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SOCIAL NEUROSCIENCE

Catherine J. Norris

In the early 1990s, an ad executive named Herbert Weinstein was accused of strangling his wife to death and then throwing her body out the window of their apartment in Manhattan in an attempt to make the crime look like a suicide (Rosen, 2007). His defense argued that Weinstein should not be held responsible for his behavior, given the presence of an abnormal arachnoid cyst in his brain. Ultimately, the prosecution allowed Weinstein to plead guilty to a lesser crime, that of manslaughter, rather than allowing his brain scans to be submitted as evidence, as they were worried the jury would be unduly swayed. Although this is an extreme example of the relationship between brain and social behavior, it raises serious questions about the nature of guilt and responsibility for one's actions; questions that are central to the field of psychology. If our (social) behavior is determined by the brain, are we responsible for our own actions when there is a neurological abnormality or defect? Clearly, the connection between brain function and behavior is critical. Social neuroscience is a subfield of psychology that has developed to better understand social behavior by studying the brain and body, and the reverse.

What Is Social Neuroscience?

A general, broad definition of social neuroscience is the use of neuroscientific methods—including those drawn from the fields of psychophysiology, neuropsychoimmunology, and behavioral endocrinology—to study social psychological questions and processes. In other words, social neuroscience encompasses the use of the body and brain to understand social behavior, as well as the impact of social behavior on the function of the body and brain. Social neuroscience is not defined by its methods or its populations, and draws from research on biological systems, organisms, animals, and humans, although the current chapter will focus on the latter. Thus, the field of social neuroscience is by definition multimodal and interdisciplinary and often requires collaborative research incorporating perspectives from multiple specialists in diverse areas.

Although the biological influences on psychological processes have often been viewed as reductionistic and therefore unhelpful for understanding social behavior, the roots of social neuroscience were planted long ago. Gordon Allport, the father of research on attitudes, defined an attitude as "a mental and *neural* state of readiness, organized through experience, exerting a directive or dynamic influence upon the individual's response to all objects and situations with which it is related" (Allport, 1935, p. 810). The inclusion of the brain as essential for understanding a fundamental

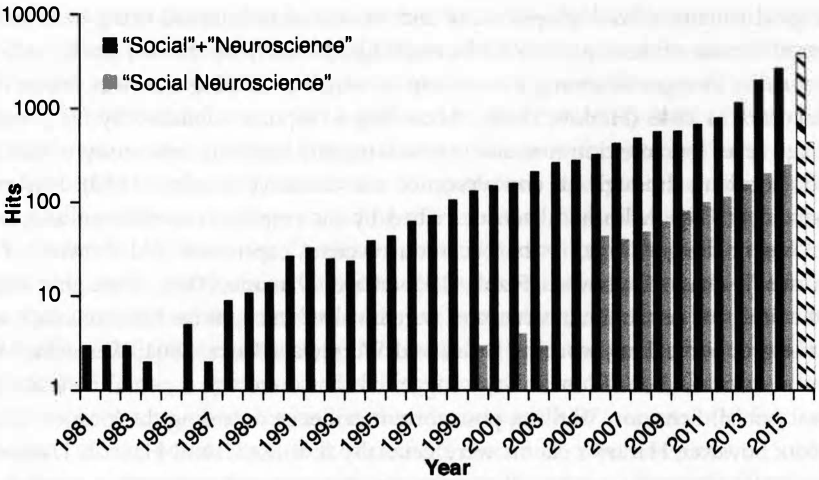

FIGURE 6.1 Results From Two PubMed Searches: One for the Union of the Terms "Social" and "Neuroscience " (dark gray) and a Second for the Term "Social Neuroscience" (light gray).

Note: The scale of the *y*-axis is logarithmic. Results for the year 2016 (striped bars) are projected based on occurrences in the first four months of the year; 1,338 for "social" and "neuroscience" and 152 for "social neuroscience."

concept such as an attitude is notable in the absence of advanced neuroimaging or other methodological tools necessary for the measurement of such influences. Indeed, the growth of the field of social neuroscience has been strongly driven both by the advent of methodological innovations such as functional magnetic resonance imaging (fMRI) and commercially available systems for collection of electroencephalography (EEG) and psychophysiological signals, such as electrodermal activity (EDA) and electromyography (EMG), and the necessity for developing indirect measures for investigating socially sensitive topics, such as race bias, as well as cognitive and emotional processes difficult to unearth through pure introspection.

A recent search of the PubMed database for the union of the terms "social" and "neuroscience" in article titles, abstracts, and key words since the year 1981 (i.e., the year in which the two terms began to coincide annually) reveals tremendous growth, from 2 occurrences in 1981 to over 2,700 in 2015 (and projected to be over 4,000 in 2016; Figure 6.1). This search, however, may overestimate the true prevalence of work that combines these theoretical perspectives. A second search for the term "social neuroscience" shows the same pattern, from a single use in 1994 to just over 250 appearances in 2015 (and projected to be 450 in 2016). Given that this search is conservative in scope as it ignores related terms, such as social cognitive neuroscience, psychoneuroimmunology, social psychophysiology, and others, it vastly underestimates the growth in literature while still capturing the rise in interest and publication rates. In addition, a quick search on Amazon for "social neuroscience" in books reveals 5,855 matches, including textbooks, conference proceedings, and books produced for the popular press. Clearly, combining biological and psychological perspectives to understanding social behavior has gained in both appreciation and perceived utility.

A Brief History

Although the advent of neuroimaging techniques, compact and ambulatory systems for collection of psychophysiological signals, smart phones, and other technological advances have greatly furthered the field of social neuroscience, its roots are firmly planted in careful, systematic observation of neurological patients who displayed social and emotional deficits following brain damage. Perhaps the most famous of these patients is Phineas Gage, the unlucky railroad worker who exhibited major personality changes following an accident in which a tamping iron was driven through his prefrontal cortex in 1848 (Harlow, 1848). According to reports published by his physician, John Harlow, Gage never lost consciousness and was walking and speaking coherently within minutes of the horrific accident, although his convalescence was extensive (Harlow, 1848). Harlow reported that post-incident Gage, who had been described by his employers as efficient and capable pre-incident, "was no longer Gage," as he became irreverent, capricious, and showed no regard for societal norms (Damasio, Grabowski, Frank, Galaburda, & Damasio, 2005). Though it was acknowledged at the time that certain brain structures were involved in cognitive functions such as language, based on the groundbreaking work by Broca and Wernicke (Broca, 1861; Wernicke, 1875/1994), Harlow's observations about Phineas Gage suggested that there was a neural basis for personality and rational (social) behavior. Without postmortem evidence regarding the location and extent of Gage's lesion, however, Harlow's claims were generally dismissed, until Hannah Damasio and her colleagues (2005) obtained Gage's skull and the tamping iron and recreated its possible trajectory. Their results indicated that both Broca's area and the motor and supplementary motor cortices were likely intact; whereas the bilateral ventromedial prefrontal cortices bore the brunt of Gage's injuries. These findings, along with those from other neurological cases, contributed to the conclusion that the ventromedial prefrontal cortex plays a critical role in emotion and its utility in guiding decision-making in the social realm (Damasio et al., 2005).

Phineas Gage was just one of many neurological cases that led researchers to the conclusion that—just as there are neural mechanisms critical for higher level human capacities such as language, perception, and memory—emotion and social reasoning are also served by neural networks, and the study of their deficits can shed light on normal human functioning. A second notable example is that of S. M., a female patient with a genetic condition called Urbach-Wiethe disease that resulted in the bilateral destruction of her amygdala, a midline brain structure that is part of the limbic system (Adolphs, Tranel, Damasio, & Damasio, 1994). The case of S.M. provides a strong counterpart to that of Phineas Gage, in that the extent and exact location of Gage's damage was unknown during his lifetime, whereas S. M.'s damage has been thoroughly examined using neuroanatomical measures, including structural magnetic resonance imaging (MRI), and is known to be confined to the amygdalae. S. M. has been studied extensively, and her behavioral deficits have been well documented. Most notably, S. M. is impaired in her recognition of fear expressions (Adolphs et al., 1994), does not appear to experience fear (e.g., when viewing film clips, interacting with spiders, and entering a haunted house; Feinstein, Adolphs, Damasio, & Tranel, 2011), misjudges unapproachable and untrustworthy faces (Adolphs, Tranel, & Damasio, 1998), and fails to show typical fear conditioning, while maintaining declarative memory for an association between a novel and a fear-inducing (loud noise) stimulus (Bechara et al., 1995). In sum, S. M. is often described in the media as the "woman with no fear" (Babcock, 2014), and her case has led many to conclude that the human amygdala is critical for the recognition and experience of fear.

The cases of Phineas Gage and S. M. underscore the contributions that have been made to the field of social neuroscience through the study of brain-damaged patients. They also, however, highlight some of the major issues presented by using neuroscience methods to study social psychological processes. In the case of Phineas Gage, the extent and location of his lesion was both unknown and uncontrolled (the strongest evidence of his injuries being localized to the bilateral ventromedial PFC comes from posthumous study of his skull; Damasio, Grabowski, Frank, Galaburda, & Damasio, 1994), meaning that his observed behavioral deficits may be due to damage to particular structures, damage to connectivity between affected and intact structures, or possibly even the trauma (or recuperation from the injury) itself. Furthermore, Gage was not subjected to controlled laboratory investigations to examine his behavioral deficits; reports were primarily published by one individual—his physician, Harlow—based on casual observation. Certainly, these data have been instrumental in advancing thinking about the contributions of neurological findings to the study of social and emotional behavior, but require both caution in interpretation and careful, scientific examination. Indeed, Gage and other patients with ventromedial prefrontal lesions inspired researchers to develop behavioral tasks for systematic study of impairments in the role of emotion in guiding decision-making, including the Iowa Gambling Task (IGT; Bechara, Damasio, Damasio, & Anderson, 1994; see also Dunn, Dalgleish, & Lawrence, 2006 for a critical review).

Although the extent and location of S.M.'s damage are well-known and -documented (i.e., bilateral amygdala), many of the same concerns are applicable when using that knowledge along with her behavioral deficits to make assumptions regarding links between behavior and brain localization of function. Through systematic, scientific examination of S.M.'s deficits in socioemotional processes, researchers have often concluded that the amygdala is "responsible" for fear. Careful study has ruled out the possibility that these deficits extend to other emotions, as S.M. does not exhibit deficits in processing other emotional facial expressions (e.g., disgust, happiness, anger) or in the experience of those emotions (Adolphs et al., 1994). It is still possible, however, that fear simply represents one manifestation of a more global human function. Indeed, complementary data from other approaches suggests that the amygdala is implicated in the processing of stimuli with biological relevance (Pessoa & Adolphs, 2010; Adolphs, 2010), of which fear is a subcategory. More recently, researchers have used positron emission tomography (PET) to demonstrate an association between amygdala activation and positive emotions (Hamann, Ely, Hoffman, & Kilts, 2002), suggesting that the role of the amygdala in emotional processing is not confined to fear.

Both of these examples demonstrate the need for careful experimental work and cautious interpretation of observed relationships between neural activation and behavior. Importantly, such criticisms extend far beyond the examination of lesioned individuals and have become more significant as the psychological construct of interest becomes more difficult to define and study. Cacioppo and Berntson (1992; Cacioppo, Hawkley, & Berntson, 2003) have written extensively on both the benefits and complications of taking multilevel approaches, in which research bridges levels of representation of either brain or behavior, to studying broad psychological concepts. They state that "the level of organization of psychological phenomena can vary from the molecular, to the cellular, to the tissue, to the organ, to the system, to the organism, to the physical environment, to the sociocultural context" (Cacioppo & Berntson, 1992, p. 1020). Some researchers perform single-level analyses, staying within one level of this organization, and study the behavioral components of major depressive disorder (MDD) within individuals. Others may cross levels, by studying the sociocultural or neurochemical factors that may contribute to the onset of MDD. Clearly, both approaches are critical for a thorough understanding of the disorder, and an understanding of both is essential for the development of interventions and treatments for MDD. The complexity of investigating these questions, however, increases dramatically as a function of the number of levels crossed. The field of social neuroscience by definition relies on multilevel analysis and must therefore be particularly sensitive to issues regarding the crossing of multiple levels. Although these issues are beyond the scope of the current chapter, any student of social neuroscience should be familiar with the complications of multilevel analysis (Cacioppo & Berntson, 1992; Cacioppo et al., 2003) and should be encouraged to exercise caution in interpretation of results generated by such an approach.

Chapter Overview

The current chapter is divided into three sections. The first section will cover the literature on how we understand the self in the context of others, including topics such as self-awareness, social cognition, theory of mind, perspective taking, and emotional responses and regulation of those responses. The second section will address the research on how we *respond* to others, covering studies on empathy, altruism, and cooperation; social rejection and exclusion; and intergroup processes including social perception and categorization, stereotyping, and prejudice. I refer to this section as *responding* to others rather than *interacting* with others for two reasons: first, few of the studies in the second section utilize actual interpersonal interactions, but instead focus on solitary participants engaging in laboratory-based experimental paradigms designed to mirror real-world encounters; and second, the past few years have seen a surge of studies examining dyadic and group interactions in a wide variety of settings. The third section of the chapter will focus on these exciting new developments on interpersonal interactions in the field of social neuroscience. Given the impossibility of covering an entire field in a single chapter, each topic section will begin with a summary of a paper outlines some of the central issues and findings. Following will be a brief description of other relevant and more current studies.

Understanding the Self in the Context of Others

It is often said that everyone knows what the self is, yet philosophers and psychologists alike have struggled with defining, delineating, and understanding the concept, as well as its implications for how we make sense of ourselves and the world around us. Humans are arguably one of the few species that have an intuitive sense of self, of being an independent entity with volition and unique experiences, and this ability is critical for our perceptions of our own actions, of others' actions, and of our interactions. Self-awareness, the capacity to recognize that oneself is separate and independent from others, has often been studied in both humans (typically infants or young children) and other species (most notably chimpanzees, dolphins, and elephants) using the mirror self-recognition task, in which a mark (e.g., an odorless dye) is placed on the individual's head (or other clearly visible physical location) before being positioned in front of a mirror. Self-recognition is said to be present if the individual does not merely inspect the mirror or look for a nearby conspecific, but touches or otherwise reacts to the mark on their physical being (Amsterdam, 1972; Bard, Todd, Bernier, Love, & Leavens, 2006; Gallup, 1970). Studies have shown that chimpanzees and human infants (24-month olds) respond equally on the mark test (Bard et al., 2006), and researchers have suggested that this ability indicates conscious awareness of oneself as separate from others. This basic cognitive facility is thought to be important for self-evaluation and social comparisons, and is thus critical for higher level social behavior. Furthermore, self-awareness also suggests that perhaps the self, as well as information about the self, may be prioritized in social cognition, including how we remember information, how we perceive the world, and how we understand others.

Self-Knowledge

In a now classic study, Kelley and his colleagues (2002) sought to determine whether knowledge about the self is uniquely represented within the human brain. Their study was founded on the robust finding from the memory literature that knowledge about the self is remembered better than other types of semantic information (i.e., the self-reference effect in memory [SRE]; Klein, 2012; Symons & Johnson, 1997). Kelley and his colleagues (2002) argue that there are two explanations for the SRE in memory: first, that the self is a unique construct that facilitates encoding and retrieval of information (Rogers, Kuiper, & Kirker, 1977), and second, that there is nothing *unique* about the self, but that the SRE arises from more elaborative encoding of information that is self-relevant (Klein & Loftus, 1988). The authors used fMRI to examine these two hypotheses. Participants judged a series of trait adjectives either as (a) upper vs. lower cased, (b) other-relevant or not ("Does this describe President George Bush?") or (c) self-relevant or not ("Does this describe you?"). Results indicated greater activation of the left inferior frontal gyrus (IFG) and the anterior cingulate cortex (ACC) during semantic encoding (self and other) trials compared to nonsemantic encoding (case) trials, consistent with a typical depth-of-processing effect. In addition, however, a region of the medial prefrontal cortex (MPFC) showed greater activation to self than to other or to case judgment trials, consistent with that hypothesis that the self is unique and that the observed SRE is not due simply to increased depth of processing.

Kelley and his colleagues (2002) used fMRI to effectively test two competing hypotheses regarding the psychological processes underlying the self-reference effect in memory. Other researchers have followed up on this research in a number of ways. Mitchell, Banaji, and Macrae (2005) argued that simulation theory, the idea that we use our own experiences and knowledge about ourselves to understand the mental states of others, would predict that the MPFC should be implicated when individuals are asked to make mentalizing judgments about similar others, in addition to making judgements about themselves. Indeed, activity of the MPFC was correlated with self-reported perceived similarity of others, but only when individuals were asked to attend to the mental states of those others. Ochsner and his colleagues (2002) used fMRI to explore the idea that self-knowledge can be attained via direct appraisals, our beliefs about ourselves, reflected appraisals, or our beliefs about how others view ourselves. Both direct and reflected appraisals were associated with increased activation of the MPFC, suggesting again that the MPFC is implicated in self-awareness.

In addition to providing evidence that self-knowledge may be a construct that is uniquely structured in the brain, findings from the initial study conducted by Kelley and his colleagues (2002) also shed light on a broader question regarding the nature of neural activity. Specifically, self-judgments were associated with greater *relative* MPFC activity as compared to other and case judgments, but activity in all three conditions was found to be a *decrease* from baseline. In other words, when performing any of the judgment tasks, the MPFC showed deactivation, but less so for self-judgments than for other or case judgments. This finding is consistent with research on the brain's *default network* (cf. Buckner, Andrews-Hanna, & Schacter, 2008), a neural system that is active when individuals are not focused on external events or tasks. A large body of research has shown that the default network is instead active when individuals are focused on internal tasks, such as thinking about the self, thinking about the perspectives of others, engaging in autobiographical memory retrieval, or thinking about the future (Buckner et al., 2008). Thus, research on the neural structure of self-knowledge has both shed light on the psychological processes involved in thinking about the self and contributed to our understanding of default brain function.

Theory of Mind

The ability to think about and remember self-relevant information is clearly important for the human species; the field of social neuroscience has begun to investigate the neural mechanisms underlying this ability and in the process has shown that the MPFC is strongly implicated in self-referent tasks and is part of a broader default network responsible for internally focused cognitions. The self is also, however, critical for how we understand others. Indeed, Mitchell and colleagues (2005) argued that we use our own experiences and knowledge about ourselves to understand the mental states of others. The ability to reason about and make inferences of other individuals' behaviors based on our understanding of their minds is called *theory of mind* (ToM; Saxe & Kanwisher, 2003), and is also critical for the human species. ToM requires more than acknowledging the physical presence of another as separate from the self; it includes the recognition that the mind of another is also separate from the self and involves the reasoning about the contents of another's mind.

Saxe and Kanwisher (2003) extended existing neuroscience research on ToM by attempting to isolate the underlying processes. Participants read stories while functional neuroimages were collected. The two important story types were *false belief stories*, in which participants must infer a hidden mental process to understand the behavior of a character (e.g., a mother discards newspaper strips that are, unbeknownst to her, critical for her son's paper mache project), and *mechanical inference stories*, in which participants must infer a hidden physical process to understand the "behavior" of a nonhuman agent (e.g., water left in a hot pot on the stove overnight disappears). Arguably, the critical difference between these conditions is whether participants are reasoning about mental or physical states (additional analyses were conducted to address potential confounds, including sociality and task difficulty). fMRI data revealed greater bilateral activation of the temporoparietal junction (TPJ) when participants reasoned about mental as compared to physical states, and the authors argue that the TPJ is thus a critical structure for reasoning about the minds of other people. A great many studies have replicated these findings, as evidenced by a number of review articles (cf. Koster-Hale & Saxe, 2013; Saxe, 2006).

One important criticism of the research on the role of the TPJ in theory of mind is that the TPJ (particularly the right TPJ) is also implicated in attention switching, when individuals are required to switch their attention to task-relevant stimuli (Mitchell, 2008). Saxe and her colleagues (Scholz, Triantafyllou, Whitfield-Gabrieli, Brown, & Saxe, 2009) have responded by showing that ToM and endogenous attention selectively activate different regions of the TPJ. This debate illustrates an important discussion point for neuroscience research; namely, that there is rarely (if ever) a one-to-one mapping between psychological process and neural (or physiological) mechanism (Cacioppo & Berntson, 1992; Cacioppo et al., 2003). The TPJ may be important for ToM because of its role in performing a secondary skill required to make inferences about other peoples' minds.

Perspective Taking

Theory of mind is a basic human characteristic that is required for making inferences about others' behaviors. Taking this a step further, ToM may also help us take the perspective of others; understand their reasoning about their own behavior from their point of view. And by truly attempting to understand others' minds, we may begin to understand not only how they act but also how they feel. ToM, perspective taking, and empathy, or a sense of similarity between one's own experienced emotions and the emotions expressed by someone else (Decety & Lamm, 2006), are intricately linked. One dominant theory proposed to explain how we understand others' behaviors, thoughts, and feelings is *simulation theory*, which suggests that mental simulation is critical for this uniquely human behavior (Gordon, 1986, 1992). Following the discovery of mirror neurons, neurons that respond both when observing and performing an action, in nonhuman primates, researchers proposed that the mirror neuron network may be critical for simulation (and thus for ToM, perspective taking, and empathy), via behavioral mechanisms such as imitation and mimicry (Gallese & Goldman, 1998). In an initial study examining the role of the mirror neuron network in empathy in humans, Carr, Iacoboni, Dubeau, Mazziotta, and Glan (2003) instructed participants to either observe or imitate facial expressions of emotion while functional neuroimages were collected. Both observing and imitating activated similar neural regions, including the inferior frontal gyrus (IFG) and superior temporal sulcus (STS), two regions proposed to be part of the human mirror neuron network (Iacoboni, 2009). In addition, the insula and amygdala, two subcortical structures implicated in emotional processing, also were active when participants observed and imitated others' emotions. Notably, all regions showed greater activation during imitation than during observation. Carr and colleagues' (2003) results fall short of their initial aim, however, given that no link between imitation and empathy is provided. And a long-standing debate over the purported existence of mirror neurons in humans continues even today (Caramazza, Anzellotti, Strnad, & Lingnau, 2014; Hickok, 2014; Marshall & Rossman, 2014).

Another approach that researchers have taken to understand perspective taking and empathy is to examine individuals' imagined responses to their own versus another's pain. Jackson, Brunet, Meltzoff, and Decety (2006) asked individuals to imagine a painful stimulus either from a first-person perspective (i.e., this is happening to you) or from a third-person perspective (this is happening to someone else) and found greater activation of the rTPJ during imagining another's perspective/pain than when imagining one's own pain, consistent with the possibility that the TPJ is implicated in perspective taking. Furthermore, using the same first- versus third-person perspective approach, Decety and his colleagues have shown that the rTPJ (or right inferior parietal cortex) is implicated in perspective taking of simulated actions (Ruby & Decety, 2001) and of social emotions (Ruby & Decety, 2004). Thus, both theory of mind tasks that require reasoning about the (false) contents of another person's mind and perspective taking tasks that require a proposed simulation of another's actions or feelings are associated with activation of the right temporoparietal junction.

Emotion and Emotion Regulation

Social neuroscience has been crucial in furthering research on constructs such as the structure of self-knowledge, theory of mind, and perspective taking, all of which were initially studied using carefully developed behavioral paradigms. The field of emotion research, however, has been characterized from its onset by the use of multiple methods and an interdisciplinary approach, likely due to the difficulty of accurately introspecting about one's own emotional states, as well as the fact that emotion has always been widely recognized as having both a physiological, physical component in addition to a psychological, cognitive component (James, 1884). Although James argued that felt emotional states are the product of lower sensory systems that produce a physical response to a relevant stimulus (e.g., "we feel sorry because we cry, angry because we strike, afraid because we tremble" [p. 248]), as early as the 1920s Cannon (1927) argued that the physical and psychological manifestations of emotions occur simultaneously and that subcortical structures of the brain (specifically the thalamus) were specialized for producing emotional responses and expressions. Emotion researchers have therefore often turned to psychophysiological measures to study these elusive responses. Vrana, Spence, and Lang (1988) pioneered the use of the startle eyeblink reflex as a probe for emotional responses, as they found that eyeblink amplitudes in response to a loud acoustic stimulus were largest when individuals viewed unpleasant emotional images, middling to neutral images, and smallest to pleasant emotional images. Lang, Greenwald, Bradley, and Hamm (1993) also found that facial muscular activity as measured by electromyography (EMG) over the corrugator supercilii (i.e., brow) and zygomaticus major (cheek) muscles corresponded to self-reported valence judgments of emotional stimuli (also see Larsen, Norris, & Cacioppo, 2003), whereas electrodermal activity (EDA, previously known as the Galvanic skin response or skin conductance) corresponded to self-reported arousal judgments of emotional stimuli.

These examples focus on peripheral psychophysiological measures used to measure emotional responses. The past 20 years or so have seen a surge in the use of central measures, including both neuroimaging (PET, fMRI, MEG) and event-related brain potentials (ERPs), in the study of emotion. For example, Ito and her colleagues (1998) examined the negativity bias, the tendency to respond more strongly to unpleasant than to equally extreme and arousing pleasant stimuli, using ERPs and found that the late positive potential (LPP) of the ERP was larger to both unexpected unpleasant and unexpected pleasant images as compared to neutral context images, but was even larger to unpleasant compared to pleasant. Additional studies have replicated this negativity bias (Norris et al., unpublished data), although some have argued that it changes over time (Wood & Kisley, 2006). Initial neuroimaging studies examined the neural regions and networks activated by emotional stimuli; meta-analyses have focused on networks implicated in emotional processing as a function of induction method (cf. Phan, Wager, Taylor, & Liberzon, 2002) and on regions specialized for positive/negative valence and/or approach/withdrawal motivation (Wager, Phan, Liberzon, & Taylor, 2003). More recent meta-analyses have shown that there is little correspondence between discrete emotions (e.g., sadness, happiness, anger, surprise) and activation of isolated neural regions (Lindquist, Wager, Kober, Bliss-Moreau, & Feldman Barrett, 2012) and instead argue for a constructivist perspective, in which neural regions engaged in basic psychological processes are implicated in various emotional experiences.

Perhaps more critically for the field of neuroscience has been the study of emotion regulation, or the control of one's own emotional responses. In an initial study of the consequences of instructed emotion regulation on self-reported, behavioral, and physiological responses, Gross (1998) asked participants to either simply watch a series of disgusting films, to think about the film in such a way that would minimize their emotional responses (i.e., *reappraisal*), or to behave in such a way that someone watching them would not know how they were feeling (i.e., *suppression*). Psychophysiological measures (e.g., skin conductance, a measure of arousal) and somatic activity (i.e., actual movement) were collected during the films, and self-reported emotional responses (including disgust) were collected following the films. Participants were also videotaped during the films and their behavioral and emotional responses were coded. Results showed that participants instructed to reappraise reported experiencing less disgust than did those who watched or suppressed; however, this pattern of results could be due to reappraisal participants falling subject to demand characteristics (i.e., instructions told them to minimize their feelings of disgust). Importantly, behavioral data indicated that both regulation groups showed less expressive and somatic activity. Taken together, these results indicate that not all regulation is the same, and that instructed regulation may decrease behavioral responses but not always impact self-reported affective responses. Furthermore, physiological data showed that reappraisal was effective at minimizing arousal, whereas suppression was not—in fact, physiological arousal was *higher* when participants suppressed than when they watched. The inclusion of physiological data allowed Gross (1998) to draw conclusions about the impact of two regulation strategies on emotional responses that could not have been made otherwise, and represent a stride forward in understanding the efficacy of different forms of regulation. However, questions regarding the mechanisms by which reappraisal decreases emotional reactivity remained unanswered.

Drawing from Gross's (1998) initial study and attempting to explore these underlying mechanisms using fMRI, Ochsner, Bunge, Gross, and Gabrieli (2002) asked participants to reappraise negative scenes in unemotional terms. Compared to trials on which participants were asked to simply attend to negative scenes, reappraisal of negative scenes was associated with decreased self-reported negative affect, decreased activation of the amygdala and the medial orbital frontal cortex (MOFC), and increased activation of the ventral lateral prefrontal cortices (vLPFC). The authors suggest that this pattern indicates that, when instructed to reappraise, individuals may engage prefrontal control mechanisms, which in turn down regulate activation of the amygdala, likely through down-regulation of the MOFC (which provides an anatomical bridge between the vLPFC and amygdala). In fact, increased activation of the vLPFC during reappraisal vs. attend trials correlated with decreased activation of both the MOFC and the amygdala, supporting the authors' hypotheses. Additional analyses also revealed that increased activation of a region of the anterior cingulate cortex (ACC; BA 24) during reappraisal trials correlated with decreased negative affect ratings, suggesting a direct role of the ACC in down-regulation of experienced (or at least reported) negative affect. In sum, Ochsner and his colleagues (2002) demonstrated that fMRI could be a useful tool for understanding the mechanisms underlying the reappraisal of negative affect, and, in doing so, paved the way for researchers to use neuroimaging methods to examine emotional processes.

Ochsner and his colleagues (2004) followed up on this initial study by investigating the shared and unique neural mechanisms implicated in the up- and down-regulation of negative affect. Compared to a neutral "look" condition, both up- and down-regulation were associated with increased activation of prefrontal and anterior cingulate regions implicated in cognitive control. Amygdala activation also varied as a function of regulation, decreasing during down-regulation and increasing during up-regulation. Combined, these findings constitute a replication and extension of their previous work and demonstrate that regulation, regardless of direction, relies on a common underlying control network that may influence amygdala reactivity. However, up- and down-regulation also recruited unique regions: up-regulation was associated with increased activation of prefrontal regions associated with emotion knowledge (left rostromedial PFC), whereas down-regulation was associated with increased activation of prefrontal regions associated with behavioral inhibition (right lateral and orbital PFC).

In addition, participants were assigned to either use a self-focused regulatory process, in which they were instructed to either increase their subjective closeness (up-) or distance (down-regulation) to negative scenes, or a situation-focused regulatory process, in which they were instructed to reinterpret events as depicted in their situational context by imagine them getting worse (up-) or better (down-regulation). As predicted, self-focus also recruited regions associated with self-knowledge processing (i.e., the medial PFC; Kelley et al., 2002), while situation-focus recruited regions associated with external focus (lateral PFC). Based on these and other results, Ochsner and Gross (2005) argue that although regulation may activate a central cognitive control networks, different kinds of regulation rely on different prefrontal regulatory regions.

Social neuroscience research on emotion regulation has not only illuminated the mechanisms underlying emotional reactivity and its moderation, but has also shed light on mental health disorders such as depression. Unipolar depression has been associated with increased and sustained amygdala reactivity (Abercrombie et al., 1998) and with decreased or disrupted activation of the dorsolateral prefrontal cortex (Johnstone, Van Reekum, Urry, Kalin, & Davidson, 2007). These patterns have been observed both on traditional emotion regulation tasks (Johnstone et al., 2007) and on independent tasks, such as rating of emotional words (increased amygdala activity) and digit sorting (a purely cognitive task; decreased DLPFC activity; Siegle et al., 2007). Furthermore, the relationship between DLPFC and amygdala activation also appears to be decreased in unipolar depression, although these patterns are not homogenous across depressed individuals (Siegle et al., 2007). These findings are suggestive of a number of mechanisms underlying depression, including increased emotional reactivity, decreased regulation of emotional responses, or dysregulated communication between neural regions implicated in these processes. Using neuroimaging and other methods to understand disruption of emotion regulation networks in mental health disorders such as depression may lead to better treatments and interventions.

Responding to Others

Self-awareness and the structure of self-knowledge, theory of mind and perspective taking, and emotion and emotion regulation are central to human functioning. Given that humans are a social species, these processes are critical for guiding how individuals understand not only themselves but also other conspecifics. To flourish in our social world, we must be able to not only understand ourselves, but we must also effectively communicate and respond to others. Many believe that the expansion of the human brain evolved due to the complex demands of dealing with others—competing or cooperating with them, deceiving or empathizing with them, understanding or misjudging them. These processes are critical for survival in a social species, and we turn now to a consideration of the neuroscience research that has contributed to our understanding of the mechanisms underlying how we respond to others.

Empathy, Altruism, and Cooperation

Empathy, defined previously as a sense of similarity between one's own experienced emotions and the emotions expressed by someone else (Decety & Lamm, 2006), is thought to be critical for how we respond to others and is dependent on our ability to take the perspective of someone else. Singer and her colleagues (2004) used fMRI to examine individuals' responses to their own versus a loved one's pain. Female participants were scanned while either they or their romantic partner received a painful stimulation to their right hand. As expected, receiving pain activated the "pain matrix," a network of brain regions implicated in the experience of physical pain (Davis, 2000; Peyron et al., 2002), including the primary and secondary somatosensory cortices, primary motor cortex, bilateral insula, anterior cingulate cortex (ACC), thalamus, brainstem, and cerebellum (Singer et al., 2004). More importantly, participants also exhibited activation of the ACC and the bilateral insula, regions of the pain matrix more associated with the emotional or affective aspects of pain than the physical aspects, when their partners received pain, indicating shared neural networks during experienced and empathic pain. Regions of the pain matrix associated with the physical aspects of pain, including the somatosensory and motor cortices, were not activated when individuals observed their partners experiencing pain, suggesting that empathy for pain involves emotional but not physical pain. Furthermore, individual differences in empathy as measured by self-reports correlated with activation of the ACC and insula, such that more empathic individuals exhibited increased activation of these regions when they observed their partner in pain. These findings dovetail with those presented by Decety and Jackson (2004), who used an indirect, imagery-based manipulation of experienced versus empathic pain. Indeed, a recent meta-analysis has confirmed that across nine independently conducted studies using both picture-based and cue-based (e.g., Singer et al., 2004) paradigms, the ACC and insula are implicated in empathy for pain (Lamm, Decety, & Singer, 2011).

Empathy, sharing another's feelings, may be required for prosocial behavior or actually acting to help someone experiencing pain or another negative emotion. Morrelli, Rameson, and Lieberman (2014) used a picture-based paradigm to investigate neural responses during empathy for individuals depicted experiencing pain. Outside of the fMRI scanner, participants also completed a "daily helping checklist" on 14 consecutive evenings, in which they indicated whether they had performed each of 11 different helping behaviors, including picking up a dropped item or holding a door or an elevator. Replicating previous research, empathy for pain was associated with activation of the bilateral insula and the ACC, in addition to regions thought to be part of the human mirror neuron network (e.g., inferior parietal lobule [IPL], inferior frontal gyrus [IFG]). In addition, the septal area, a region previously associated with prosocial behavior (Inagaki & Eisenberger, 2012), was active during empathy for pain, and activation of the septal area was correlated with self-reported daily helping. Thus, Morelli and colleagues (2014) effectively showed that neural activation of the septal area in response to another's pain is related to frequency of prosocial behavior in real life.

Another aspect of responding to others concerns social interactions that require competition versus cooperation. Both behaviors require perspective taking and theory of mind, as we must consider the desires and needs of an interaction partner to determine the most appropriate (and profitable) response in any situation. Cooperation and competition have often been studied using economic decision-making games, such as the ultimatum game and the prisoner's dilemma. Decety, Jackson, Sommerville, Chaminade, and Meltzoff (2004) manipulated cooperative and competitive mindsets in participants as they played a computerized game with a confederate, and also examined neural activation when they played alone. fMRI results showed a shared pattern of neural responses in a frontoparietal network, indicating that both cooperation and competition (compared to solo play) implicated regions associated with executive functions, and the insula, associated with autonomic arousal. However, cooperation also uniquely engaged the orbitofrontal cortex (OFC), whereas competition uniquely engaged the medial PFC. The authors argue that cooperation and competition, both of which require considering another's perspective and mindset, require greater attention and executive functioning than solo play. Based on previous research indicating the role of the orbitofrontal cortex in processing positive feedback, they also suggest that cooperation may be associated with greater implicit reward (Decety et al., 2004). Greater activation of the medial PFC during competition may be consistent with an increased focus on the self and one's own performance.

Consistent with Decety and colleagues' (2004) conclusions that cooperation may be intuitively rewarding, Rilling et al. (2002) found increased activation of the OFC and the nucleus accumbens (also associated with both primary rewards, like food and sex, and secondary rewards, like monetary gains) during mutual cooperation on a prisoner's dilemma game. The authors argue that this pattern of findings may reinforce reciprocal altruism, a type of prosocial behavior that may motivate individuals to cooperate instead of not reciprocating favors, in players. In a separate study, Rilling, King-Casas, and Sanfey (2008) found that unreciprocated cooperation on the prisoner's dilemma game was associated with increased activation of the bilateral anterior insula, implicated in autonomic arousal, and the left hippocampus, a neural structure strongly implicated in episodic memory. These results may suggest both an increase in arousal and better encoding of the event when individuals' cooperative behavior is not returned.

Using the ultimatum game, in which one player proposes a split of $10 (the "giver") and a second can accept or reject it (the "receiver"), rejection of offers increases as a function of the amount of deviation from a fair split. In other words, a $5/$5 split is accepted by most players, whereas an $8/$2 split is rejected more often than a $7/$3 split. Sanfey, Rilling, Aronson, Nystrom, and Cohen (2003) found that activation of the insula, associated with arousal and disgust, in receivers increased as the unfairness of offers increased. Importantly, receivers are less likely to reject unfair offers if they are made by a computer than by another player, and insula activation to unfair offers was greater when made by a another player than by a computer. This finding highlights the social nature of human cooperation; we are more affected by and responsive to uncooperative humans than to inhuman machines.

Indeed, Fehr and Rockenbach (2004) argue that human cooperation is unique, in that "humans frequently cooperate with genetically unrelated strangers, often in large groups, with people they will never meet again, and when reputation gains are small or absent" (p. 784). Fehr and Rockenbach (2004) review the literature on strong reciprocity—the tendency toward altruistic punishment and reward—which they believe is critical for human cooperation. De Quervain and colleagues (2004) used PET to examine the neural correlates of altruistic punishment, or the unrewarded and sometimes costly tendency to punish social defectors. Using a sophisticated experimental paradigm, the authors showed that the dorsal striatum, a region implicated in reward processing, exhibited stronger activation during effective punishment (i.e., in which a defector actually received financial punishment) than during symbolic punishment (in which a defector did not receive financial punishment), suggesting that altruistic punishment may be intrinsically rewarding. Furthermore, participants with more dorsal striatum activation were willing to incur higher costs to effectively punish defectors. Altruistic punishment may be one mechanism that humans have developed to encourage cooperation in social interactions.

Empathy, cooperation, and altruism may not, however, be equally allocated to all conspecifics; we may show ingroup members, individuals like us, preferential treatment. Mathur, Harada, Lipke, and Chiao (2010) investigated the neural basis of extreme empathy and altruism for ingroup and outgroup members in Caucasian-American and African-American participants. Participants viewed scenes depicting ingroup and outgroup members in pain or not in pain (i.e., in a neutral context). Behaviorally, all participants expressed more empathy for and were willing to donate more money (i.e., exhibit greater altruistic motivation) to help targets in pain than not in pain; however, African-American participants also exhibited greater empathy and altruistic motivation for their ingroup than their outgroup (Caucasian-American participants showed no group differences). In addition to all participants exhibiting activation of the affective regions of the pain matrix to targets in pain, African-American participants also showed greater activation of the medial PFC to ingroup targets in pain than to outgroup targets in pain. Furthermore, the ingroup bias in medial PFC activation also correlated with increased empathy for and altruism toward ingroup members in pain. The authors argue that these results could indicate that a stronger attachment between self-identity and group membership may underlie increased empathy and altruism toward ingroup members.

Social Rejection, Loneliness, Exclusion

In addition to shedding light on social psychological processes, social neuroscience has also changed the way that we think about brain function. One now classic study that is often held as an example of this (and that has fostered a lengthy discussion about the nature of the relationship between neural and psychological processes) sought to investigate the neural mechanisms underlying social rejection. Eisenberger, Lieberman, and Williams (2003) subjected participants to multiple rounds of Cyberball, an online ball tossing game, while undergoing fMRI. Importantly, participants were included by two players in one block and were excluded in a second block. Results showed greater activation of the anterior cingulate cortex (ACC), a neural region implicated in the experience of physical pain (cf. Rainville, Duncan, Price, Carrier, & Bushnell, 1997), when participants were excluded versus included, and greater activation of the ACC during exclusion correlated with higher self-reported ratings of distress. The authors concluded that the ACC might have been "co-opted" to respond to social as well as physical pain. Although the original study has received much critique in the field (Rogachov, Cheng, & DeSouza, 2015; Wager et al., 2016), the results challenged the way that researchers thought about the function of neural regions and networks. Eisenberger and Lieberman (2004) have argued that the ACC may be best conceived of as a primary component in a more general neural alarm system that is activated when an individual is threatened in some way, whether physical or psychological. In general, this line of research has raised questions about such topics as the utility of reverse inference in neuroimaging research; the study of neural activation at the level of regional patterns, entire structures, or broader networks; the adoption of neural networks by other related psychological processes; statistical approaches in neuroscience research; and even the neural representation of psychological processes such as physical or social pain.

Importantly, many researchers have continued to pursue the study of social rejection and exclusion in order to provide a better understanding of these processes. For example, Somerville, Heatherton, and Kelley (2006, Somerville, Heatherton, & Kelley, 2010) developed a new paradigm to help dissociate social rejection from expectancy violation, under the assumption that being excluded from a game of Cyberball during a second round of play confounds these processes. They found that difference regions of the ACC are implicated in social rejection (ventral ACC) and in expectancy violation (e.g., receiving negative feedback when expecting positive; dorsal ACC; Somerville et al., 2006), and that self-esteem moderated these effects (Somerville et al., 2010). Such follow up studies extend the research on social exclusion and rejection by carefully attending to multiple processes underlying these high-level, complex states, while also addressing questions regarding neural function.

Cacioppo and his colleagues (2009) have taken a complementary approach to understanding the neural mechanisms underlying social pain by studying naturally occurring individual differences in self-reported loneliness, or the stable psychological experience of feeling alone. Rather than examining acute responses to rejection in the laboratory, Cacioppo and his colleagues (2009) looked at how chronically lonely individuals responded to emotional images that were either social (i.e., contained people) or nonsocial (did not contain people). Although self-reported emotional responses to the images did not differ as a function of loneliness, fMRI results indicated that lonely individuals showed greater activation of the bilateral visual cortex to unpleasant social versus unpleasant nonsocial images than did nonlonely individuals; whereas activation of the bilateral temporoparietal junction (TPJ) showed the opposite pattern, with nonlonely individuals showing greater activation to unpleasant social versus unpleasant nonsocial images than lonely individuals. Given past research on the contributions of these two regions to psychological processes, the authors tentatively suggest that lonely individuals may pay more attention to pictures of distressed others (given visual cortex activation), but that nonlonely individuals may engage in more perspective taking when viewing pictures of distressed others (TPJ; Ruby & Decety, 2004). Furthermore, neural responses of the ventral striatum to pleasant images showed a crossover interaction, with lonely individuals showing greater activation to pleasant *nonsocial* images and nonlonely individuals showing greater activation to pleasant *social* images. Given the role of the ventral striatum in reward processing (cf. O'Doherty, 2004), these data suggest that people are not as rewarding to chronically lonely individuals as they are to nonlonely individuals (Cacioppo, Hawkley, Norman, & Berntson, 2011).

It's important to note that many of these findings are subject to criticism based on their reliance on reverse inference, or the assumption that activation of a neural region may be indicative of a psychological process that has previously been associated with that region. However, studies such as this may shed further light on the psychological processes that underlie chronic loneliness (or other negative psychological states), which may help direct interventions and treatments focused on their easement.

Intergroup Processes: Stereotypes, Prejudice, Discrimination, and Race Bias

Perhaps one of the research areas that has benefited most from incorporating a neuroscientific perspective and methods to study social psychological questions is that of intergroup processes, including social categorization, stereotypes, prejudice, and discrimination. Clearly, understanding intergroup processes is critical for any culture, and the field of social psychology has led this investigation throughout its long history. Yet, such processes can be difficult to study in an egalitarian society, both due to lack of ability to accurately introspect on internal processes (Nisbett & Wilson, 1977) and to reporting biases driven by either societal standards or desire for positive self-presentations. Researchers realized the need for creativity in their assessment of individuals' attitudes and feelings toward members of other social groups (as well as their own self-reported group membership; Alexander and Fisher, 2003), giving rise to such approaches as the "bogus pipeline," in which participants are convinced that (sham) physiological equipment can detect the direction and extremity of their "true" feelings (Jones & Sigall, 1971). A meta-analysis conducted on 31 bogus pipeline (BPL) studies revealed reliable decreases in socially desirable responses (Roese & Jamieson, 1993). It is not surprising, therefore, that social neuroscientists have adopted multiple psychophysiological and neuroimaging methods to study intergroup processes.

In 2000, two landmark studies examined neural responses to members of racial outgroups; specifically, both Hart and colleagues (2000) and Phelps and colleagues (2000) focused on neural responses in the amygdala to ingroup versus outgroup faces. Although it might be assumed that given these similarities, the two studies should show convergent results and draw parallel conclusions, methodological and theoretical differences between the two research groups led to slightly divergent perspectives. Hart and colleagues (2000) recruited both self-identified Black and White participants and showed both Black and White faces. Their analysis collapsed across race and instead focused on "ingroup" (White participants viewing White faces; Black participants viewing Black faces) versus "outgroup" (White participants viewing Black faces; Black participants viewing White faces) responses in the amygdala. In addition, trials were divided into early and late scans to allow for an investigation of amygdala responses over time. Perhaps surprisingly, they found no differences in amygdala responses to ingroup versus outgroup faces in the early scan, but a larger (maintained) amygdala response to outgroup versus ingroup faces in the late scan. Hart and colleagues (2000) argue ingroup faces elicit a faster habituation of the amygdala response than do outgroup faces, and that this finding is consistent with the interpretation that individuals show more rapid familiarization of ingroup versus outgroup members.

Phelps and colleagues (2000) examined amygdala responses to White (ingroup) versus Black (outgroup) faces in a group of all White participants. They also found no group differences to White versus Black faces during early trials, consistent with Hart and colleagues (2000). However, they did note that there was variability in individuals' responses, with a majority showing greater amygdala activation to Black versus White faces. Importantly, this variability was related to indirect measures of race bias using the eyeblink startle paradigm (Amodio, Harmon-Jones, & Devine, 2003) and the race bias version of the Implicit Association Test (IAT; Greenwald, McGhee, & Schwartz, 1998). White participants exhibiting stronger amygdala responses to Black versus White faces also tended to show larger eyeblink startle responses to Black versus White faces and a stronger implicit race bias on the IAT. To support their conclusions that the variability in amygdala activation to Black versus White faces was "a reflection of culturally acquired knowledge about social groups filtered through individual experience" (p. 733), the authors conducted a second experiment that was identical in methods and analysis but used familiar and well-liked Black and White faces in both the fMRI and IAT tasks. As predicted, there was no overall pattern of larger amygdala responses to Black or White faces, and the variability in these differences did not correlate with either eyeblink startle or IAT scores. Thus, using familiar and well-liked Black and White faces eliminated the effect. Taken together, Hart and colleagues (2000) and Phelps and colleagues (2000) both showed that larger amygdala responses to outgroup versus ingroup faces seems to be driven by a lack of familiarity (and consequent slower habituation) with outgroup members.

Following these two pioneering studies, a great number of researchers have utilized fMRI and other neuroimaging methods to investigate the mechanisms underlying stereotypes, prejudice, discrimination, and race bias. One limitation of these methods, however, is their relatively slow temporal resolution. ERPs allow researchers to investigate how such processes unfold over time, also shedding light on the stage at which social categorization and intergroup biases emerge and begin to affect behavior. Using ERPs, Ito and Urland (2003) found that within 100 ms of presentation, Black faces elicited more attention than did White faces in mostly White participants, and notably that gender was categorized 50 ms *after* race. This research is important as it investigates social categorization of individuals from multiple categories; Ito and her colleagues have followed up by using ERPs to look at the categorization of mixed or ambiguous race individuals. Correll, Urland, and Ito (2006) used ERPs to investigate the mechanisms underlying the *shooter bias*, the tendency for individuals to "shoot" armed Black men more quickly and frequently than armed White men in a videogame simulation. They found that the shooter bias was predicted by knowledge of the cultural stereotype of Blacks, and that this relationship was mediated by differences in the amplitudes of the P200 and N200 components of the ERP to Black versus White targets, suggesting that differential attention to outgroup members is a mechanism that drives the shooter bias. In addition to ERPs, other psychophysiological measures have been used to study race bias. Amodio et al. (2003) showed that eyeblink startle amplitudes were larger to Black than to White faces, but only for individuals low in internal motivation to respond without prejudice (Plant & Devine, 1998), suggesting that individuals who do not internalize the goal to act unprejudiced respond more negatively to Black targets.

Importantly, researchers have begun to investigate the neural correlates of changes in intergroup processes. Van Bavel, Packer, and Cunningham (2008) randomly assigned participants to one of two mixed-race (Black and White) teams in a modified version of the minimal groups paradigm, which has previously shown that arbitrary assignment to a group can foster ingroup favoritism (Tajfel, 1970). Following two learning tasks in which participants learned and were tested on their memory for ingroup vs. outgroup members, participants performed a team member categorization task in the fMRI scanner and subsequently rated their liking for all targets (both ingroup and outgroup members, both Black and White targets). Liking ratings revealed ingroup favoritism, with ingroup members liked more than outgroup members; and this effect was not moderated by race, indicating that Black and White ingroup members were equally liked. fMRI results showed greater activation of the fusiform gyrus, the amygdala, the orbitofrontal cortex (OFC), and the dorsal striatum to ingroup than to outgroup members, and these results were not moderated by race. The ingroup effect in the fusiform gyrus, a region implicated in face processing, is consistent with previous results indicating a bias toward processing ingroup (and indeed, own-race; Golby, Gabrieli, Chiao, & Eberhardt, 2001) faces. Although the amygdala has in the past been strongly associated with negative affect, the current results are more consistent with the interpretation that the amygdala is sensitive to biological (or motivational) relevance. This conclusion is supported by greater activation of the OFC and dorsal striatum, two regions associated with reward processing, to ingroup versus outgroup faces (Van Bavel et al., 2008). Thus, a simple minimal groups paradigm effectively increased not only self-reported liking of team members, but also affected the neural processes associated with responses to ingroup members (deeper processing of faces, increased motivation, increased reward). The malleability of perceptions of and neural responses to (arbitrarily assigned) group members may have implications for the reduction of outgroup bias more broadly.

Interacting With Others

Although the field of social neuroscience is, by definition, concerned with how we understand, respond to, and interact with other people, it is notable that much of the field's research focuses on individuals acting alone, in the solitude of an fMRI or PET scanner or a sound-attenuated, electrically isolated chamber. We study perspective taking by asking participants to imagine what someone depicted in an image is thinking, instead of utilizing paradigms that allow individuals to interact naturally and require perspective taking (e.g., the director task; Keysar, Lin, & Barr, 2003, and see Dumontheil, Küster, Apperly, & Blakemore, 2010 for an adaptation of this paradigm for use with fMRI). We examine cooperation using a computerized economic decision-making task that ultimately has no impact on a future relationship or the possibility of real reciprocity, instead of creating realistic scenarios in which cooperation has consequences for participants. We investigate race bias and prejudice by measuring brain activation in response to novel, unfamiliar faces from different races, absent of context, participants' backgrounds, or additional interpersonal cues. The general reliance in social neuroscience on studies focused on the individual rather than those that incorporate an interpersonal component is likely due to at least three factors: first, limitations introduced by the dominant methods of the field, including psychophysiology (which often requires electrically and audibly quiet rooms for data collection) and neuroimaging (placing an individual in a scanner constrains the ability to examine interactions naturally; second, examining social questions at the dyadic or group level requires highly complex data analyses, given the co-dependence between observations; and third, the laboratory environment provides a high degree of control, allowing researchers to minimize confounds and noise, while maximizing psychological realism.

One of the most exciting current directions in social neuroscience, however, is towards the study of people interacting with people. An example of this approach that we have already discussed is that of work on empathy for pain; Singer and her colleagues (2004) pioneered the use of actual pain simulation applied to a participant *or her romantic partner* while neuroimaging data were collected. Although this paradigm allows for the investigation of a *single* brain responding to a present, real-life social stimulus, it represents an attempt to examine responses to others *in vivo* (and notably, results generalize to more typical empathy paradigms, including picture-based approaches; Lamm et al., 2011). We turn now to research that examines how individuals interact with others.

A critical question for psychological research in general is the degree to which findings replicate across contexts: in social psychology, this question concerns whether an individual responds the same when alone versus when with a stranger, with a friend, or in front of an audience. We have known throughout the history of psychology that the social context has an impact on behavior, as arguably the first social psychological study showed that cyclists ride faster in the presence of pacers or competitors than when alone (Triplett, 1898; but see Strube, 2005). Similarly, Fridlund (1991; Fridlund, Kenworthy, & Jaffey, 1992) showed that positive and negative facial expressions were augmented in the presence of a real or imagined audience, and suggested that the social context may have a stronger impact on facial expressions than the experience of emotion itself. One criticism of this initial study, however, was its reliance on self-reports; Hess, Banse, and Kappas (1995) replicated the work using facial electromyography (EMG) and found that, indeed, social context (i.e., strangers versus friends) did have an impact on emotional expression—but it is more complicated than Fridlund originally argued. Thus, the inclusion of psychophysiological data clarified the role of the social context on emotional expressions.

Importantly, Hess and her colleagues (1995) found that the nature of the social relationship was also critical; expressions were different when in the presence of a friend versus a stranger. Many dyadic studies have capitalized on existing relationships (e.g., friends, romantic partners) to study how both presence of another person and both nature and quality of the existing relationship affect neural and behavioral responses. Coan, Schaefer, and Davidson (2006) examined the social regulation of threat responses by collecting fMRI data while female participants completed a threat of shock task, in which visual cues either predicted safety (no shock) or threat (20% chance of shock) on individual trials. Critically, participants held the hand of either their husband or a male experimenter (i.e., relative stranger) in two critical blocks of trials, and were alone in a third block. The authors observed widespread reduction of neural activation in regions associated with emotional and behavioral responses to threat when wives held the hands of their husbands, and attenuated reduction when they held the hands of a male stranger. Furthermore, marital satisfaction predicted greater reductions of activation in the insula, superior frontal gyrus, and hypothalamus, regions implicated in threat responses, when holding the hands of their husbands but not the stranger, suggesting that not only the immediate social context, but also the relationship history and quality were effective at reducing neural responses to threat.

Coan and his colleagues (2006), along with Singer and her colleagues (2004), introduced a new paradigm to the fMRI literature that allowed for the investigation of how social relationships and interactions can impact responses to stimuli such as pain and threat. Neuroimaging methods, however, have not typically allowed for simultaneous data collection in two (or more) interacting individuals (although this is changing). Instead, researchers have used psychophysiological measures to examine bodily signals in two interacting individuals. For example, Gottman, Coan, Carrere, and Swanson (1998) found that when newlywed couples engaged in a discussion about a marital issue in the laboratory, lack of physiological soothing of the male (in addition to a number of other factors) predicted divorce. More recent studies have investigated the role of not only the individuals' physiological responses, but the *synchrony* or covariation of those responses in predicting outcome factors. Helm, Sbarra, and Ferrer (2014) examined the covariation of respiratory sinus arrhythmia (RSA; a measure of parasympathetic activation) in interacting heterosexual romantic couples, and found that both males' and females' RSA responses were associated with their partners' previous RSA responses, and that this covariation was stronger for couples with higher relationship satisfaction. A number of theoretical (e.g., Butler & Randall, 2013) and analytical (e.g., Helm, Sbarra, & Ferrer, 2012; McAssey, Helm, Hsieh, Sbarra, & Ferrer, 2013) innovations have been introduced that will pave the way for future advances in the study of synchrony between individuals.

Indeed, researchers have already begun to examine synchrony of EEG activity during interpersonal interactions as a way of understanding social behavior. Using an iterated prisoner's dilemma game, Fallani and colleagues (2010) examined EEG connectivity in individual brains as well as relationships between brains while pairs of (unfamiliar) participants made cooperative and noncooperative decisions. The authors introduce the concept of a "hyper-brain network" to examine interbrain links, and found that fewer interbrain links and higher modularity between partners predicted noncooperative decisions. In other words, patterns of EEG across partners directly related to how individuals played the game. In a motor imitation task, Dumas, Nadal, Soussignan, Martinerie, and Garnero (2010) found that participants did, indeed, engage in more synchronous than nonsynchronous activity both when instructed to imitate and when not instructed to imitate (i.e., they exhibited spontaneous synchrony). Furthermore, behavioral synchrony was associated with interbrain synchrony of a particular frequency band of the EEG (alpha-mu) over right centroparietal regions, including the right temporoparietal cortex (TPJ). The authors suggest that these findings are consistent with the role of the TPJ in understanding others' actions and taking the perspective of others, and then interbrain synchrony of right TPJ activation may predict synchronous behavior within dyads.

Yun, Watanabe, and Shimojo (2012) conducted a study that uniquely complements this previous research by first having pairs of participants engage in a cooperative interaction and then examining the effects on imitation and EEG synchrony. As expected, cooperative interaction increased motor imitation (of simple fingertip movements) and neural synchrony, most notably in the inferior frontal gyrus (IFG; a region implicated in the human mirror neural network) and the medial frontal regions (implicated in mentalizing). Thus, increased behavioral mimicry following cooperation may be driven by synchronous brain activation in either mirroring or mentalizing networks.

In sum, researchers are making great strides toward studying interacting social brains, a direction that is likely to shed new light on how we understand social cognitive processes such as perspective taking, theory of mind, empathy, cooperation, and even race bias. Liu and Pelowski (2014) and Wheatley, Kang, Parkinson, and Looser (2012), among others, have written excellent reviews of the issues inherent in taking a "two-person neuroscience" (2PN) approach to understanding social processes, as well as the mechanisms required for synchrony and the consequences of synchrony for social behavior. The study of interacting brains has great promise for the future of the field of social neuroscience.

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