mother smiling (relative to the mother not smiling and a stranger smiling or not smiling).

Viewing pictures of one's romantic attachments has typically produced dorsal striatum activity (Aron et al., 2005; Bartels & Zeki, 2000); however, one study that subliminally primed the name of one's loved one has reported increased ventral striatum activity (Ortigue, Bianchi-Demicheli, Hamilton, & Grafton, 2007). Similar to the network associated with seeing cues associated with one's own child, adult attachment studies have observed relationships between anxious attachment style and activity in the amygdala and dorsal ACC during relationship distress or hostile feedback paradigms (Gillath, Bunge, Shaver, Wendelken, & Mikulincer, 2005; Lemche et al., 2006). In addition, another study reported that avoidant attachment was associated with diminished ventral striatum feedback during supportive feedback from a stranger (Vrticka, Andersson, Grandjean, Sander, & Vuilleumier, 2008).

Finally, a few studies have examined grief responses by prompting individuals to think about the recent loss of a significant other (e.g., mother recently dying of cancer or a romantic relationship that recently ended). These studies have typically observed greater activity in the dorsal ACC and anterior insula, consistent with a social pain account of grief, and in the posterior cingulate (Gundel, O'Connor, Littrell, Fort, Lane, 2003; O'Connor et al. 2008). One study (O'Connor et al., 2008) examined the neural differences among individuals who were showing a normal level of recovery from grief compared with those with complicated grief, which refers to a persistent grief that is not following the normal recovery pattern. Complicated grief was associated with increased ventral striatum activity, relative to noncomplicated grief, when responding to cues related to the deceased. This activity was also associated with self-reported yearning for the deceased, suggesting that ventral striatum activity may reflect current desires for connection with the deceased that typically abate over the course of several months of normal, noncomplicated grief.

Attitudes and Attitude Change

Attitudes are one of social psychology's oldest constructs (Thurstone, 1928). People's attitudes are of great interest because they are believed to predict an individual's behavior in a variety of attitude-relevant situations. In contrast to our intuitions, self-reported attitudes are often poor indicators of subsequent behaviors. This has led researchers to examine the existence and predictive efficacy of implicit attitudes (Fazio & Williams, 1986), to assess attitudes in the aggregate (Ajzen, 2001), and to identify the critical role of behavioral intentions linking attitudes to behaviors (Gollwitzer, 1999). To date, the neuroscience of attitudes has largely focused on the neural correlates of attitudinal evaluation and the neural correlates of attitude change.

Attitudinal Evaluation

Several studies have examined which brain regions are more active when expressing attitudinal evaluations (e.g., how good is it?) compared with when control judgments are made (e.g., how symmetrical is it?). There is substantial variability in the activations reported across studies of attitudinal evaluation. This may be a result of the diversity of attitude objects examined in different studies. The objects examined include geometric shapes (Jacobsen, Slotkin, Westerveld, Mencl, & Pugh, 2006), paintings (Kawabata & Zeki, 2004), music (Brattico, Tervaniemi, & Picton, 2003), social concepts (Cunningham et al., 2004), unfamiliar faces (O'Doherty et al., 2003), famous names (Cunningham, Johnson, Gatenby, Gore, & Banaji, 2003; Zysset, Huber, Ferstl, & von Cramon, 2002), and current political candidates (Kaplan, Freedman, & Iacoboni, 2007). The most frequently observed activations in these studies occur in the bilateral ventrolateral PFC, along with a host of mentalizing and self-referential brain regions, including the medial PFC, dorsomedial PFC, posterior cingulate, TPJ, and temporal pole.

When subjects report their evaluations, it is difficult to know what psychological processes are occurring to generate this evaluation. For instance, evaluations are sometimes constructed in the moment, and other times they are retrieved from memory. Sometimes people feel comfortable expressing their attitudes, and other times they engage in effortful mental processes to shape the expression of an attitude for public consumption. Evaluations also vary in valence and arousal, and therefore task materials that vary on these dimensions across studies could produce different results as well. Some of these elements have been examined. With respect to valence, positive and negative attitudes have been associated with left and right lateral PFCs, respectively (Cunningham, Espinet, DeYoung, & Zelazo, 2005). In contrast, attitudinal intensity or arousal has been associated with the amygdala and ventromedial PFC (Cunningham et al., 2004). Self-reported efforts to control one's evaluation have been associated with activity in the ventrolateral PFC, dorsolateral PFC, dorsal ACC, medial PFC, and precuneus. In contrast, being exposed to liked or disliked attitude objects without expressing an evaluation has been associated with activity in the ventral striatum (Aharon et al., 2001) and amygdala (Cunningham et al., 2003), respectively, suggesting that these regions may play a role in implicit attitudes.

More recently, an area of research referred to as neuromarketing has begun examining branding effects that bear a close relationship to attitude processes. The most significant of these studies recreated the Pepsi challenge inside the scanner (McClure et al., 2004). In the classic advertising campaign from the 1970s, it was found that despite overwhelming self-reported preference for Coke, when each drink was tasted without labels, Pepsi was more often preferred. The implication is that Coke is preferred because of the brand association rather than its taste. In this study, subjects tasted Coke and Pepsi on a series of trials, but could see the brand labels on only some of the trials. They observed that in the absence of labels, ventromedial PFC activity was associated with drink preference, consistent with this region's common association with hedonic experience (Trepel, Fox, & Poldrack, 2005). In contrast, when the brand labels were available, preferences were associated with dorsolateral PFC and hippocampal activity, suggesting a role for higher cognitive and memory processes.

Attitude Change

The first neuroscience investigation of attitude change explored cognitive dissonance processes in patients with anterograde amnesia (Lieberman, Ochsner, Gilbert, & Schacter, 2001). Cognitive dissonance reduction usually refers to the change in attitudes or beliefs that occur when one has freely chosen to engage in a behavior that conflicts with a previously held attitude or belief. For instance, in the free choice paradigm, an individual ranks his or her preferences for several items in a category (e.g., kitchen appliances; Brehm, 1956) and then chooses which of two closely ranked items he or she would like to own; the subject then finally re-ranks all of the items. The classic finding is that the selected item goes up in the re-rankings, whereas the unselected item goes down in the re-rankings. The dissonance account suggests that choosing between evenly liked items is at odds with previously ranking them as similar and that by "spreading the alternatives" in one's updated rankings, the selected items comes to look as though it was an obvious choice all along. Of course, to outsiders, this looks like post hoc rationalization.

Several early accounts of cognitive dissonance processes suggested that dissonance reduction processes were relatively explicit and slow, occurring over a long period of time after the conflictual behavior occurred (Festinger, 1964; Hovland & Rosenberg, 1960; Steele, Spencer, & Lynch, 1993). According to this model, an individual must be consciously aware that he or she has engaged in counter-attitudinal behavior, attribute the resulting dissonance feelings to this specific conflict, and then engage in effortful processing to change this attitude over time. Lieberman et al. (2001) compared attitude changes in amnesics and healthy controls because it is unlikely that amnesics would recognize that they have engaged in a behavior that conflicts with a previously expressed attitude. Despite this impairment, amnesics showed as much attitude change as control subjects, suggesting that the conventional account of cognitive dissonance effects relies too heavily on controlled processing mechanisms being deployed slowly over time. Multiple electroencephalograph (EEG) studies also suggest that dissonance effects may occur more quickly than previously assumed (Harmon-Jones, Gerdjikov, & Harmon-Jones, 2006; Harmon-Jones, Harmon-Jones, Fearn, Sigelman, & Johnson, 2008).

Stereotyping and Intergroup Processes

Perceiving Race

Neuroscience research on stereotyping and related intergroup processes represents a microcosm of the larger social cognitive neuroscience landscape, including studies of social perception, implicit attitudes, self-like processing of others, and self-control. This is also one of the areas of social cognitive neuroscience where ERP studies vastly outnumber fMRI studies (for review, see Amodio, 2008; Bartholow & Dickter, 2007; Kubota & Ito, 2009).

A number of fMRI studies have examined the perception of Black and White faces. Across these studies, inverse affective and perceptual effects have emerged. On one hand, greater amygdala activity in response to Black versus White faces (Lieberman et al., 2005; Ronquillo et al., 2007) suggests a possible negative evaluative response to or greater emotional evocativeness of Black faces. In contrast, greater activity in the FFA to ingroup versus outgroup faces (Golby, Gabrieli, Chiao, & Eberhardt, 2001; Lieberman et al., 2005) has been interpreted as reflecting greater perceptual expertise with ingroup faces.

These results are paralleled by ERP studies (Ito & Urland, 2003), which reveal some early components that are more responsive to outgroup faces (N100, P200) and another early component that is more responsive to ingroup faces (N200), which has been linked to FFA activity (Allison et al., 1994).

Although these early ERP components are not modulated by race-related encoding goals (Ito & Urland, 2005), both race-based categorization and individuation goals have been associated with diminished amygdala responses to Black faces in fMRI studies. Wheeler and Fiske (2005) observed diminished amygdala activity when subjects judged a target's food preference. In contrast, Lieberman et al. (2005) observed diminished amygdala activity during the labeling of a target's race, similar to the effects of affect labeling. Along the same lines, a study of stigma (Krendl, Macrae, Kelley, Fugelsang, & Heatherton, 2006) reported less amygdala activity when subjects' judgments were explicitly focused on the stigma, compared with when they were not. In addition, amygdala responses to race have been modulated by skin darkness (Ronquillo et al., 2007) and the direction of a target's eye gaze (Richeson, Todd, & Trawalter, 2008).

Implicit Attitudes

Other neuroimaging studies have examined the relationship between attitudes and amygdala responses to Black faces, relative to White faces. Most notably, an early fMRI study (Phelps et al., 2000) observed that amygdala activity to Black faces was correlated with the strength of negative implicit attitudes toward Blacks but was not correlated with an explicit measure of racism. Similarly, another study (Cunningham, Johnson et al., 2004) reported greater amygdala activity to Black faces versus White faces only when the faces were presented subliminally, suggesting potential self-regulation under supraliminal conditions. In this study, implicit attitudes were associated with amygdala activity during subliminal presentations but not during supraliminal presentations. Somewhat surprisingly, a patient with amygdala damage showed normal implicit racial attitudes (Phelps, Cannistraci, & Cunningham, 2003), although the lesion was acquired in adulthood and other social processes have been spared for amygdala lesions acquired in adulthood (Shaw et al., 2004). In contrast, patients with ventromedial and medial PFC damage do not produce implicit attitude effects (Milne & Grafman, 2001).

Controlling Bias

Given that stereotype-based expectations can lead to systematically biased behavior (Payne, 2001) and given that most individuals are motivated to be or appear nonbiased, self-regulation processes are often brought online in order to guard against having biased thoughts, feelings, or behaviors toward outgroup members. Multiple fMRI studies have observed a network almost identical to those seen in other forms of self-control (ventrolateral PFC, dorsolateral PFC, dorsal ACC, supplementary motor area) more active in conditions in which subjects are exposed to Black faces under conditions where bias could be revealed (Cunningham, Johnson et al., 2004; Richeson et al., 2003). In addition, work with ERPs (Amodio et al., 2004; cf. Bartholow et al., 2005) has shown evidence of a fast response in the dorsal ACC, called the error-related negativity response, during the Weapons Identification Task (Payne, 2001) on trials that reveal bias. Critically, the dorsal ACC response on a particular trial predicted greater controlled processing during the subsequent trial. This suggests that this activation is an internal indicator of potential bias and the need to be more careful on ensuing trials.

Naturally, there are situations in which individuals do not mind acting on the basis of ingroup favoritism. People want members of their ingroups to succeed and obtain their fair share of resources, at a minimum. One study observed neural responses associated with this ingroup bias in the absence of pressure to be unbiased (Rilling, Dagenais, et al., 2008). Subjects were separated into groups using a minimal group paradigm manipulation; they then played prisoner dilemma games with ingroup and outgroup members. Approximately one third of the subjects reported feeling differently when playing against an ingroup member than an outgroup member. This subsample, but not the sample as a whole, produced greater activity in the dorsomedial PFC and right TPJ, both regions in the mentalizing network, when playing with an ingroup rather than with an outgroup member. In other words, playing with an ingroup player may have produced more mentalizing about the perspective of the other player.

Being the Target of Prejudice

Although the vast majority of intergroup studies, both behavioral and neuroimaging, have examined the perceiver's side of bias, a handful have examined the reactions of the targets of prejudice. In the behavioral literature, stereotype threat (Steele & Aronson, 1995) is the most widely used paradigm for examining the effect of stereotypes on the target of those stereotypes. In these studies, subjects for whom a stereotype exists (e.g., females are bad at math) perform a stereotype-relevant task (e.g., a math test) that either is characterized as measuring their ability or is characterized in nonability terms (e.g., it is a game). The standard finding is that stereotype targets perform worse on these tasks when they believe the task is diagnostic of their ability, and these results are explained in terms of anxiety over confirming the stereotype. In other words, if a female is anxious or distracted, thinking that poor performance on a math test will confirm negative math stereotypes about women, this may limit the woman's ability to focus on task, thus creating a self-fulfilling prophecy.

Two fMRI studies have examined the neural correlates of stereotype threat (Krendl, Richeson, Kelley, & Heatherton, 2008; Wraga, Helt, Jacobs, & Sullivan, 2006; see also Masten et al., under review). In both studies, increased stereotype threat was associated with increased rostral ACC activity. Given that this region has been associated both with emotional experience and with the regulation of emotions, it is difficult to interpret the significance of this common activation from just these two studies. In one of the studies (Wraga et al., 2006), increased activity in the rostral ACC was marginally associated with poorer task performance. However, this could be explained either as distress interfering with task performance or as attention to regulating one's distress interfering with task performance. An ERP study (Forbes, Schmader, & Allen, 2008) found that those in a stereotype threat condition who responded to the task by devaluing its significance produced smaller error-related negativity responses to their own errors, suggesting less self-monitoring as a consequence of devaluing.

IV. HOW SOCIAL COGNITIVE NEUROSCIENCE CONTRIBUTES TO SOCIAL PSYCHOLOGY

Now that we have reviewed where dozens of social psychological processes occur in the brain, anyone would be forgiven for believing that social cognitive neuroscience is little more than phrenology. Knowing that social processes can be localized within the brain is not all that interesting. What is the alternative hypothesis? That they will be localized in your elbow? A cognitive neuroscientist who has taken a shine to the social side of things might respond that brain mapping is essential to understanding what different brain regions do. How can we really understand what a brain region does if it is examined using only abstract decontextualized stimuli that cognitive psychologists typically use? A complete understanding of the brain will be constituted only if the brain is studied while situated in all its social psychological glory.

A social psychologist would likely respond that it is all fine and well that neuroscientists want to probe their favorite brain regions using social psychological paradigms to figure out what those regions do. But what does that do for social psychology? Is our social psychology improved at all by looking at the brain? Are there social psychological theories that should be updated in light of social cognitive neuroscience data? Is there conventional wisdom in our field that needs to be reconsidered or looked at in a fresh light because of brain data? Do neuroscience methods allow us to ask social psychological questions that have gone unanswered for years? If the answer to any of these questions is yes, then social psychology needs the tools of neuroscience just as surely as it needed the tools of cognitive psychology a few decades ago.

Can social cognitive neuroscience answer all of social psychology's questions? Of course not. No method can. Neuroimaging is no more a panacea than reaction time measures or introspective self-reports. Indeed, for most of the interesting findings from the history of social psychology, neuroimaging would have been a far worse tool than those already used by social psychology. During a typical fMRI session, a person lays prone in the scanner wearing goggles that allow the subject to see a video feed; the subject responds during tasks almost exclusively with button boxes limited to a few buttons, and there are constant loud noises during scanning. Finally, experimental trials from each condition of interest often must be repeated dozens of times, meaning that any task for which trial repetition will necessarily contaminate the psychological phenomenon is off limits. Despite these limitations, there are specific ways in which neuroscience can contribute to our social psychological enterprise that should matter even to social psychologists uninterested in the brain. The remainder of this section discusses some of the ways that social cognitive neuroscience can and has contributed to the mission of social psychology.

Brain Mapping

Knowing where social psychological processes occur in the brain does matter for at least a few reasons. First, animal research and cognitive neuroscience have made significant progress in figuring out the computations performed by particular brain regions. This knowledge can be drawn on to generate preliminary inferences about the kinds of subprocesses subserving macrolevel social processes. That is, social processes usually encompass multiple component processes simultaneously or in rapid sequence, and identifying the involvement of brain regions with well-characterized functions can help us identify which corresponding psychological processes may contribute to the total mental act. For instance, imagine that when individuals watch one person greeting another person, a region of the lateral temporal cortex known to be primarily involved with semantic processing (Noppeney & Price, 2004) was activated, compared with some control task. One might infer that watching this social episode is comprehensible to us because we retrieve social scripts from semantic memory. Alternatively, imagine that watching this greeting activates the mirror system. This finding might suggest that people understand social episodes through simulation rather than semantic coding. Incidentally, it could be the case that both the mirror system and semantic processes are activated when observing the greeting. One of the advantages of neuroimaging over standard behavioral testing is that multiple systems can be interrogated simultaneously and often without eliciting a behavioral response from subjects that would require particular instructions and an attentional set that might contaminate the natural attitude of the subject.

Brain mapping discoveries are the beginning, not the end, of the process for social cognitive neuroscience. Once the regions involved in a social process are identified, one can then more carefully interrogate those regions in future studies that focus on hypothesis testing. As social psychologists, we are used to our everyday experiences serving as the anecdotal database from which we design studies. Brain mapping studies are the way that social cognitive neuroscientists create an anecdotal database.

In many cases, it might be argued that brain mapping is telling us something we already know from other existing behavioral research, and that is a fair criticism. However, we should ask ourselves what the value of a neuroimaging study would have been, had it come first. Would it have updated our social psychological theories just as the behavioral research did? If so, it indicates that neuroimaging data can constrain our theories (Kihlstrom, 2006); it is just a historical accident that the behavioral study came first. Surely in the future there will be times when the neuroimaging study will come first and make significant contributions.

Convergences

Although social cognitive neuroscience is still a young discipline, one of its most exciting contributions is a series of findings in which two experiences that seem quite different from each other phenomenologically, or were thought to be only metaphorically related, actually rely on overlapping neural processes. The assumption is that if two processes rely on common brain regions, then they rely on common computational processes as well. It is exceedingly difficult to demonstrate that two psychological events that feel different from each other share a great deal at the computational level (Kosslyn, 1999). Yet such demonstrations are a critical component to advancing social psychological theory. We group psychological phenomena into domains of study based on whether phenomena feel similar or meet some set of logical criteria; however, additional progress would be made if psychological phenomena were grouped based on their deep structure.

Social Metaphors Are Not So Metaphorical

A number of social psychological phenomena have now been linked to nonsocial phenomena in ways that raise the possibility that descriptions of social experience may be far less metaphorical than once thought. Social rewards such as positive social feedback or being treated with respect (Izuma et al., 2008; Tabibnia et al., 2008) activate the ventral striatum in much the same way that winning money or eating chocolate does. The experience and regulation of social pain are associated with brain regions involved in the experience and regulation of physical pain (Eisenberger & Lieberman, 2004). The sense of insult in response to unfair treatment and the experience of disgust in response to sensory stimuli are both associated with activity in the anterior insula (Borg, Lieberman, & Kiehl, 2008; Calder et al., 2000; Hsu, Anen, & Quartz, 2008; Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003; Wicker, Keysers, et al., 2003). In each of these cases, the social phenomenon seems less abstract and more embodied in light of these linkages. In addition, these unexpected convergences have led to behavioral studies that would not have been done otherwise. For instance, behavioral studies have examined the relationship between social and physical pain sensitivity (DeWall & Baumeister, 2006; Eisenberger, Jarcho, Lieberman, & Naliboff, 2006), with one recent experiment finding that taking Tylenol reduced self-reported feelings of social rejection (DeWall et al., in press).

The linkage of social to physical pain changes our conceptual understanding of social rejection and the need for social connection. Maslow's (1943) hierarchy of needs orders our needs (from most basic to least basic) as biological, safety, belonging, esteem, and self-actualization. In other words, biological and safety needs are critical to survival, and the rest are more or less gravy. However, deficits in social connection cause a form of pain just as deficits in other survival needs cause a form of pain (e.g., hunger, thirst, cold). It seems that evolution has a special painful place for deficits in basic survival needs, and social connection has made the cut. It has been speculated that because mammalian young are born relatively helpless, incapable of securing their own food, water, and shelter, continued social connection with their caregiver(s) is their primary means of survival. Knowing that social rejection activates the same pain processes as other survival need deficits allows us to think differently about social connection's place in our hierarchy of needs (Baumeister & Leary, 1995; Lieberman & Eisenberger, 2009).

Using the Self to Understand Similar Others

Other work has shown convergences within social cognition that have been hypothesized but never clearly demonstrated. For instance, although it is not surprising that people would use their knowledge of themselves to make sense of others, until recently there had been no hard evidence one way or the other. Studies by Mitchell, Macrae, and Banaji (2006) provide compelling evidence that we do use ourselves to make sense of at least some people. Specifically, they showed that the same region of the medial PFC is active when making self-referential judgments and judgments about a similar other but that this region is not active when making judgments about a dissimilar other. Such findings open up a variety of opportunities to hypothesize about how targets will be differentially understood and treated based on the relative contributions of the medial PFC or dorsomedial PFC (Harris et al., 2005).

Empathy

Knowing that experiencing physical pain and seeing others in physical pain recruit the same neural systems makes an important contribution to empathy research (Singer et al., 2004). When someone says, "I feel your pain," we can certainly quibble about whose pain they are feeling, but for the first time there is evidence they are really feeling someone's pain rather than merely entertaining an abstract idea. This often-replicated overlap also provides an experimental paradigm for testing various important aspects of empathy theories in the future because the modulation of this overlap by situational and personality factors can be easily assessed (Singer et al., 2006).

Direct and Reflected Self-appraisals

Social psychologists and sociologists have long hypothesized about the role that others' evaluations of us have on our own self-views (Cooley, 1902; Mead, 1934). As compelling and influential as this symbolic interactionist account has been over the years, there has been surprisingly little empirical evidence to support it. Behavioral research has focused on the overlap in the content of direct and reflected self-appraisals. Neuroimaging, however, allows us to examine the overlap in the structures supporting different kinds of appraisals. It might be expected that asking a 12-year-old boy what his best friend thinks of him would recruit brain regions known to be involved in self-referential processing and also brain regions known to be involved in mentalizing. Here, the adolescent is being asked to reflect on the mental state of another person and to derive a self-evaluation from this. The fact that adolescents recruit both of these systems when asked to make a direct appraisal of themselves (e.g., what do you think of yourself?) is more surprising. This finding constitutes preliminary evidence of reflected appraisals being spontaneously generated even when they have not been asked for (Pfeifer et al., 2009). Adults do not show broad activation of the social cognition network when making self-referential judgments. Note that if asked to make a direct self-appraisal, neither adolescent nor adult is likely to spontaneously use reflected appraisal language in their replies, but these neuroimaging data suggest that adolescents are doing something social when making direct self-appraisals. What this something is requires further investigations.

To be sure, these convergences are open to multiple interpretations. They are new findings that need further interrogation. However, each suggests new conceptual understandings of social phenomena and may inspire a variety of behavioral and neuroscience studies to follow up on these leads. New findings are rarely ends in themselves. However, each of these findings is part of a social psychological conversation, and suggests that neuroscience can indeed have a seat at the table and even have something worth saying to social psychologists now and then. It is also worth noting that in each of the preceding examples, knowing which brain regions are involved is relatively superfluous to the relevance of the findings for social psychology. One need not have an interest in neuroanatomy to find an overlap in how the brain processes social and nonsocial rewards quite compelling. One need never know that the ventral striatum is the point of convergence for this to be relevant. The anatomy can be left to the anatomists, but the investigation of such overlaps provides a method for conceptual advances within social psychology.

Dissociations

A basic tenet of all psychological research is that if two processes or performances can be dissociated on some dependent measure such as reaction time, then the processes are distinct from one another. Neuroscience research is no different. When lesion studies observe that damage to region A produces deficits in task X but not in task Y, compared with damage to region B, which produces deficits in task Y but spared performance in task X, this is taken as strong evidence that task X and Y rely on different psychological processes. Similarly, when an fMRI study reveals that different brain structures tend to be active during tasks X and Y, this too suggests different psychological processes may be at work. In some cases, these differences are quite relevant to social psychological theories.

Social Cognition Is Special

Perhaps the single best example of a neuroimaging study challenging the traditional understanding of a social psychological finding comes from Mitchell et al. (2004). In a classic behavioral study, subjects read passages with the goal of either memorizing the material for later testing or forming a social impression of the target in the passage (Hamilton, Katz, & Leirer, 1980). The surprising finding was that the impression formation goal led to better performance on a subsequent memory test, even though those with an impression formation goal did not know the test was coming and those in the memorization condition did. The generally accepted explanation of these results was depth of processing (Craik & Tulving, 1975), such that social encoding was believed to be a deeper, more elaborative form of encoding than encoding with a memorization goal.

Mitchell and colleagues (2004) replicated this paradigm in the scanner and discovered what those earlier studies could not. Social and nonsocial encoding do not just differ quantitatively on a depth of processing dimension. Rather, they rely on qualitatively dissociable processes. Countless studies have shown that successful memorization (i.e., encoding that leads to later retrieval success) is associated with activity in left ventrolateral PFC and the medial temporal lobes (Wagner et al., 1998). Mitchell found that activity in these regions did predict retrieval success in the memorization condition but did not predict retrieval success in the social encoding condition. Instead, retrieval success in the social encoding condition was associated with activity in the dorsomedial PFC. This finding strongly calls into question the depth of processing account and instead suggests that there is something qualitatively different about social encoding. Regardless of how one evaluates the significance of this problem, it is a clear case in which the inference from the behavioral data was wrong and the neuroimaging evidence provided a clear and compelling case for distinct processes operating in social and nonsocial encoding. Upon learning the results of this study, one must update one's understanding of this phenomenon based on these neuroimaging data.

Social by Default

One of the most significant discoveries in the past decade of cognitive neuroscience research is the *default network.* These regions are highly activated when a subject is at rest (i.e., when not being given any experimental task to perform) (Raichle et al., 2001) and show highly coordinated activity with each other at rest (Fox et al., 2005). They become less active when cognitive tasks are performed (Greicius, Krasnow, Reiss, & Menon, 2003; Shulman et al., 1997), to the extent that the cognitive tasks are more demanding (McKiernan, Kaufman, Kucera-Thompson, & Binder, 2003), but when active during cognitive tasks, they tend to be associated with producing errors (Boly et al., 2007; Li, Yan, Bergquist, & Sinha, 2007; Weissman, Roberts, Visscher, & Woldorff, 2006). At rest, these regions produce activity that is inversely correlated with activity in brain regions supporting common cognitive tasks (Fox et al., 2005).

What is striking is that this default network could easily be mistaken for a self and social cognition network. All of the regions that are highly active at rest (dorsomedial PFC, medial PFC, ventromedial PFC, precuneus, TPJ in almost all studies, with fusiform gyrus and temporal poles also appearing with some frequency) are among the regions that figure most prominently in this review of social cognitive neuroscience. The implication is obvious. When left to their own devices, people think about themselves and their social lives (D'Argembeau et al., 2005; Gusnard et al., 2001; Iacoboni et al., 2004; Mason et al., 2007; Wicker, Ruby, Royet, & Fonlupt, 2003).

Put a different way, the brain's default focus is social. Only when something nonsocial, like a working memory task, requires it to direct its resources elsewhere does it momentarily stop focusing on the social. Social psychologists might find this to be obvious, but to funding agencies, the media, and your grandparents this kind of finding really helps to firm up the significance of what we study (the fact that the size of the prefrontal cortex across species correlates the typical group size in each species is a good one to throw out there too; Dunbar, 1998).

It should be noted that it was recently reported that anesthetized unconscious monkeys still had increased activity in the default regions (Vincent et al., 2007; see also Fransson et al., 2007). This raises a fascinating issue, one that should be relevant to social psychologists (and not just impress their grandparents). Does the brain show these social cognition activations at rest because this is what we choose to think about in our spare time? Or is it the case that we tend to focus on social and self-related thinking in our spare time because high baseline activity in these regions biases us, in a sense priming us, to think about these things? Has evolution progressed in such a way that it has proved adaptive to have our spare thought biased toward processing and reprocessing information about ourselves and the social world?

Automaticity and Control

At the end of the 1990s, great attention was being devoted to the Implicit Association Test (Greenwald, McGhee, & Schwartz, 1998) as a method for assessing implicit attitudes. On one hand, large numbers of social psychologists were conducting Implicit Association Test studies because among implicit measures it was straightforward to use and produced strong experimental effects with relatively modest sample sizes. On the other hand, there was a great deal of controversy over what the Implicit Association Test measured and whether what it measured could legitimately be called implicit. At one point, so the story goes, the *Journal of Personality and Social Psychology* had a moratorium on publishing any additional Implicit Association Test papers until it was clear that it really assessed implicit attitudes. When Phelps and colleagues (2000) reported that the strength of amygdala responses to images of Black faces was strongly associated with Implicit Association Test scores but not with explicit attitude scores, this was generally received as significantly strengthening the case that the Implicit Association Test truly measured implicit attitudes. The amygdala has long been thought to primarily engage in automatic processes, given its phylogenetic history, its early position in the visual processing stream, its role in fear conditioning in rodents, and the fact that subliminal presentations of fear expressions activate this region. If the Implicit Association Test scores, but not explicit attitudes, are associated with amygdala responses, then there is a good chance the Implicit Association Test is measuring something implicit. Thus, neuroimaging findings help distinguish implicit from explicit attitudes and clarify the interpretation of one of the most commonly used social psychological instruments.

As with implicit and explicit attitudes, several dual-process models within social psychology (Chaiken & Trope, 1999) posit some combination of automatic and controlled processes believed to share the work in various domains (e.g., persuasion, attribution, self-knowledge, empathy). Automatic processes are fast, resistant to interruption, independent of conscious intention, or outside of awareness, whereas controlled processes are slow, interruptible, intention-driven, and accessible to awareness (Wegner & Bargh, 1998). There are several remaining important questions about dual-process models. For instance, are automaticity and control two ends of a spectrum in which the same processes and representations are employed but with differing levels of efficiency? Or are there distinct automatic and controlled processes that differ qualitatively and may be sensitive to different types of inputs, store information differently, and respond differently as a function of context? If there are separate processes, how many sets of dual-processes exist? One scientist (Kruglanski et al., 2003) hyperbolically suggested that there might be 30 sets of dual-processes based on the fact that a contemporary volume on dual-process models (Chaiken & Trope, 1999) had 30 chapters, each putting forth a dual-process model with only minimal connections made between the different models. Because experiences in different domains of social psychology feel so different from one another and have such different outcomes, it is hard to assess whether dual-process models in these domains (e.g., persuasion and stereotyping) rely on common processes. Similarly, because different underlying processing architectures can produce the same behaviors, it can be difficult to identify which processing architectures are really at work (Gilbert, 1999).

Neuroimaging has been quite informative in general in helping to tease apart processes that are implicit, automatic, nonconscious, or reflexive from those that are explicit, controlled, conscious, or reflective (Lieberman, 2009a; Satpute & Lieberman, 2006). For instance, explicit learning is impaired in anterograde amnesiacs but not in patients with Parkinson's disease, whereas implicit learning is impaired in patients with Parkinson's disease but not in anterograde amnesiacs (Knowlton, Mangels, & Squire, 1996). Based on the neural deficits associated with each neuropsychological impairment, neuroimaging studies have shown that implicit learning is associated with basal ganglia activations, whereas explicit learning has been associated with medial temporal lobe activations (Lieberman, Chang, Chiao, Bookheimer, & Knowlton, 2004; Poldrack et al., 2001). Moreover, these regions appear to be in competition such that if one region is relatively active during task performance, the other tends to be correspondingly deactivated.

In one particularly elegant study, Foerde, Knowlton, and Poldrack (2006) trained subjects on two tasks known to be learnable using both implicit and explicit processes. For one task, subjects were trained under cognitive load; the other task was learned without cognitive load. When there was no cognitive load task, thus facilitating explicit learning strategies, activity in the medial temporal lobe during training was associated with performance accuracy at a follow-up test session. When there was cognitive load during training, thus interfering with explicit learning strategies, activity in the medial temporal lobe during training was associated with performance at test; instead, activity in the basal ganglia was associated with later performance. Critically, the behavioral performances were equivalent in both conditions. In other words, behaviorally there was no evidence that different underlying psychological processes were supporting performance at test, but neuroimaging revealed that there were indeed different processes at work. These results strongly suggest that there are two separate processes that operate at different times and in different contexts. Although there may be a smooth transition in observable performance as learning and performance switch from being controlled to automatic, the underlying neural responses argue for qualitatively distinct processes.

Although social cognitive neuroscience research has rarely set out to compare automatic and controlled variants of social cognition, a number of studies have had conditions that would at least roughly meet the criteria allowing for such a comparison. Lieberman (2007) reviewed the findings from several domains of social cognition. Six brain regions were reliably invoked during controlled, but not automatic, forms of social cognition; these regions included the lateral PFC, lateral parietal cortex, medial PFC, dorsomedial PFC, precuneus, and medial temporal lobe. Four regions were reliably invoked during automatic, but not controlled, forms of social cognition; these regions included the amygdala, ventromedial PFC, lateral temporal cortex, and ventral striatum.

These results suggest an answer to the first of the lingering dual-process questions: Are there really separate automatic and controlled social processes? The findings are more consistent with an account of separate automatic and controlled processes, rather than an account wherein single processes are called automatic when they operate efficiently and called controlled when they operate inefficiently. Rather, it appears that with training, the brain regions responsible for automatic processes slowly develop computational algorithms to support task performance, and as these processes come online, brain regions supporting controlled processing are needed less and less.

These data also speak to the second lingering question of how many sets of dual-processes exist. Although no definitive answer is available, the review (Lieberman, 2007) found that brain regions involved in automatic or controlled processes tended to each be involved in a variety of automatic or controlled processes. For instance, the ventromedial PFC has been associated with automatic aspects of self-knowledge, decision making, emotional experience, and attitudes, whereas right ventrolateral PFC has been associated with inhibitory control over behavior, thought, emotion, attitudes, and perspective (Cohen & Lieberman, in press). Thus, it appears that the same networks responsible for automatic and controlled processing in one social psychological domain may deal with automatic and controlled processing in other domains as well. The phenomenologically different inputs in each social domain may produce different outputs but still make use of a shared dual-process architecture. This may help explain phenomena such as ego depletion (Baumeister, Bratslavsky, Muraven, & Tice, 1998), in which self-control efforts in one domain undermine subsequent self-control efforts in another domain. From the perspective of the brain, the processing resources from the same brain regions may be required for both tasks, and thus the brain is not starting fresh when moving from one task to another.

Such neuroscience findings may also help update our understanding of the relationship between automaticity and control more broadly. Similar to the implicit and explicit learning findings, in a number of the reviewed studies (Lieberman, in press), increasing activity in controlled processing regions was associated with decreased activity in automatic processing regions such as the amygdala. For instance, looking at an emotional picture nonreflectively leads to reliable amygdala activity. However, labeling the emotional content of the same picture reflectively leads to reliable right ventrolateral PFC activity and correlated decreases in amygdala activity. From the typical view of automaticity, it is difficult to explain how amygdala activity in response to an emotional picture would be diminished by the addition of a conscious reflective process. The amygdala response occurs when such pictures are presented subliminally (Morris et al., 1998; Whalen et al., 1998), a gold standard for automaticity. Automatic processes are believed not to rely on the common pool of controlled processes resources; thus, conscious reflective processing should not take away any resources that the amygdala needs to respond. Additionally, by definition, automatic processes that can be triggered without one's intentions (e.g., through subliminal presentations) are believed to be immune to interruption from conscious processing. Finally, the controlled process in question directs attention to the emotional aspects of the stimulus and thus is unlikely to reduce amygdala activity through distraction effects.

Although difficult to explain from a social cognition perspective, from a cognitive neuroscience perspective, these results are quite amenable to explanation. There are brain regions that, independent of one another, show evidence of possessing the operating characteristics of automatic or controlled processes, as commonly defined. However, these brain regions are also interconnected in a multitude of ways, including functionally inhibitory connections. In other words, the amygdala may process emotional inputs in an automatic fashion that requires no controlled processing resources to operate; however, the amygdala may also be anatomically linked with regions of the prefrontal cortex that can inhibit the amygdala's functioning if they are activated. Although such results do not in themselves demand a rewriting of all the rules of automaticity and control, they do suggest aspects that are worth reconsidering and testing as this new channel of data becomes available.

Internal and External Self-Focus

The mirror self-recognition test (Gallup, 1970) is used to test whether a particular species possesses self-awareness. Consequently, it is rather surprising that the network of brain regions involved in recognizing oneself in a picture and the network of brain regions involved in reflecting on one's feelings, preferences, and traits are completely nonoverlapping networks (Lieberman, 2007). External self-focus (i.e., visual self-recognition) is reliably associated with a lateral frontoparietal network in the right hemisphere, whereas internal self-focus (i.e., reflecting on one's psychological characteristics) is reliably associated with a medial frontoparietal network. What's more, the activity in these two networks at rest tend to be inversely correlated with one another (Fox et al., 2005). This separation of the neural networks supporting internal and external self-focus calls into question whether the mirror self-awareness test is actually an index of the ability to reflect on the psychological aspects of oneself or is limited to an ability to recognize the physical manifestations of oneself, perhaps a precursor to, rather than evidence of, true self-awareness.

Potentially the greatest implication of this dissociation is that it may help explain why nearly all human beings maintain some intuitive belief in mind–body dualism, even when rationally admitting that dualism is a nonstarter logically (Lieberman, 2009a). Although the broad strokes of Descartes' brand of dualism focused on the existence of two strata—the material and the immaterial, the impact of dualism largely follows from imputing material and immaterial aspects to each individual (i.e., mind and body). Part of the reason that this discredited theory is so compelling is that everyone has experiences that feel like a struggle between two aspects of the self. When we "drag ourselves out of bed," this fits nicely with the notion that there is a mind that somehow forces the unwilling body out of bed.

However, the clean division between the brain regions involved in internal self-focus (i.e., focusing on one's mind) and external self-focus (i.e., focusing on one's body) suggests that mind–body dualism may be a particularly sticky notion because our brain cleaves our perceptions of ourselves into these components whether we ask our brain to or not. Just as sights and sounds are automatically processed by separate neural networks and give rise to irreducibly distinct sensations, perhaps the separate processing streams for reflecting on one's own mind and body produce the irreducible experience of dualism.

Future Questions

Expected or unexpected convergences and dissociations in the brain regions responsible for particular social processes help group these processes into the appropriate psychological bins. Neuroscience techniques allow for other kinds of insights and hypothesis testing as well, although at this point, very little of this work has been done. For instance, as cognitive neuroscientists refine their understanding of the basic computations performed by different regions, activation in different networks can serve as an indicator that certain psychological processes have been invoked (c.f. Poldrack, 2006). This is not to suggest that we will be able to look at the brain and know whether someone is reading Haruki Murakami or Italo Calvino anytime soon, but we may be able to have some idea of whether a person is at least recruiting self-processes in a very general way, which would be useful.

Starting in the 1970s, a variety of self-serving or egocentric biases were reported on. For instance, people who live together each tend to believe they are responsible for a disproportionate amount of the housework that gets done (Ross & Sicoly, 1975). Similarly, after being asked if they would walk around wearing a giant sign saying "Eat at Joe's" for a small payment, regardless of the choice they made, subjects tended to believe most other people would make the same choice as they did (Ross et al., 1977). Rival accounts of these self-serving biases (Greenwald, 1980; Nisbett & Ross, 1980) led to countless studies attempting to show whether these effects were due to motivational processes intended to justify a person's own behavior and positions or were due to cognitive processes that tended to be biased as a result of the structure of information processing and the information sample available for consideration (e.g., a person is aware of all the housework done by oneself but only a portion done by a roommate). Because studies often provided positive evidence for their position without providing evidence against the alternative account, the debate eventually lost steam and was believed by many to be irresolvable (Tetlock & Levi, 1982). If neuroimaging can assess the extent to which self-related or motivational processes are at work, it should be possible to fruitfully revisit this debate. In all likelihood, both motivational and cognitive processes can contribute to these effects, but neuroimaging might reveal individual differences in the source of these biases across individuals, which in turn might relate to different psychological consequences (e.g., resistance to being challenged).

In the 1990s, research on automatic goals, motives, and behavior was (and continues to be) enormously influential (Dijksterhuis & Bargh, 2001). The fact that priming "impression" leads people to act as if they have an impression formation goal (Chartrand & Bargh, 1996), that priming "succeed" can produce an array of motivational phenomena (Bargh, Gollwitzer, Lee-Chai, Barndollar, & Trötschel, 2001), and that priming "elderly" can lead people to walk more slowly (Bargh, Chen, & Burrows, 1996) are extraordinary findings. Nevertheless, it is unclear from these findings alone whether automatic and nonautomatic variants of these processes are in fact one and the same. The assumption within this literature is that they are the same, but this has remained an assumption. Neuroimaging may be relatively uniquely positioned to address this question because it can clearly show whether two putative processes are relying on common or distinct neural networks.

Automatic goals, motives, and behaviors fall into the broader category of phenomena that are real but seem a bit magical. There are other linkages that always seem a bit magical as well, such as the functioning of placebo effects, hypnosis, and the impact of social support on health (after controlling for specific health care provided by supporters). In each of these cases, it's hard to tell a straightforward compelling story about why the phenomena occur because each is at odds with our basic dualistic notions that beliefs can change beliefs and overt behavior but beliefs cannot change low-level perceptual or physiological responses (i.e., our more mechanistic processes). In each case, neuroimaging data are starting to reveal where in the brain the magic happens (Eisenberger, Taylor, Gable, Hilmert, & Lieberman, 2007; Kosslyn, Thompson, Costantini-Ferrando, Alpert, & Spiegel, 2000; Wager et al., 2004), and this will allow for further interrogation of these brain regions and how their neurocognitive function might produce the observed results. Neuroscience is hardly a cure-all, but these are the kinds of problems for which neuroscience methods may shed new light and prompt new programs of behavioral research.

V. CONCLUSIONS AND THE NEXT DECADE

This chapter has provided a history of social cognitive neuroscience, the neural landmarks that have been laid down for hypothesis testing in various domains of social psychology, and an exploration of the specific ways in which social cognitive neuroscience directly contributes to the mission of social psychology. Given the number of pages devoted to each of these sections, there is no denying that the emphasis of the past decade has been on brain mapping far more than hypothesis testing. This is not surprising, because for neuroimaging research, the hypothesis testing phase generally follows the brain mapping phase. But a more significant factor in the relative balance between brain mapping and hypothesis testing is that doing the kind of social cognitive neuroscience studies that ask and answer the questions of social psychology is hard, much harder than doing a brain mapping study to see what lights up. Indeed, making truly meaningful contributions to social psychology using any methodology is hard because our phenomena are counterintuitive, our subjects are moving targets trying to figure out the purpose of our experiments, and our experiments must recreate just the right ecologically valid experiences within ethically acceptable limits, while still assessing the appropriate dependent variables. All of this is made that much harder when subjects are essentially lying in coffin-like confinement, unable to move, unable to speak, and needing several repetitions of each trial type to extract detectable signals from the noise.

Social cognitive neuroscience studies that address social psychological questions will only be carried out to the extent that social psychologists want to ask those questions and make a commitment to conducting social cognitive neuroscience studies, either on their own or with collaborators. Cognitive neuroscientists who are interested in using social psychological paradigms to clarify what different brain regions do have every right to do so. They are pursuing their intellectual passion and they should. There is no reason why they should suddenly care about the enduring questions of social psychology anymore than social psychologists should suddenly care about the enduring issues in neuroscience.

It is incumbent upon social psychologists to make use of neuroscience for their own ends. And this is nothing new for social psychologists. In the 1970s, social psychology reinvented itself in large measure by co-opting the methods of cognitive psychology for its own purposes. Whether social psychologists choose to embrace the methods of neuroscience to pursue our mission is still an open question. Nevertheless, this alone will determine whether the next review of social cognitive neuroscience, a decade from now, will have a better balance between brain mapping studies and studies that move social psychology forward.

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