

Chapter 15

Social Neuroscience

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People have

through the adaptive capacities of the cortex, attained the levels of intelligence and the power of inhibition and control which are prerequisite for civilized society. The chief contributions of the cortex to social behavior may be summarized as follows: (1) It underlies all solutions of human problems, which are also social problems, and makes possible their preservation in language, customs, institutions, and inventions. (2) It enables each new generation to profit by the experience of others in learning this transmitted lore of civilization. (3) It establishes habits of response in the individual for social as well as for individual ends, inhibiting and modifying primitive self-seeking reflexes into activities which adjust the individual to the social as well as to the non-social environment. Socialized behavior is thus the supreme achievement of the cortex. (Allport, 1924, p. 31)

In arguably the first major textbook of social psychology, Allport (1924) chose to begin with an examination of the physiological basis of human behavior. It is scarcely surprising, therefore, that the topic of social neuroscience should stand with other research areas in any comprehensive coverage of social psychology. Yet, for most of the past century, relatively few social psychologists have emphasized its biological nature (with notable exceptions to be discussed shortly). Within the past decade or so, however, a biological revolution has taken place within many areas of psychological science, including social psychology, with an increasing emphasis on the use of neuroscience methods to understand human behavior. The field of neuroscience reflects the interdisciplinary effort to understand the structure, function, physiology, biology, biochemistry, and pathology of the nervous system. From a psychological perspective, however, the term *neuroscience* typically is used to refer primarily to the study of the brain. Of interest is how the brain gives rise to affect, cognition, and behavior.

Social neuroscience, a term first used by John Cacioppo and colleagues (e.g., Cacioppo & Berntson, 1992), is an emerging field that uses the methods of neuroscience to understand how the brain processes social information. It involves scholars from widely diverse areas (e.g., social and personality psychology, neuroscience, psychiatry, philosophy, anthropology, economics, sociology) working together to

understand fundamental questions about human social nature. The core challenge of social neuroscience is to elucidate the neural mechanisms that support social thought and behavior. From this perspective, just as there are dedicated brain mechanisms for breathing, seeing, and hearing, the brain has evolved specialized mechanisms for processing information about the social world, including the ability to know ourselves, to know how others respond to us, and to regulate our actions to co-exist with other members of society. The problems that are studied by social neuroscience have been of central interest to social psychologists for decades, but the methods and theories that are used reflect recent discoveries in neuroscience. Although in its infancy, there has been rapid progress in identifying the neural basis of many social behaviors (see Baron-Cohen, Lombardo & Tager-Flusberg, 2013; Harmon-Jones & Inzlicht, 2016; Stanley & Adolphs, 2013).

The goal of this chapter is to (a) sketch a brief history of the field of social neuroscience, (b) describe the major techniques—including their strengths and limitations—used to study the social brain, (c) discuss some of the brain regions and structures that are likely to be of greatest interests to social psychologists, and (d) explain why understanding the brain is important for understanding social minds and behaviors.

A Brief History of Social Neuroscience

Although the rise of the use of neuroscience methods has accelerated over the past decade or so, it is important to understand how it has, since the 1800s, permeated psychological thinking as we seek to understand how those methods can be useful for understanding social cognition and behavior.

The Intellectual Backdrop

By the beginning of the 20th century, anatomists had a reasonably good understanding of the basic structures of the brain. What was less clear, however, is how these structures worked to produce thought and behavior—much less how the brain created complex mental activities such as those associated with attitudes, prejudice, or love. One early attempt to map brain function to thought and behavior was phrenology. Phrenologists such as Franz Gall and Johann Spurzheim identified social constructs such as self-esteem as being reflected by enlargements on the skull (the area to feel for bumps in the skull indicating high self-esteem is just at the crown at the back of your head).

Although the theory that brain functions are associated with specific patterns of bumps on the skull is now discredited, the idea that discrete regions of the brain are specialized for different tasks was quite insightful. Early case histories of individuals with brain damage also provided considerable evidence for localized functions. For social and personality psychologists, the most important early case was that of Phineas Gage, a 25-year-old railroad foreman from New Hampshire who suffered extensive damage to his frontal lobes when a blast charge he was preparing accidentally ignited and propelled his tamping iron—an iron bar roughly one yard long and 3.2 inches in diameter that was used to prepare explosive charges—through his left cheekbone, into his brain, and out the top of his head. Physicians of the period were initially incredulous at the possibility that anyone could sustain such a massive trauma to the brain and survive, but Gage seemed otherwise unaffected by the blast, conversing casually with both his workers and his physician, John Harlow (Macmillan, 2000). Following this extraordinary accident, remarkable changes in Gage's personality and social behavior were noted. Formerly thought of as honest, reliable, and deliberate (Harlow, 1868), Gage was afterwards described as “gross, profane, coarse, and vulgar, to such a degree that his society was intolerable to decent people” (Anonymous, 1851; attributed to Harlow; see

Macmillan, 2000). Importantly, then, Gage's injuries produced specific social deficits without impairing other capacities, such as language or intelligence.

Although Phineas Gage was a notable example of how localized brain damage can cause social deficits, this case alone did not spur increased interest in the brain basis of social thought and behavior. Indeed, for the next hundred years, physicians and neuroscientists were more interested in how the brain supported sensory and cognitive functions such as memory, vision, motor planning, and language. In the latter 20th century, the question of how the brain produces the social mind finally resurfaced.

Renewed interest in the social brain originated, in part, from a few perceptive cognitive neuroscientists who noticed that the brain damage they were studying had interesting social implications. One such neuroscientist, Michael Gazzaniga, was studying “split brain” patients who had their corpus callosum (the connective tissue between the two brain hemispheres) severed to control their epilepsy thereby rendering the two hemispheres unable to communicate with each other. His work revealed that the sense of self, a question of deep interest to social psychologists, may be dependent on the left hemisphere where language is located (Gazzaniga, 1985). This was discovered by giving a command to a split brain patient's right hemisphere only. Upon showing the command “get up” to the right hemisphere, the split brain patient would rise out of his chair. Gazzaniga would then ask why he was getting up (knowing full well the reason was the command shown). Because language resides in the left hemisphere, the split brain would have to use his left hemisphere to answer the question—the hemisphere that did not see the command. Would the patient simply say, sensibly, “I don't know”? Gazzaniga found that, no matter what the command, the patient would make up a plausible (but incorrect) story. These studies revealed that the left hemisphere is important for developing a narrative story about ourselves and why we do what we do.

The integration between social psychology and cognitive neuroscience accelerated sharply around the turn of the 21st century, creating the new field of social neuroscience. Since that time, there has been an explosion of research linking specific brain areas with particular social behaviors and mental processes (for reviews, see Gazzaniga, 2009). We now know that there is some localization of function but that many different brain regions participate to produce behavior and mental activity (Adolphs, 2009; Lieberman, 2010). That is, although there is considerable support for the general idea of specialization, virtually every behavior involves the joint activity of many brain regions. This new understanding has been greatly accelerated by the use of new brain imaging methods.

The Major Techniques

Although a multitude of different methods to measure brain activity have been developed, they tend to group into three categories. The first category, including electroencephalography (EEG) and event-related potential (ERP), relies on measuring the electrical activity (and its associated magnetic consequences) in the brain. These methods are optimized for assessing the timing of brain activity (i.e., they are high in temporal resolution) but are limited in their ability to localize the origins of that brain activity (i.e., they are low in spatial resolution). The second category, including positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), is based on tracking blood flow (and its correlates) that accompanies neuronal activity. These methods are relatively high in spatial resolution, but because of the rather sluggish nature of blood flow, they are low in temporal resolution. Both of these categories passively measure brain activity. A third category of techniques are those that actively perturb brain activity to address causal questions about the roles brain areas play. Here, we describe some of the major techniques that are used

in social neuroscience and end the section with a brief discussion about future directions in neuroscience methods and the field's evolving understanding of best research practices.

Passive Imaging Methods: High Temporal Resolution

EEG was the first noninvasive method of brain mapping developed for humans. It is based on the principle that neural activity produces electrical potentials that can be recorded by electrodes placed on the scalp. Because EEGs register all brain activity, the signal is noisy, and it cannot provide information about specific changes in brain activity in response to a stimulus or cognitive task. This problem is remedied by using ERP. During ERP experiments, the trials are repeated numerous times, and the EEG signals following those trials are averaged together to create an average waveform of the brain's response to the experimental event. Perhaps the most important feature of ERP is that it provides a temporally precise record of brain activity. The use of ERP methods has provided psychologists with insights into a number of important social behaviors, including identifying unique patterns that are associated with perceiving members of an outgroup, at least for those who score high on measures of racial prejudice (Ito, Thompson, & Cacioppo, 2004). An excellent review of social neuroscience findings using ERP describes the method as being useful for understanding person perception, stereotyping, attitudes and evaluative processes, and self-regulation (Bartholow & Amodio, 2009). Most recently, electrocorticography (ECoG) or intracranial EEG is allowing social neuroscientists to record electrical activity by implanting electrodes directly on the exposed brain tissue of patients. While the technology is the same, these "depth electrodes" provide a much stronger signal because they are close to the actual neurons rather than recording neural activity through the skull.

A technique related to EEG but with increased spatial resolution is magnetoencephalography (MEG), which measures magnetic fields that are produced by the electrical activity of the brain. Unlike EEG, MEG does not require electrodes but rather uses special sensors that detect magnetic fields. MEG has the same temporal resolution as EEG, but because magnetic signals are not distorted by the skull, as are EEG signals, its signal localization is considerably better. In a study of the effects of social exclusion on self-control failure using MEG, Campbell et al. (2006) found that social exclusion affected frontal lobe regions typically involved in executive control of attention.

Passive Imaging Methods: High Spatial Resolution

Brain activity is not only associated with the electrical activity of neurons but also with associated changes in metabolic processes. Brain imaging methods track these changes to understand which areas of the brain are most active for a given task. PET, the first imaging method developed, involves injecting a relatively harmless radioactive substance into the blood stream. Using a PET scanner, researchers can then track this radiation as blood travels through the brain, resulting in a map of brain activity in three-dimensional space. The resulting image identifies the neural structures engaged in specific cognitive tasks. PET has one major disadvantage: The use of radioactive substances places an inherent limitation on the number of trials that can be used and, accordingly, tends to yield studies with low statistical power. Moreover, it can take a long time to image the entire brain, and so trials themselves need to last for an extended period. For reasons of safety as well as the ability to use many more trials, most current brain imaging is conducted using fMRI, to which we now turn.

Similar to PET, fMRI measures brain activity by tracking metabolism associated with blood flow, but it does so noninvasively (i.e., nothing is injected into the blood stream). Thus, a single fMRI study can contain hundreds of trials, thereby greatly enhancing the power of the study. Functional MRI does not

measure blood flow directly. Rather, fMRI employs a strong magnetic field to assess changes in the blood-oxygen level dependent (BOLD) response at particular cortical sites after they have become active, which is an indirect measure of blood flow. Specifically, the BOLD signal is derived from the ratio of oxygenated to deoxygenated blood at cortical locations throughout the brain.

Active Manipulation Techniques

It is commonly known that functional neuroimaging data only suggest brain regions that may be engaged during a given behavior; correlations between behavior and localized brain activity cannot establish a causal brain-behavior linkage. One way to address such a hypothesis would be to conduct a lesion study in which specific brain regions were damaged while leaving other areas relatively intact. Ethics committees, however, tend not to encourage lesioning our undergraduate research participants. Fortunately, transcranial magnetic stimulation (TMS) allows for the temporary experimental disruption of neural activity in relatively circumscribed cortical regions while individuals engage in a cognitive task (Jahanshahi & Rothwell, 2000; Walsh & Cowey, 2000; Wig, Grafton, Demos, & Kelley, 2005). During TMS, a powerful electrical current flows through a wire coil that is placed on the scalp over the area to be stimulated. As electrical current flows through the coil, a powerful magnetic field is produced that interferes with neural function in specific regions of the brain. If multiple pulses of TMS are given over extended time (known as repeated TMS), the disruption can carry over beyond the period of direct stimulation. Studies using TMS to create a virtual lesion in the superior temporal sulcus (STS) have demonstrated interference in the perception of eye gaze direction (Pourtois et al., 2004), reduced accuracy in detecting biological motion from point light displays (Grossman, Battelli, & Pascual-Leone, 2005), and interference with processing facial expressions indicating anger (Harmer, Thilo, Rothwell, & Goodwin, 2001). By selectively disrupting the function of a brain region with TMS, scientists can make causal conclusions about whether and, if so, how these regions play a role in a given thought process or behavior.

Transcranial direct current stimulation (tDCS) also manipulates brain activity, but in a less invasive way than TMS. Rather than disabling a region with a strong magnetic pulse, tDCS applies weak electrical currents to the scalp to excite neural activity. By applying tDCS over a specific region associated with a particular behavioral response, researchers can increase the likelihood of that response. In social neuroscience, tDCS has been used to modulate a person's mood and emotion, the ability to perceive others' emotions, empathize, and make decisions (for a review, see Boggio et al., 2016). Recently, Maréchal, Cohn, Ugazio, and Ruff (2017) reported that stimulating the dorsolateral prefrontal cortex, a region associated with self-regulation, made participants more likely to act honestly even if doing so was contrary to their financial self-interest. Although promising as a method to influence social thought and behavior, the relative newness of tDCS mean that the limits and long-term consequences are as yet unknown.

Future Advances and Best Practices

Every year, new advances in hardware and analytical tools get us closer to maximizing both spatial and temporal resolution. Furthermore, teams of researchers are working hard to make neuroimaging more portable and conducive to studying the kind of behavior that social psychologists care about. At present, most techniques require participants to sit or lie motionless while being scanned, with even a couple of millimeters of head motion rendering data unusable. However, newer techniques such as functional near-infrared spectroscopy (fNIRS) provide fMRI-like images of brain activity while allowing participants

to move and speak, albeit with reduced spatial resolution. Every year, neuroscientists and physicists are working toward better tools that will allow us to study the neural basis of social behavior with better technical precision and in more ecologically valid ways.

Besides technological advances, the field is also invested in establishing best practices for data collection and analysis. Most imaging methods are necessarily correlational and therefore prone to all the inherent limitations of correlational methods (see Vul, Harris, Winkielman, & Pashler, 2009). The advent of tools such as TMS and tDCS allow for some causal validation, but transcranial stimulation is limited to cortical areas near the skull and therefore can only have an indirect effect on mental processes that involve deeper structures. Assessing patients who have brain injury can provide complementary evidence for the causal involvement of a brain region for a given psychological function. Understanding how the brain gives rise to the social mind, therefore, requires integrating multiple sources of data rather than relying on data from a single technique or paradigm.

A deep understanding of mind and brain also relies on research practices that maximize the reliability of that data. Like other scientific disciplines, the field of social neuroscience is undergoing a sea change spurred by questions of replicability. In public discussion and private implementation, better practices for the collection and analysis of data are being established to increase confidence in findings reported. In the recent past, fMRI studies could be published with very few participants—a research practice driven by the high hourly costs of using fMRI. Now, studies must be adequately powered, requiring many more participants. Furthermore, new statistical understanding has led to better practices of how data are analyzed to avoid bias including separating data into training and testing samples and preregistering the proposed analyses.

A more conceptual concern is the difficulty in localizing specific psychological functions to discrete brain regions. There have now been several thousand imaging studies of a variety of psychological functions. It is now clear that many brain regions are activated across numerous cognitive and social tasks (Mitchell, 2009; Ochsner, 2007). Thus, when a researcher finds a particular activation in an imaging study, it is not always obvious what that activation indicates. An area may be activated across a broad array of disparate cognitive tasks because those different tasks share some common psychological process (i.e., semantic processing, memory, selecting among competing stimuli). In these cases, the activation may have little to do with the research question of greatest interest to the investigator. As in all areas of science, the value of any one imaging study depends on the care with which the experimental tasks are designed, and deep advances in our understanding about human thought and behavior will be achieved in the aggregate, across many studies and approaches. With that in mind, what is our best understanding to date about how the brain supports social thought and behavior?

Building a Social Brain

How do you build a social brain? Or what does the brain need to do to allow it to be social? In this section, we describe a conceptual framework for understanding the social brain. The overarching assumption is that the brain evolved over millions of years as an organ that solves adaptive problems, which, for humans, are frequently social in nature. Early human ancestors needed to recognize faces of friends and foes, identify potential mates and evaluate them in terms of desirability, understand the nature of group relations, and so on. Humans evolved a fundamental need to belong, which encourages behavior that facilitates cohesive groups (Baumeister & Leary, 1995; Bowlby, 1969). Effective groups shared food, provided mates, and helped care for offspring. As such, human survival has long depended on living within groups; banishment from the group was effectively a death sentence. Baumeister and Leary (1995) argued that the

need to belong is a basic motive that activates behavior and influences cognition and emotion and that it leads to ill effects when not satisfied. Indeed, even today, not belonging to a group increases a person's risk for a number of adverse consequences, such as illnesses and premature death (Cacioppo, Hughes, Waite, Hawkley, & Thisted, 2006).

Initial findings using neuroimaging revealed that some neural regions appear to be associated with processing social information as compared to general semantic knowledge. For instance, Mitchell, Heatherton, and Macrae (2002) showed that when participants make judgments about whether a word describes a person (e.g., assertive, fickle) or an object such as fruit (e.g., sundried, seedless), various brain regions, particularly the medial prefrontal cortex (mPFC), were associated more with person judgments. Similarly, Mason, Banfield, and Macrae (2004) found that when participants made judgments about whether an action (e.g., running, sitting, biting) could be performed by a person or a dog, the mPFC was once again associated with judgments about people. Thus, the brain seems to treat other humans as a special class of stimuli. Here, we examine the implications of that notion.

The Building Blocks of the Social Brain

Converging evidence suggests that the human brain comes hardwired to find other humans interesting. Within 48 hours of life, newborns attend more to faces than any other objects, listen longer to human voices than other sounds, and gaze longer at upright versus upside-down displays of biological motion (Goren, Sarty, & Wu, 1975; Johnson, Dziurawiec, Ellis, & Morton, 1991; Simion, Regolin, & Bulf, 2008; Vouloumanos & Werker, 2007). Since babies lack knowledge about the world, this initial interest in other beings is likely driven by simple, perceptual cues. Indeed, two dots and a line are enough to grab an infant's attention but only if those shapes are presented in the configuration of a face: two dots for eyes and a line for nose (Goren, Sarty, & Wu, 1975). However primitive, having an innate set of "life detectors" affords two important benefits. First, it increases the chance of survival by ensuring that infants detect those who are likely to feed, protect, or eat them. The second, perhaps less obvious, benefit is that cleaving the world into animate and inanimate halves establishes a foundation upon which social thought can be built (Wheatley, Milleville, & Martin, 2007).

The layering of social understanding upon a framework of animacy is demonstrated across child development. By 5 months of age, infants infer goal-directedness in a moving human hand but not a moving rod (Woodward, 1998) and, by 18 months, attribute intentions to human actors but not machines (Meltzoff, 1995). Thus, early on, we impute thoughts, feelings, and actions only to the subset of the world that can think, feel, and act in return. In this way, the initial step of detecting life conserves precious cognitive energy—a finite resource that people are loathe to expend (Fiske & Taylor, 1991). Detecting animacy avoids such effort-wasting missteps as greeting doors or wondering why the lamp is such a poor conversationalist. Evidence from neuroscience suggests that these early "life detectors" are housed in two regions of the temporal lobe: ventral temporal cortex for the detection of human form (faces, bodies) and lateral temporal cortex for the detection of human dynamics (sound, motion).

Detecting Faces

Faces pack a wealth of information into a relatively small space. People are such experts at recognizing faces that they can effortlessly pick out their relatives in a crowd, evaluate people as potential mates, and understand that the two categories are independent. Given the importance of faces to daily life, it has been suggested that face perception and recognition hold a privileged status in the human brain. Indeed, one of the most robust findings in social neuroscience is that viewing faces activates a section of cortex

more than any other kind of stimuli including nonface objects, scrambled faces, and inverted faces (Ishai, Ungerleider, Martin, Maisog, & Haxby, 1997; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997). This region is located bilaterally (one per hemisphere) on the underside of the human brain and is dubbed the fusiform face area (FFA). Among faces, this region is particularly responsive to human faces compared to visually matched doll faces, suggesting a sensitivity to faces that appear to have minds attached (Looser, Guntupalli, & Wheatley, 2012; Wheatley, Weinberg, Looser, Moran, & Hajcak, 2011). Lesions to the FFA can create prosopagnosia: the selective inability to recognize the identity of faces (Duchaine & Nakayama, 2005; Tranel, Damasio, & Damasio, 1998).

The structural properties of a face not only provide the identity of a person but also the raw material for attraction. In one study, subjects were asked to report the gender of various faces while lying in an fMRI scanner. Although subjects were not judging attractiveness at the time, blood-flow activity in orbitofrontal cortex (OFC) correlated with subjects' later ratings of the attractiveness of those faces. OFC, a region associated with the evaluation of reward, was activated more by faces later deemed attractive relative to faces deemed unattractive (O'Doherty et al., 2003). As one might predict, sexual preference modulates this activity: Male faces evoked a greater response in this region for homosexual men and heterosexual women while female faces evoked a greater response for heterosexual men and homosexual women (Kranz & Ishai, 2006).

Other face-sensitive regions of cortex have been identified that may work in tandem with the FFA to support other percepts (what we perceive) and inferences based on the invariant features of a face (e.g., for a study on gender, see Kriegeskorte, Formisano, Sorger, & Goebel, 2007; for a study on trustworthiness, see Oosterhof & Toderov, 2008). However, the face is more than a collection of features; it also provides a canvas for facial expressions that convey transitory emotional and mental states. Reading facial expressions, along with other dynamic cues such as gestures and voice intonation, relies on a different region of temporal cortex right above the ears.

Detecting Speech and Motion

The overwhelming majority of research on facial identity and expressions employs static photographs. However, faces and bodies are in a perpetual state of motion that must be detected rapidly and decoded for biologically relevant meaning (e.g., intent to harm). A useful method of showing how people can extract social information through movement was discovered by Johansson (1973) who attached small lights to the joints of actors and filmed them in a dark room. A static snapshot of this stimulus looks like a random series of dots, but in motion the dots are immediately recognizable as biological motion. Such "point light" stimuli have been used with great effect to show that movement alone can convey gender, emotion, even personality (Atkinson, Dittrich, Gemmell, & Young, 2004; Clarke, Bradshaw, Field, Hampson, & Rose, 2005; Heberlein, Adolphs, Tranel, & Damasio, 2004; Pollick, Lestou, Ryu, & Cho, 2002). Dynamic stimuli such as these are processed by a neural pathway distinct from that used to process structural facial features: the STS (Allison, Puce, & McCarthy, 2000; Beauchamp, Lee, Haxby, & Martin, 2002; Grossman et al., 2005; Haxby, Hoffman, & Gobbini, 2000). Consistent with a layering of social understanding upon the detection of biological motion, fMRI studies have revealed that the STS in adult subjects is particularly tuned to motion that expresses social meaning, such as intentional actions and emotional gestures (Pelphrey, Morris, & McCarthy, 2004). And those with compromised functioning in this brain region (e.g., those with autism) are less accurate at identifying the emotion expressed in movement by point light videos in which actors move around "angrily" or "happily" in a dark room with only small lights visible that are attached to their joints (Dakin & Frith, 2005).

The STS is adjacent to that supporting the detection of biological sound. Several studies have shown that the superior temporal gyrus is activated by the sound of other human beings relative to similarly

complex nonspeech sounds and underpins the ability to understand emotion in tone of voice (Beaucousin et al., 2007; von Kriegstein & Giraud, 2004). In normal daily life, the ability to hear emotion in a person's voice is taken for granted, but losing that ability (aprosodia) can have devastating social consequences. A recent meta-analysis found that schizophrenia patients were more than one standard deviation below the mean of healthy controls in recognizing tone of voice cues to emotion. The impairment was so large that the authors concluded it "was one of the most pervasive disturbances in schizophrenia that may contribute to social isolation" (Hoekert et al., 2007). In sum, the superior temporal cortex appears to be particularly attuned to the detection of human voice and movement and instrumental in decoding the many dynamic configurations of social meanings.

The specialized regions of cortex for the detection and understanding of human faces, voice, and motion are highly interconnected not only with each other but as nodes within larger, interacting circuits that support the full breadth of social understanding including self-identity, ability to empathize, and the regulation of our behavior in accordance with social norms. We now discuss a conceptual model of the neural basis of such components.

Components of the Social Brain

Given the fundamental need to belong, there needs to be a social brain system that monitors for signs of social inclusion/exclusion and alters behavior to forestall rejection or resolve other social problems (Krendl & Heatherton, 2009). Such a system requires four components, each of which is likely to have a discrete neural signature. First, people need self-awareness—to be aware of their behavior so as to gauge it against societal or group norms. Second, people need to understand how others are reacting to their behavior so as to predict how others will respond to them. In other words, they need "theory of mind" (ToM) or the capacity to attribute mental states to others. This implies the need for a third mechanism, which detects threat, especially in complex situations. Finally, there needs to be a self-regulatory mechanism for resolving discrepancies between self-knowledge and social expectations or norms, thereby motivating behavior to resolve any conflict that exists.

This does not mean that other psychological processes are unimportant for social functioning. Indeed, capacities such as language, memory, and vision, along with motivational and basic emotional states, are generally important for functioning within the social group. However, fully intact neural circuits underlying memory and vision, for example, are not necessary for being a good group member. By contrast, people with fundamental disturbances in the primary components of self, ToM, threat detection, or self-regulation have profound and often specific impairments in social function. Recall the case of Phineas Gage who had severe social impairments while having most of his mental facilities intact.

Unlike many other aspects of cognition, almost everything we know about the social brain has been uncovered in the last couple of decades. Fortunately, the emergence of social neuroscience has been both rapid and far-reaching, and thus, despite its infancy, this approach has already netted a substantial number of reliable empirical findings about how the brain gives rise to human sociality.

Component 1: Self Awareness

Survival in human social groups requires people to monitor their behavior and thoughts to assess whether those thoughts and behaviors are in keeping with prevailing group (social) norms. According to Baumeister (1998), "the capacity of the human organism to be conscious of itself is a distinguishing feature and is vital to selfhood" (p. 683). The topic of self may be among the most near and dear to social and personality psychologists. In social neuroscience, the study of self-reflection has provided one of the best examples

of how neuroimaging might be especially useful as a tool to resolve theoretical debates when traditional behavioral methods are unable to do so. This section uses this example to demonstrate how neuroscience was able to resolve the age-old debate about whether the self is "special."

In the 1980s, a major debate in social psychology was whether information processed about the self is treated separately from other types of information or in the same manner (Bower & Gilligan, 1979; Klein & Kihlstrom, 1986; Klein & Loftus, 1988; Maki & McCaul, 1985; Markus, 1977). The first line of evidence in favor of the view that self is special emerged from the pioneering work of Tim Rogers and his colleagues (Rogers, Kuiper, & Kirker, 1977), who showed that when trait adjectives (e.g., happy) were processed with reference to the self (e.g., "Does happy describe you?"), subsequent memory performance was better than when the items were processed only for their general meaning (e.g., "Does happy mean the same as optimistic?"). This self-referential effect in memory has been demonstrated many times (Symons & Johnson, 1997) and shows that information processed about the self is special. Indeed, even people who can remember very little can often remember information that is self-relevant. For instance, patients who suffer from severe amnesia (resulting from brain injury or developmental disorders) retain the ability to accurately describe whether specific traits are true of the self (Klein, 2004). Even patients with Alzheimer's disease who suffer severe temporal disorientation and have difficulty recognizing their own family have shown evidence of self-knowledge (Klein, Cosmides, & Costabile, 2003).

Other researchers argued that self plays no special or unique role in cognition but that the memory enhancement that accompanies self-referential processing can be interpreted as a standard depth-of-processing effect (Greenwald & Banaji, 1989; Klein & Kihlstrom, 1986). From this perspective, the self is quite ordinary; people remember things about themselves more because, as that information comes in, they attend to and think about that information more than they do for other things they care less about.

Research on this question eventually withered, in part because the opposing theories made identical behavioral predictions; namely, better memory for items that were processed in a self-referential manner. Herein lies the tremendous advantage of using brain imaging. Neuroimaging techniques are ideally suited for resolving debates for which competing theories make identical behavior predictions. An initial attempt to examine the neural substrates of the self-reference effect used PET. Unfortunately, as previously discussed there is a limit to the number of trials that can be presented using PET, and the researchers did not obtain a statistically significant self-reference effect (Craik et al., 1999). Nonetheless, their results were intriguing in that during self-reference processing trials they did find distinct activations in frontal regions, notably the mPFC and areas of right prefrontal cortex. Observing the statistical-power limitation of PET, Kelley et al. (2002) used event-related fMRI in an attempt to identify the neural signature of self-referential mental activity. In a standard self-reference paradigm, participants judged trait adjectives in one of three ways: self ("Does the trait describe you?"), other ("Does the trait describe George Bush?"), and case ("Is the trait presented in uppercase letters?"). These judgments produced the expected significant differences in subsequent memory performance (i.e., self > other > case).

More important, however, they enabled the researchers to test the competing explanations that have been offered for the self-reference effect in memory. Previous functional imaging studies have identified multiple regions within the left frontal cortex that are responsive when thinking deeply something being learned (Buckner, Kelley, & Petersen, 1999; Demb et al., 1995; Gabrieli et al., 1996; Kapur et al., 1996; Kelley et al., 1998; Wagner et al., 1998). Thus, if the self-reference effect simply reflects the operation of such a process, then one would expect to observe elevated levels of activation in these left frontal areas when traits are judged in relation to self. If, however, the effect results from the properties of a unique cognitive self, then one might expect self-referential mental activity to engage brain regions that are distinct from those involved in general semantic processing. The results

were clear: The left inferior frontal region, notable for its involvement in semantic processing tasks, did not discriminate between self and other trials. Instead, Kelley et al. (2002) observed selective activity in areas of prefrontal cortex, notably mPFC, suggesting that this region might be involved in the self-referential memory effect. In a later study, Macrae et al. (2004) demonstrated that activity in mPFC could predict whether a person would subsequently remember terms encoded with reference to self, providing more compelling evidence linking the activity in mPFC to self-memory processes. Thus, neuroimaging was able to resolve a social psychological debate about the self could not be resolved with behavioral methods alone.

Since these early studies, social neuroscience has made excellent strides in identifying brain regions that are involved in processing information about the self. For example, many neuroimaging studies have replicated the involvement of this mPFC region in tasks that require participants to judge their own personality traits (e.g., Heatherton et al., 2006; Johnson et al., 2002; Macrae, Moran, Heatherton, Banfield, & Kelley, 2004; Pfeifer, Lieberman, & Dapretto, 2007) or report on their preferences and opinions (Ames, Jenkins, Banaji, & Mitchell, 2008; Jenkins, Macrae, & Mitchell, 2008; Mitchell, Macrae, & Banaji, 2006), compared to judging these characteristics in others. Although the cognitive aspects of self-reflection involve mPFC, the emotional consequences of those responses (i.e., whether the response indicates positive or negative things about the rater) appear to be coded in the ventral anterior cingulate cortex, which is adjacent to mPFC (Moran et al., 2006). This area turns out to be important for interpersonal relations, which we discuss later in this chapter.

The issue of whether the self is somehow "special" remains somewhat contentious (see Gillihan & Farah, 2005), but the imaging literature is quite clear regarding tasks that involve self-awareness. They activate mPFC in imaging studies (Gusnard, 2005).

It is interesting to note that converging evidence from patient research also indicates that frontal lobe lesions, particularly to the mPFC and adjacent structures, have a deleterious effect on personality, mood, motivation, and self-awareness. Patients with frontal lobe lesions show dramatic deficits in recognizing their own limbs, engaging in self-reflection and introspection, and even reflecting on personal knowledge. Indeed, frontal lobe patients are particularly impaired in social emotions (Beer et al., 2003). Interestingly, damage to this region can lead to deficits in the organization of knowledge about one's preferences. Fellows and Farah (2007) have reported that, when asked to indicate their attitudes toward various stimuli, patients with mPFC lesions show unusually large discrepancies between testing sessions, suggesting that damage to this region leads either to failures to retrieve knowledge of one's attitudes or instability in otherwise stable aspects of selfhood.

It is important to be clear that there is no specific "self" spot of the brain, no single brain region that is responsible for all psychological processes related to self. Rather, psychological processes are distributed throughout the brain, with contributions from multiple subcomponents determining discrete mental activities that come together to give rise to the human sense of self (Turk, Heatherton, Macrae, Kelley, & Gazzaniga, 2003). Various cognitive, sensory, motor, somatosensory, and affective processes are essential to self, and these processes likely reflect the contribution of several cortical and subcortical regions.

The extent to which we include others in our self-concept has been a topic of particular interest for social psychologists. Theories of intimacy and personal relationships might suggest that the self-reference effect is affected by the closeness of a relationship with the other used as a target. Indeed, Aron and colleagues define closeness as the extension of self to incorporate the other (Aron & Aron, 1996; Aron & Fraley, 1999; Aron, Aron, Tudor, & Nelson, 1991). Consistent with this idea, recent research has found that the brain encodes friendship in terms of distance from self (Parkinson & Wheatley, 2014; Parkinson, Liu, & Wheatley, 2014) and that close friends have strikingly similar neural responses to a variety of stimuli from comedy to music videos (Parkinson, Kleinbaum, & Wheatley, 2018).

Component 2: Mentalizing

Perhaps the most important attribute of the social brain is the ability to infer the mental states of others to predict their actions (Amodio & Frith, 2006; Gallagher & Frith, 2003; Mitchell, 2006). The underlying assumption—that behavior is caused by mental states—has been called taking an “intentional stance,” ToM, and “mind perception” (Epley & Waytz, 2010), and the adoption of this assumption is an important developmental milestone. Testing whether young children possess ToM usually involves telling them stories in which false beliefs must be inferred. In one well-known example, a child is shown two dolls: Sally and Ann. Sally has a basket, and Ann has a box. The child watches as Sally puts a marble in the basket and leaves. While Sally is gone, “naughty” Ann takes the marble out of the basket and puts it in the box. Then Sally returns. The child is asked: “Where will Sally look for the marble?” The correct response requires understanding that Ann moved the marble *unbeknownst* to Sally and that Sally thus holds a false belief that the marble is still in the basket. Healthy and IQ-matched Down syndrome children succeed at this task around the age of four (Baron-Cohen, Leslie, & Frith, 1985). Before that time, children have difficulty grasping that a person can believe something decoupled from reality.

It is perhaps not surprising that patients with impoverished social relationships do poorly on ToM tasks. Four-year-old autistic children have a failure rate of 80% on the Sally–Ann task (Baron-Cohen, Leslie, & Frith, 1985). If the task requires the added difficulty of understanding what a person thinks about *another* person's beliefs or thoughts (i.e., second-order mental state attribution), the failure rate in autistic individuals is even higher (Baron-Cohen, 1989). Difficulty representing another's thoughts is a hallmark of autism that endures throughout the lifespan. Research with patients and healthy adults has converged on two brain areas that are consistently modulated by tasks requiring the inference of mental states: the temporal parietal junction (TPJ) and the mPFC though additional areas may also be recruited depending on the task (Molenberghs, Johnson, Henry, & Mattingley, 2016). Healthy adult volunteers recruit these areas when inferring mental states from expressions in photographs, attributing mental states to animations of geometric shapes, and imputing mental states to characters in cartoons and stories (Frith & Frith, 1999; Molenberghs et al., 2016).

TPJ. An early social psychological study by Heider and Simmel (1944) showed our proclivity to infer social meaning from motion. In this seminal study, subjects spontaneously inferred intent, emotion, gender, and even personality in simple animations of interacting geometric shapes. Subsequent research demonstrated that various types of human motion express emotional, motivational, and intentional states (e.g., communicative gestures, gaze shifts) and that these motions have been associated with activity in the superior temporal sulcus extending into the TPJ (Castelli, Happe, & Frith, 2002; Haxby et al., 2000; Martin & Weisberg, 2003). Some researchers have speculated that there are adjacent but distinct areas within this region of cortex that support related but dissociable functions, such as the recognition of biological motion, recognition of mental states from motion cues, and the ability to mentalize regardless of whether motion cues are present. The last ability appears to be associated primarily with the TPJ, which has been implicated in perspective-taking (Saxe & Powell, 2006) as well as how we perceive our own body in space. TMS disruption to this region produces impairments in the ability to imagine how one's body looks from another's perspective (Blanke et al., 2005). Thus, this region appears to facilitate the ability to contemplate different spatial and mental perspectives from one's own (Saxe & Kanwisher, 2003; Mitchell, 2008). Consistent with the developmental trajectory mentioned earlier, the maturation of white matter tracts between TPJ and prefrontal cortex predicts the development of ToM in early childhood (Weismann et al., 2017).

Medial prefrontal cortex. The second area that is consistently activated by mentalizing is the mPFC, although typically a region of this brain structure slightly higher than observed for self-referential processing. Activity in this region has been associated with the perception of pain and tickling, as

well as autobiographical memory and aesthetic judgment. Across these seemingly disparate studies, a common denominator has emerged: mPFC appears to support the ability to *attend* to the mental states that give rise to experience. That is, to create an explicit representation of what one thinks or feels *about* X. Recent research suggests that this area is also important for taking the perspective of another person (i.e., “How would you feel if you were person X”). This suggests that being able to represent our own subjective experience plays a central role in the ability to understand the subjective experience of others (Jenkins, Macrae, & Mitchell, 2008; Mitchell, Banaji, & Macrae, 2005; Mitchell, Heatherton, & Macrae, 2002).

Mentalizing allows us to infer the intentions of others, thereby learning about their likely future behavior. For this reason, social neuroscientists studying morality are particularly interested in the brain processes that allow us to reason about another's mental states, such as whether an act was committed intentionally or unintentionally (Decety & Wheatley, 2015). Although the act committed may have been the same, the state of another's mind allows us to predict the likelihood of it happening again and thus whether a person that committed a crime is an ongoing threat.

Component 3: Detection of Threat

One value of having ToM is that it supports a third mechanism, threat detection, which is particularly useful in complex situations such as dealing with ingroup or outgroup members (i.e., with members of their own group or members of other groups).

Ingroup threats. If humans have a fundamental need to belong, then there ought to be mechanisms for detecting inclusionary status (Leary, Tambor, Terdal, & Downs, 1995; Macdonald & Leary, 2005). Put another way, given the importance of group inclusion, humans need to be sensitive to signs that the group might exclude them. Indeed, there is evidence that people feel anxious when they face exclusion from their social groups (Baumeister & Tice, 1988). Thus, feeling socially anxious or worrying about potential rejection should lead to heightened social sensitivity. Indeed, research has demonstrated that people who worry most about social evaluation (i.e., the shy and lonely) show enhanced memory for social information, are more empathetically accurate, and show heightened abilities to decode social information (Gardner, Pickett, & Brewer, 2000; Gardner, Pickett, Jefferis, & Knowles, 2005; Pickett, Gardner, & Knowles, 2004).

Social psychologists have documented the pernicious effects of interpersonal rejection threat on mood, behavior, and cognition (Smart & Leary, 2009). Most prominent is a study by Eisenberger, Lieberman, and Williams (2003) who found that the dorsal region of the anterior cingulate cortex was responsive during a video game designed to elicit feelings of social rejection when virtual interaction partners suddenly and surprisingly stopped cooperating with the research participant. Since this initial study, other studies have also implicated the anterior cingulate cortex, although some of them find a more ventral (lower) rather than dorsal (higher) region (Somerville, Heatherton, & Kelley, 2006). Adolescence may be a particularly sensitive period for social evaluation (Masten et al., 2009; Somerville, 2013). Within adolescents, greater self-reported susceptibility to peer influence was associated with greater activity in the ventral anterior cingulate cortex during social rejection (Sebastian, Viding, Williams, & Blakemore, 2010).

Outgroup threats. Not all threats, however, are related to social exclusion. Just as people naturally fear dangerous animals (e.g., poisonous snakes and spiders, tigers, wolves), they also face harm from other humans who might like to harm them. Indeed, other group members can transmit disease, act carelessly and place bystanders at risk, waste or steal vital group resources, or poach one's mate. Similarly, people from other groups also can be dangerous when competition for scarce resources leads to intergroup violence. Hence, there is also a need for mechanisms that detect threats from outgroup members.

The most common area identified as relevant to threat from outgroup members is the amygdala. In perhaps the first social neuroscience study that used functional neuroimaging, cognitive neuroscientist

Elizabeth Phelps, social psychologist Mahzarin Banaji, and their colleagues used fMRI to study racial attitudes. They showed White college students pictures of unfamiliar Black and White faces while they scanned brain activity (Phelps et al., 2000). For those subjects who score high on an implicit measure of racial bias (see Chapter 12), the unfamiliar Black faces activated the amygdala, a brain structure that is involved in fear response and recognition (Whalen, 1998; Whalen & Phelps, 2009). It is important to note that the amygdala is only one of several neural areas engaged during the evaluation of an outgroup member. Interestingly, emerging research from neuroimaging has revealed that areas of the prefrontal cortex involved in cognitive control are also engaged in these tasks. For instance, Cunningham et al. (2004) showed that the amygdala responded to pictures of Black faces when presented very quickly (30 ms). However, when the faces were presented for a longer duration (525 ms), the amygdala response was dampened and instead increased activation was observed in the prefrontal cortex. The authors argued that the heightened activation in the prefrontal cortex may have been inhibiting the automatic response elicited by the amygdala.

People who possess stigmatizing conditions that make them seem less than human, such as the homeless, also activate regions of the amygdala (Harris & Fiske, 2006), as do the physically unattractive and people with multiple facial piercings (Krendl, Macrae, Kelley, Fugelsang, & Heatherton, 2006). Considered together, it is clear that evaluating outgroup members—particularly those whom may pose a physical threat—involves activity of the amygdala. So, what function does the amygdala serve in the social context? It has long been thought to play a special role in responding to stimuli that elicit fear (Blanchard & Blanchard, 1972; Feldman Barrett & Wager, 2006; LeDoux, 1996). From this perspective, affective processing in the amygdala is a hard-wired circuit that has developed over the course of evolution to detect biologically relevant stimuli (e.g., threats to survival). But, like any other brain region, the amygdala is multifaceted with multiple subparts and different roles. Although one role is to detect threat, another is to detect who may need our help. People with psychopathy—who tend to be low in empathy and relatively insensitive to danger—tend to have smaller amygdalae on average compared to healthy controls, and their amygdalae are less responsive to signals of distress in others (e.g., fearful facial expressions). In contrast, extraordinary altruists such as people who donate one of their kidneys to a stranger tend to have larger amygdalae that are more responsive to signals of distress (Marsh et al., 2014). How brain areas such as the amygdala keep us safe from physical and social threats while also inciting us to safeguard others from these threats is an ongoing and vibrant area of research.

Component 4: Self-Regulation

A unique aspect of human behavior is the ability to regulate and control thoughts and actions, an ability commonly referred to as self-regulation. Self-regulation allows people to make plans, choose from alternatives, focus attention on pursuit of goals, inhibit competing thoughts, and regulate social behavior (Baumeister, Heatherton, & Tice, 1994; Baumeister & Vohs, 2004; Metcalfe & Mischel, 1999; Wegner, 1994). Extensive evidence from neuroimaging and patient research demonstrates that the prefrontal cortex is imperative in successfully engaging self-regulatory processes, as befitting its label as “chief executive” of the brain (Goldberg, 2001). Abundant patient and neuroimaging research has identified discrete brain regions within prefrontal cortex that are critical for self-regulation (for reviews, see Heatherton & Wagner, 2011; Ochsner, Silvers, & Buhle, 2012): primarily, the lateral prefrontal cortex (involved in inhibition), the OFC (involved in regulating primary physiological drives), and the ACC (involved in conflict resolution).

The lateral prefrontal cortex is associated with planning, choice, the control of memory and working memory, and language function (see D’Esposito et al., 1995; Dronkers, Redfern, & Knight, 2000; Fuster, Brodner, & Kroger, 2000; Goldman-Rakic, 1987). Damage to this area often results in patients’ experiencing an inability to inhibit unwanted thoughts and behaviors (Pandya & Barnes, 1987). Damage to the OFC,

which controls our behavioral and emotional output and how we interact with others (Dolan, 1999), often results in striking behavioral changes, including increased aggression (e.g., Rolls, Hornak, Wade, & McGrath, 1994). It is also linked to personality changes such as indifference, impaired social judgment and responsiveness, poor self-regulation, lack of impulse control, and poor judgment and insight (Damasio, 1994; Stone, Baron-Cohen, & Knight, 1998; Stuss & Alexander, 2000). Patients with OFC damage, like Phineas Gage, often cannot inhibit desires for instant gratification and thus may commit thefts or sexually aggressive behavior (Blumer & Benson, 1975; Grafman et al., 1996).

The ACC is essential for initiating actions, evaluating conflicts, and inhibiting otherwise dominant responses, processes heavily involved in self-regulation (Kerns et al., 2004). The ACC is functionally dissociated into the dorsal (higher) region that evaluates cognitive conflict, and the ventral (lower) ACC that evaluates emotional conflict (Bush, Luu, & Posner, 2000). Recall that ventral ACC is active during social evaluation and rejection. The ACC is often engaged whenever any kind of “supervisory input” is required (Badgaiyan & Posner, 1998). In fact, it is widely accepted that the ACC is somehow involved in evaluating the degree and nature of conflict, whereas other parts of the brain (particularly the PFC) may be involved in resolving the conflict itself (Botvinick, Cohen, & Carter, 2004; Cohen, Botvinick, & Carter, 2000; Kerns et al., 2004).

Emerging neuroimaging research has sought to more clearly identify the neural structures in self-regulation by examining the structures engaged in emotion and cognitive regulation. Ochsner, Bunge, Gross, and Gabrieli (2002) showed participants highly negative pictures and instructed them either to “attend” (study the picture and be aware of, but not try to alter, their feelings toward it) or “reappraise” (reinterpret the picture in such a way that it would no longer elicit a negative response) the photograph. The authors found that reappraising the photographs led to decreased subjective negative affect, and this was reflected in a reduction of activity in the amygdala and OFC and increased activation in the lateral and mPFC, as well as in the anterior cingulate cortex. Since the case of Phineas Gage, we have known that damage to certain prefrontal regions is associated with a lack of impulse control and self-regulatory difficulties more generally. The role of lateral PFC regions in regulating social emotions appears to be among the most robust findings in social neuroscience.

The Next Frontier

In this chapter, we have touched briefly upon several lines of research linking different kinds of brain activity to different aspects of human social behavior. Collectively, these studies reveal that there is no monolithic region or cognitive process that underlies all of social behavior but rather a constellation of processes and regions that give rise to the full social repertoire. New tools enable new analyses and new discoveries; the integration of previously siloed fields reveals a more complete picture of the whole.

Each individual study covered so far has relied on elegant empirical paradigms designed to isolate one stimulus feature or mental process at a time. This approach has yielded robust and reliable findings—an important benchmark for any new scientific field. Yet, in actuality, none of these features or processes exists in isolation. Social behavior is a messy, multifaceted affair in which the brain must process all of these components as they operate in parallel and interactively with each other. The question is, having stepped out of nature, how do we step back in? How do we study how the parts work together to create the real social world?

The next frontier in social neuroscience involves studying brains in more realistic, interactive social contexts. There is a new emphasis on using rich, naturalistic stimuli (e.g., movies rather than static photographs) and computational approaches that allow natural patterns to reveal themselves in the

resulting data (Jack, Crivelli, & Wheatley, 2018). In neuroscience, this includes studying brain activity as people watch movies and then using the recorded activity patterns to reveal what different parts of the brain were most active at which times. For example, Wagner, Kelley, Haxb, and Heatherton (2016) observed that the dorsal medial PFC was particularly activated whenever a scene in a movie involved social interaction.

Social neuroscientists are also beginning to study how brains influence each other in real social interaction. People depend on interaction to hone ideas, forge bonds, establish norms, create information, and remain physically and mentally healthy. Despite this, the traditional neuroscientific approach has been to identify and study mental processes in isolation, with experimental paradigms focused on the individual. The reason for this has been largely pragmatic: Dark, noisy fMRI scanners and being wired up to 128 scalp electrodes are poor settings for lively conversation, not to mention either's sensitivity to motion artifact. However, new technological advances in hardware and software are enabling participants to play games with each other and even have conversations (Pfeiffer, Timmermans, Vogeley, Frith, & Schilbach, 2013; Schilbach et al., 2013). Five years from now, it is likely that we will know a lot more about how minds influence each other in real time—a truly *social neuroscience*.

Summary

Over the past two decades, the integration of cognitive neuroscience and social psychology has led to a wave of insights into the neural basis of human social cognition. In beginning to examine the neural underpinnings of social behavior, researchers have sought to identify the neural bases of cognitive processes that allow humans to perceive and understand the minds of others. The methods of cognitive neuroscience have already contributed to our mechanistic understanding of the social brain. Recent and future advances in neuroimaging promise to push our understanding even deeper; to reveal how minds influence each other at different ages and scales to create the full complexity of human social behavior.

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