Neuroscience Approaches in Social and Personality Psychology

Abstract
Social neuroscience is an interdisciplinary approach to studying the mind and behavior, noted for its appreciation for the dynamic interactions of situational and dispositional processes as they relate to neural and biological mechanisms. In this chapter, we describe the methodological approach of social neuroscience and review research that has applied this approach to address the interplay of the person and situation in the domains of social cognition, attitudes, emotion and motivation, intergroup relations, and personality. We provide critical discussion of how neuroscience may contribute to classic questions in personality and social psychology, and we describe how the social neuroscience approach promotes the integration of dispositional and situational accounts of the mind and behavior.

Keywords: social neuroscience, emotion, attitudes, intergroup, review, psychophysiology, cognitive neuroscience, personality and neuroscience

Neuroscience Approaches to Social and Personality Psychology
The recent interest in neural and biological components of social and personality psychology may seem new, but is actually a return to form for the field of social and personality psychology. Founding psychologists such as James and Wundt were trained in physiology, and they approached issues of thought, emotion, memory, and perception with a firm belief that mental processes were rooted in the brain. To these psychologists, the mind and the brain were symbiotic, and a consideration of neural processes, along with dispositional and interpersonal processes, provided a natural and comprehensive approach to understanding the mind and behavior. Early psychological research on social processes, such as bluffing to other players during a poker game (Riddle, 1925) or responding to socially taboo words and phrases (Darrow, 1929), incorporated psychophysiological measures to complement behavioral observations. Indeed, early research on intergroup interactions and prejudice used physiological measures to examine anxiety during an interracial encounter (Rankin & Campbell, 1955). Hence, physiological measures have long served as an important component of an integrated approach to social-personality psychology.

As the field of psychology developed, a shift toward behaviorism effectively vanquished the role of the mind and brain from the study of behavior, and the field of neuroscience branched away from psychology. Although research on neural function continued at lower levels of analysis (e.g., cellular and molecular), it no longer made contact with the higher-level processes of social and personality psychology. When a focus on mental function reemerged during the cognitive revolution, it was generally held separate from neural and biological function (with some notable exceptions, e.g., Cacioppo & Petty, 1983; Frith, Morton, & Leslie, 1991; Gazzaniga, 1985; Shapiro & Crider, 1969). However, with recent advances in brain imaging technology, research on cognitive neuroscience has surged over the past decade, making increasing...
contact with questions of social cognition (Ochsner & Lieberman, 2001). In this way, social and personality psychologists have begun to reintegrate neural and biological approaches into the range of methods used to understand the social mind and behavior.

In this chapter, we review the contemporary social neuroscience approach to social-personality psychology. This general approach began to appear with increasing frequency in the laboratories of social psychologists, cognitive neuroscientists, and neurologists during the late 1990s. The term “social neuroscience” was coined in print by Cacioppo and Berntson (1992; see also Carlston, 1994) and tends to describe the broad enterprise of examining the interplay of social and physiological levels of analysis. More recent formulations by Ochsner and Lieberman (2001) and Klein and Kihlstrom (1998) incorporated ideas from cognitive neuroscience and neuropsychological patient literatures, respectively, prompting new aspects of social neuroscience referred to as “social cognitive neuroscience” and “social neuropsychology.” Over the past decade, social neuroscience has been the subject of several dedicated research conferences, culminating in the formation of the Society for Social Neuroscience in 2008 and the Society for Social Neuroscience in 2010. Whereas social neuroscience was seen as a novelty at social-personality meetings merely a decade ago, it is now fully integrated into the social/personality psychologist’s methodological repertoire.

The present volume highlights the interplay of social and personality factors in studies of the mind and behavior. The social neuroscience approach fits this theme well. Integrative at its core, social neuroscience encompasses the study of personality and individual differences as well as situational and environmental effects, as they interface with cognitive processes and neural mechanisms. In this chapter, we use the term “social neuroscience” to refer to this general integrative approach, although it might just as easily be called “social-personality neuroscience.”

In what follows, we begin with an overview of the methodological approaches used in social neuroscience. We then describe social neuroscience research across major areas of social and personality psychology, with a focus on how neuroscience and physiological approaches pertain to social-personality theory.

The Social Neuroscience Approach

Broadly speaking, social neuroscience refers to an integrative approach that can be applied to any scientific question concerning social processes and the brain. However, the types of questions that are addressed with this approach vary considerably across disciplines. To the social psychologist, social neuroscience refers to an interdisciplinary research approach that integrates theories and methods of neuroscience (and other biological fields) to address social psychological questions. To a cognitive neuroscientist, it often refers to research that addresses questions about the neural substrates of social processes, with a focus on understanding neural function. To an animal behaviorist, social neuroscience research may address questions about the neural and hormonal mechanisms associated with low-level social behaviors, such as dominance and affiliation. Thus, many “social neuroscience” studies examine questions outside the typical purview of social-personality psychology, and therefore it is helpful for consumers of this literature to carefully consider the question asked by a particular study. In this section, we describe the two main types of questions asked in human social neuroscience and their corresponding methodological approaches. We also describe the critical role of reverse inference in drawing conclusions from neuroscience findings.

Brain Mapping Approach

Brain-mapping studies ask “Where in the brain is _____?” For example, Where in the brain is fear? Where is episodic memory? Where is love? Where is the self? Human brain mapping is a cornerstone of modern cognitive neuroscience. It concerns the mapping of basic psychological processes to particular regions of the brain.

Early forms of brain mapping involved the probing of exposed brain tissue by a neurosurgeon while a patient reported his or her experience. Today, relatively noninvasive neuroimaging measures, such as functional magnetic resonance imaging (fMRI), are often used for a similar purpose. In cognitive neuroscience, this approach is used to map relatively low-level psychological processes such as basic forms of sensation, perception, and specific aspects of learning and memory. As a general rule, lower-level cognitive processes can be mapped more directly onto specific physiological responses than more complex high-level processes.

In social psychology, researchers have attempted to map very high-level psychological processes, such as social emotions, the self-concept, trait impressions, and political attitudes, onto the brain as well. This is where things get trickier. For example, to study the neural basis of romantic love, researchers have scanned participants’ brains while they viewed pictures of strangers versus their significant others.
Similarly, to study the neural basis of the self, researchers have scanned the brain while subjects judged whether trait adjectives described them versus another person (Kelley et al., 2002; Mitchell, Banaji, & Macrae, 2005). Such studies apply the same logic to identifying the neural substrates of very high-level processes as neuroscientists have applied in the neural mapping of very low-level processes, such as edge detection in vision. Although high-level psychological ascriptions of brain activity may have heuristic value, they may risk obscuring the important low-level mechanisms that the observed brain activations likely represent.

A defining feature of the brain mapping approach is that it seeks to create a valid mapping of psychological processes onto a pattern of neurophysiological responses. Pure brain-mapping studies are undertaken with few prior assumptions about the psychological function of a brain region—indeed, the point of such studies is to establish ideas about function through the process of induction across multiple studies using a variety of conceptually similar tasks and manipulations. This approach is potentially useful for generating new ideas about commonalities in the cognitive processes that may underlie two otherwise distinct psychological functions. For example, some researchers have observed that social exclusion and physical pain activate a common region of the anterior cingulate cortex (figure 6.1; among many other nonoverlapping areas) and concluded that social and physical pain share some common psychological features (Eisenberger, Lieberman, & Williams, 2003; but see Sommerville, Heatherton, & Kelley, 2006). Although this approach does not tell us exactly how or why social and physical forms of pain might be related, simply because the true function of the neural activity is difficult to discern, it nevertheless provokes new ideas about potential relationships between psychological processes. But because brain activations alone are usually ambiguous with regard to their specific psychological functions, they do not always provide a reliable index of a psychological variable. Thus, the brain-mapping approach is not appropriate for testing hypotheses about the relationship between two psychological variables or the effects of an experimental manipulation on a psychological variable.

**Hypothesis Testing Approach**

The hypothesis testing approach in social neuroscience is used to test relationships between psychological variables. This approach begins with the assumption that a particular brain region reflects a specific psychological process. In this regard, it does not concern brain mapping, but instead relies on past research to have already established the validity of neural indicators. For example, a social psychologist who studies intergroup prejudice might hypothesize that implicit racial bias is rooted in mechanisms of classical fear conditioning (Amadio, Harmon-Jones, & Devine, 2003). To test this hypothesis, one might measure brain activity in the amygdala (figure 6.2)—a structure implicated in fear conditioning in many previous studies—while a participant completes a behavioral task designed to elicit implicit racial bias. In this case, the construct validity of the neural measure of fear conditioning (amygdala activity) is already reasonably established (but see Amadio & Ratner, 2011a), and the question concerns not the meaning of brain activations, but experimental effects among psychological variables. It is the hypothesis testing approach of social neuroscience that is of primary interest to social-personality psychologists.

![Fig. 6.1 Medial aspect of the left hemisphere of the brain. mPFC = medial prefrontal cortex, OFC = orbital frontal cortex.](image)

![Fig. 6.2 View of coronal slice through brain, with structures on the left side labeled. AMG = amygdala.](image)
Whereas brain-mapping studies may inform our understanding of the brain, hypothesis-testing studies attempt to inform psychological theories of the mind.

Critically, brain mapping and psychological hypothesis testing approaches should not be combined within a single experiment; major inferential problems occur as a result (Amadio, 2010a). This is because a test of a psychological hypothesis assumes that the mapping of a psychological variable to a neural structure is already established (e.g., that the neural measure has construct validity). The brain mapping approach is used to establish the mapping between a psychological variable and neural structure (i.e., to establish construct validity of the neural measure). When these approaches are combined, there is a risk of defining the neural operationalization of a psychological construct on the basis of whether it supports one’s theoretical hypothesis—an example of tautological inference.

To illustrate, imagine that a researcher wants to test the hypothesis that empathy involves self-reflection. Given previous research linking self-judgments to activity in the medial frontal cortex (mPFC, figure 6.1), he decides to use a measure of mPFC activity during an empathy task (e.g., viewing pictures of people in pain) to index the engagement in self-reflection. However, the region of mPFC that has been linked to the self is rather large and idiographic across individuals and, this area has been associated with several other psychological responses, including mentalizing, evaluation, and self-regulation. Therefore, it is difficult to know whether observed mPFC activity on a given task represents self-reflection or some other process. This ambiguity undermines the construct validity of mPFC activity as a measure of the “self”.

To deal with this problem, the researcher might simply examine a correlation between mPFC activity and scores on an empathy questionnaire to see which, if any, portions of the task-related mPFC activity might relate to empathy. But this can compound the problem. Given his hypothesis that empathy involves self-reflection, the researcher might simultaneously infer that any mPFC region correlated with the questionnaire must be the “self” region (establishing the construct) and that “self” activity is indeed associated with greater empathy (testing the psychological hypothesis). This blurs the important steps of establishing construct validity (brain mapping) and internal validity (hypothesis testing). Because the construct is validated on the basis of the hypothesis-testing correlation analysis, the logic of the test is circular (Amadio, 2010a; Barrett, 2009). This analytical approach is fairly common in social neuroscience research, primarily because the social psychological processes of interest are complex and difficult to localize. Nevertheless, this approach is problematic, and consumers of social/personality neuroscience should be aware of such practices and cautious of their use.

**Reverse Inference**

When considering the two general approaches described above, the issue of *reverse inference* is often a concern. Reverse inference refers to a form of reasoning used heavily in social and cognitive neuroscience to infer the psychological meaning of a brain activation based on previous findings (Poldrack, 2006). In some studies (e.g., simple brain-mapping studies), a psychological process is manipulated and the resulting pattern of brain activity is observed. The inference that the psychological manipulation produced the brain activity may be described as a forward inference, in that the brain activity clearly follows from the manipulation. The inference is based on the known validity of the manipulation. By contrast, the inference of a psychological process from an observed pattern of brain activity is a *reverse inference*. In this case, the precise meaning of the brain activation is ambiguous and inferred from other studies that have used a particular manipulation to activate the same area. The practice of reverse inference becomes increasingly problematic to the extent that the source of inference—in this case, a brain activation—could reflect different psychological processes (Cacioppo et al., 2003; Poldrack, 2006). In studies of low-level vision, reverse inference is a comparatively lesser problem (but still a serious issue). For example, retinotopic mapping of stimuli onto primary visual cortex provides a relatively constrained index of basic visual processing. But as psychological variables become more complex, as they do with social and personality processes, the mapping between a particular brain region and a psychological process becomes less certain. In these cases, reverse inference can be a serious problem.

All cognitive and social neuroscience studies rely on reverse inference. That is, to the extent that a neural activation is interpreted as reflecting a psychological process, the use of reverse inference is unavoidable. However, researchers can take steps to bolster the strength of a reverse psychological inference by enhancing the construct validity of a neural indicator and the strength of their experimental validation.
designs, such as through the careful use of theory, converging evidence from other studies (including animal research), and the use of behavioral tasks that provide valid manipulations of a construct and interpretable behavioral data.

What Types of Social and Personality Questions Are Amenable to a Neuroscience Analysis?
9 First and foremost, the brain is a mechanism, and an extremely complex one at that. Hence, neuroscience models and methods are especially useful for the study of psychological mechanisms, such as those involved in action control, perception, and attention. Psychological phenomena that are not mechanisms, but correspond more closely to appraisals (e.g., attitudes and beliefs), subjective psychological states, abstract psychological structures (e.g., the self), and high-level representation, may be less amenable to a neuroscience level of analysis. For a social/personality psychologist who is considering the potential benefit of a neuroscience approach, the most critical issue is whether one’s question concerns basic psychological mechanisms. Can the components of one’s mechanistic model be described in terms of low-level functions, such as perception, sensation, low-level cognition, and low-level motivation? If so, then neuroscience models may be particularly useful. If the psychological phenomena of interest cannot be conceptualized at a low level of analysis, but rather are most meaningful at a high level of construal (e.g., the self), then it may be more difficult to make valid inferential connections between psychological theory and the brain.

Methods of Social and Personality Neuroscience
37 Contemporary social neuroscience makes use of a wide range of methods that are often used in combination with the more traditional tools of personality and social psychology. In addition to new technologies for measurement, social neuroscience methodology relies on the use of careful experimental designs, valid manipulations of psychological states and processes, and careful inference and interpretation. Here, we describe the most prominent methods currently used in the field and briefly discuss their relative advantages as they relate to experimental designs, issues of construct validity, and psychological inference. A more detailed description of methods in neuroscience approaches to social and personality psychology is provided by Harmon-Jones and Beer (2009), and recent discussions of inference and validity in social neuroscience can be found in Amodio (2010a), Barrett (2009), and Cacioppo et al. (2003).

Early studies taking a social neuroscience approach primarily used peripheral physiological measures, such as electrocardiogram (e.g., heart rate), galvanic skin response (i.e., skin conductance, a measure of sympathetic activation vis-à-vis palm sweating), and electromyography (e.g., measures of facial muscle activity related to emotional expressions). More recently, neuroimaging measures have become popular. The two most common neuroimaging techniques include functional magnetic resonance imaging (fMRI), which measures the flow of oxygenated blood in the brain, and electroencephalography (EEG), which measures electrical activity produced from the firing of neuron populations. EEG is used to examine event-related potentials (ERPs), which represent a burst of EEG activity in response to a discrete event, such as a stimulus presentation or subject response. fMRI yields high spatial resolution and thus is optimal for determining the location of activity. But because it assesses slow-moving blood flow, its temporal resolution is slow. By contrast, EEG/ERP yields high temporal resolution and is thus optimal for assessing the timing of a neural process, but its spatial resolution is comparatively poor. Given their relative strengths, researchers may select fMRI or EEG methods to suit their particular question, or use both approaches in complementary studies within a program of research. Neuroimaging and psychophysiological approaches may also be combined with measures of hormones, immune factors, and DNA, for example, to provide convergent evidence for a physiological process of interest. However, as with traditional methods in social-personality psychology, the utility of these measures depends on the quality of the question, the experimental paradigm, and careful interpretation.

Major Content Areas of Social Neuroscience
In this section, we provide a broad review of the social neuroscience literature in the areas of social cognition and the self, attitudes, emotion and motivation, intergroup relations, and individual differences. Although our review distinguishes these five areas of research for convenience, their content overlaps substantially. In each area, we will integrate methods and levels of analysis, and we will discuss how research in each area has contributed to social/personality psychology theories.
Social Cognition and the Self

The earliest studies conducted at the intersection of social psychology and neuroscience examined basic processes of automaticity and control, as well as the processing involved in perceiving the self and other people. Together, these areas of research have laid the foundation for social neuroscience studies of more complex social-personality processes.

Automatic and Controlled Processing

Theories of automatic and controlled processes represent a cornerstone of modern social cognition. Mechanisms of automaticity and control also constitute a central topic in cognitive psychology, and thus a large body of cognitive neuroscience research has been devoted to their elucidation. These processes have been studied primarily in two different broad research literatures on memory and cognitive control.

Automaticity

Research on systems of learning and memory is particularly relevant to social-personality theories of automaticity and implicit processes. Traditional models of learning and memory often distinguish between neural correlates of explicit (declarative) and implicit (nondeclarative) memory processes, and neuroscience research suggests these forms of memory reflect distinct neural substrates (Squire & Zola, 1996). Although implicit and automatic refer to different properties of a process (i.e., degree of awareness vs. degree of intentionality), implicit forms of memory, such as classical fear conditioning and procedural memory (i.e., skill or habit learning), have important automatic characteristics and thus are relevant to the present discussion. Studies of nonhuman animals have identified the amygdala as a critical structure in the learning and expression of fear conditioning (LeDoux, Iwata, Cicchetti, & Reis, 1988; Fendt & Fanselow, 1999), a role that has been corroborated in fMRI studies of fear conditioning in humans (LaBar, Gatenby, Gore, LeDoux, & Phelps, 1998). The neuroscience research suggests that automatic fear-related responses function somewhat independently from other types of automatic responses.

Other research on procedural memory has focused on the basal ganglia, a set of interconnected structures that include the striatum (figure 6.2; caudate, putamen, and nucleus accumbens), globus pallidus, and their dopaminergic inputs from the midbrain (substantia nigra and ventral tegmentum). Research has identified regions of basal ganglia as being critical for implicit skill learning, such as when subjects learn response associations that are embedded implicitly in a task procedure (Foerde, Knowlton, & Poldrack, 2006; Squire & Zola, 1996). These forms of learning and memory more closely resemble the type of automatic processes studied in the social and personality psychology literature, in that they drive actions that may be activated and implemented without conscious awareness or intention. It is notable that, in recent years, studies of economic decisions and reward learning have also focused on the role of basal ganglia, but as a substrate for error prediction or the computation of reward (O’Doherty, Camerer, Schultz, & Rangel, 2008). Research has yet to resolve these different interpretations. However, given the strong anatomical connectivity between the basal ganglia and motor cortices and PFC regions linked to goal representations, the interpretation that the basal ganglia are centrally involved in goal driven behaviors (including automatic responses) remains plausible.

In the social cognition literature, automaticity is often demonstrated on sequential priming tasks, when a prime word is shown to facilitate the categorization of an associated target word (Gaertner & McLaughlin, 1983; Dovidio, Evans, & Tyler, 1986). This idea was originally adapted from cognitive psychology research on semantic associations between words, such as “bread-butter” or “doctor-nurse” (Meyer & Schaneveldt, 1971, 1976). In fMRI studies, semantic priming has been associated with activity in left posterior PFC (figure 6.3; e.g., Blaxton et al., 1996; Demb et al., 1995; Raichle et al., 1994; Wagner, Gabrieli, & Verfaellie, 1997) and temporal cortex (Rismann, Eliassen, & Blumstein, 2003; Schacter & Buckner, 1998; Squire, 1992), as well as...
reduced activity in regions linked to attention (e.g., in the parietal cortex, figure 6.3; Gabrieli, 1998). Given other research implicating the left PFC in approach-related motivation and action tendencies (Harmon-Jones, 2003), this pattern of neural correlates suggests a link between automatic semantic processes and goal-driven behavior (Amodio, 2008), consistent with the idea that “thinking is for doing” (Fiske, 1992).

Together, the neuroscience research on fear-conditioning, procedural memory and reward, and semantic associations has helped to distinguish different types of automatic processes. In doing so, they clarify the functions of automaticity and shed new light on how automatic processes operate and change. These advances have already begun to inspire new theories of implicit social cognition (e.g., Amodio & Ratner, 2011b).

Control
Cognitive neuroscience research on mechanisms of control has examined subjects’ brain activity while they completed classic cognitive control tasks, such as the Stroop color naming task, the Eriksen Flankers Task, or the Go/No-Go task. Tasks such as these typically include two main types of trials, which require either a high or low degree of control. In one set of trials, subjects make responses that are facilitated by existing semantic associations (e.g., the color-naming Stroop task), perceptual cues (e.g., the Eriksen Flankers task), or expectancy (e.g., the Go/No-Go). Responses on these trials are thought to benefit from automatic processing. On other trials, the participant must override the automatic influence in order to deliver the correct task response. Control-related behavior on these tasks has been consistently associated with activity in the anterior cingulate cortex (ACC) and PFC regions of the brain.

In particular, the ACC responds to instances when a prepotent, or automatic, response is inconsistent with the task goal, such as when the text of a color word interferes with one’s goal to name the ink color (Carter et al., 1998; MacDonald, Cohen, Stenger, & Carter, 2000). Botvinick, Braver, Barch, Carter, and Cohen (2001) proposed that the ACC serves a conflict monitoring function, such that it is involved in detecting conflict between alternative response tendencies and, when conflict arises, it signals regions of the PFC involved in implementing one’s intended response over other tendencies. Consistent with the conflict monitoring hypothesis, anatomical research on monkeys has revealed that the ACC is strongly interconnected with motor structures as well as PFC regions associated with high-level representations of goals and actions (Miller & Cohen, 2001). Some researchers have extended this theorizing to suggest that ACC activity on control tasks may simply reflect a distress signal or social pain (Eisenberger et al., 2003; Inzlicht, McGregor, Hirsh, & Nash, 2009). However, most cognitive control tasks that elicit ACC activity do not involve distress or pain, complicating this interpretation. Finally, several studies have shown that conflict-related ACC activity occurs in the absence of awareness (Berns, Cohen, & Mintrun, 1997; Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001), suggesting that it represents a preconscious component of control that initiates the engagement of more deliberative components. The findings of cognitive neuroscience research on conflict monitoring and control have been applied to questions regarding self-regulation in social-personality contexts such as stereotyping and prejudice (Amodio, Shah, Sigelman, Brazy, & Harmon-Jones, 2004; Amodio, Kubota, Harmon-Jones, & Devine 2006; Amodio, Master, Yee, & Taylor 2008; Bartholow, Dickter, & Sestir, 2006), individual differences related to anxiety and neuroticism (Amodio, Master, et al., 2008; Robinson, Ode, Wilkowski, & Amodio, 2007), political orientation (Amodio, Jost, Master, & Yee, 2007), religiosity (Inzlicht et al., 2009), and social exclusion (Eisenberger et al., 2003).

Although several regions of the PFC are activated during attempts at response control, a general pattern has been observed in the literature whereby left-sided PFC regions are associated with the implementation of intended actions, whereas right-sided PFC activity has been associated with the intentional inhibition of action (Aron, 2007). It is notable that EEG and fMRI research is almost always conducted on right-handed participants, and observed hemispheric asymmetries in patterns of control are likely related to the lateral specialization of hand (and foot) dominance (Harmon-Jones, 2006).

In sum, cognitive neuroscience research on control has highlighted different subcomponents of controlled processes, with aspects of these subcomponents have been considered in previous social and personality psychology theories (e.g., Wegner, 1994; Wegener & Petty, 1997), the neuroscience literature has provided important clarifications of these components, as well as methods for assessing aspects of control that function rapidly and without conscious awareness. Amodio, Harmon-Jones
1 **PERCEPTION OF THE SELF AND OTHERS**

2 **The Self**

3 The self is one of social-personality psychology’s most ancient and most enduring constructs (see Crocker & Canevello, chapter 11, this volume) and, not surprisingly, it was among the first constructs to be examined in neuroscientific studies of social psychological processes (e.g., Craik et al., 1999; Klein, Loftus, & Kihlstrom, 1996). Most of this research has examined brain activity associated with self-reflection and judgments about the self in comparison to judgments of others (see also Uleman & Saribay, chapter 14, this volume). Using positron emission tomography (PET) to measure cerebral blood flow, Craik et al. (1999) found that judgments of trait words as relating to the self versus others were associated with large activations in the mPFC. In a similar study that used fMRI, Kelley et al. (2002) found that reflections on one’s own traits activated a region of ventral mPFC to a greater extent than did reflecting on the traits of another person (in this study, George W. Bush). The finding of ventral mPFC activity in response to self-related judgments has been replicated in several studies (e.g., Gutches, Kensinger, & Schacter, 2007; Heatherton et al., 2006; Kircher et al., 2002; Pfeifer, Lieberman, Dapretto, 2007; Saxe, Moran, Scholz, & Gabrieli, 2006; Schmitz, Kawahara-Baccus, & Johnson, 2004; Turner, Simons, Gilbert, Frith, & Burgess, 2008; Zhang, Lawon, Guo, & Jiang, 2006; Zhu, Zhang, Fan, & Han, 2007). Studies of other aspects of the self, such as agency and self-discrepancies, have observed regions of the brain typically involved in more general aspects of visual perception, conflict monitoring, and cognitive control (Blakemore, Oakley, & Frith, 2003; Farrer et al., 2008). Thus, brain activations during self-related judgments likely pertain to the process of self-reflection, but not to other aspects of self-related processing.

4 Although neuroimaging research on the self is a popular area of research in social cognitive neuroscience, the findings of this area of research must be considered in light of some important interpretational concerns. For example, in Kelley et al. (2002), the activity level of the mPFC during judgments of the self and other was lower than activity during a baseline condition, in which participants viewed a fixation cross on the computer display. That is, self-related processing is often associated with a deactivation in mPFC activity relative to baseline. This below-baseline effect is observed in most studies of the self, and it represents a major interpretational problem. If mPFC activity reflects “self” processing, why would this region be more activated when subjects stare at a fixation point than when they are explicitly reflecting on the self? This observation has led some researchers to suggest that research participants spontaneously focus on the self when at rest (to a greater extent than when instructed to think about the self), and this observation has prompted theories about a baseline “default” network of brain activity that supports thoughts about the self and other people (e.g., Gusnard, Akbudak, Shulman, & Raichle, 2001; Gusnard & Raichle, 2001). Although the idea that humans reflect on the self and others by default is interesting, it is inconsistent with daily diary research showing that, when probed at random points during the day and asked to report on what one was doing at the moment, participants rarely (8% of 4,700 responses) reported that they were engaged in some form of self-reflection (Csikszentmihalyi & Figurski, 1982). Ultimately, a construct like “the self” is a very broad and complex construct that may not be easily localized to a circumscribed set of neural structures.

5 **Perceiving Faces**

6 Information about conspecifics and social relationships is eminent in perception and cognition, and the initial stage of social processes often begins with face perception (see Uleman & Saribay, chapter 14, this volume). Research on visual perception suggests that some components of the visual system are specialized for seeing faces, and these face-specialized processes have been localized in the fusiform gyrus in fMRI studies (figure 6.1; Kanwisher, McDermot, & Chun, 1997). Although the idea of a specialized face area has been debated, with some arguing that fusiform responses to faces reflect expertise rather than a “face module” (Haxby, Hoffman, & Gobbini, 2000), the finding that this region responds to faces more than to other objects is consistent.

7 Faces are also known to elicit a characteristic ERP component that peaks 170 ms after the presentation of a face. This “N170” component is consistently larger to faces than to nonface stimuli that are matched on other visual dimensions (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Carmel & Bentin, 2002), making it a valuable neural marker of the engagement of low-level face-specific perception processes marking the encoding of facial features (e.g., Eimer, 2000). The N170 is believed to reflect activity in multiple temporal-occipital structures linked to face processing (Deffke et al., 2007), including the fusiform (figure 6.1; e.g., Haxby, 2000).
Once an object is perceived as a face, a perceiver rapidly begins to evaluate and infer information about the individual (Todorov, Said, Engell, & Oosterhof, 2008). The process of inferring another person’s unique motives and perspectives is referred to as mentalizing, which is the process underlying one’s theory of mind (Frith & Frith, 1999). Early studies of mentalizing in the brain used PET to measure activity involved in inferences about the thoughts of other people or characters. These studies were motivated in part by an effort to understand autism and its links to deficits in theory of mind (Frith, 1989; Baron-Cohen, Tager-Flusberg, & Cohen, 1993). In this line of research, theory of mind is best characterized by tasks involving false belief or deceptive intent—tasks on which successful performance depends on one’s ability to take another person’s perspective. In an early study on this topic, Fletcher et al. (1995) examined brain activity while normal subjects read a set of short stories. Mentalizing stories involved jokes or lies as a literary device—that is, they made sense to the extent that the reader understood that a character was the victim of a lie or joke. Hence, the stories required an understanding of a character’s false belief. Control stories did not rely on such devices, but rather involved straightforward physical descriptions. Although several brain regions were activated by these stories, only the mPFC was uniquely more active during the mentalizing stories. A similar set of mentalizing activations were observed in another study when subjects viewed movies of people showing deceptive intent (Grezes, Frith, & Passingham, 2004).

Castelli, Happe, Frith, and Frith (2001) connected their findings with the attribution literature in social psychology by measuring brain activity while participants viewed a set of videos inspired by the famous Heider and Simmel (1944) animations, in which three shapes moved in an anthropomorphic fashion that implied human interaction. The authors found that the viewing of this type of animation also elicited mPFC activity, compared with control videos in which the movement of the shapes was not interpreted anthropomorphically. More recent work has linked the process of dispositional attribution to activity in the mPFC (Harris, Todorov, & Fiske, 2005; cf. Heider, 1958). Since these initial studies, a large body of research has associated activity of the mPFC with a range of tasks involving mentalizing and complex aspects of person perception (Amadio & Frith, 2006; Frith & Frith, 1999; Saxe, Carey, & Kanwisher, 2004). These tasks also typically elicit activity in regions of the superior temporal lobe (or temporal-parietal junction) and the temporal poles—regions associated with the perception of biological motion and to conceptual representations of social information, respectively (Frith & Frith, 1999). Converging findings from the developmental literature corroborate the idea that mPFC development underlies the emergence of theory of mind abilities in children (Bunge, Dudukovic, Thomason, Valdy, & Gabrieli, 2002).

Since the initial finding that mentalizing activated regions of mPFC, researchers have asked whether other forms of person perception might involve the same brain regions. A series of studies by Mitchell, Macrae, and colleagues proposed that social-cognitive aspects of person perception, such as the ascription of trait attributes to a person, might also activate areas of mPFC (even if they do not necessarily require mentalizing). For example, when subjects judged noun-adjective word pairs that described a person, compared with those describing an inanimate object, activity was found in regions of interest within the mPFC, as well as areas of the temporal cortex and the temporal-parietal junction (figure 6.3; Mitchell, Heatherton, & Macrae, 2002). This pattern of activity has been seen across several studies using similar tasks (e.g., Mitchell et al., 2005; Mitchell, Macrae, & Banaji, 2002). In response, researchers have observed activity in similar regions when simply viewing faces in an easy memory task (Gobbini, Leibenluft, Santiago, & Haxby, 2004), demonstrating that activity in this region to faces does not necessarily imply the inference of traits. Some research has found that viewing and making trait judgments of unfamiliar faces or dissimilar people is associated with activity in more dorsal regions of the mPFC, whereas more familiar and/or similar faces are associated with activity in more ventral regions, near areas activated by self-reflection (Gobbini et al., 2004; Mitchell et al., 2006). It is important to note that the split into two sentences here.
notable, however, that the mPFC is a large region of cortex, and the specific locus of person-related activity varies considerably across studies (Gilbert et al., 2006).

As with neuroimaging studies of the self, activity associated with forming impressions of both people and inanimate objects is typically lower than baseline mPFC activity (e.g., Mitchell, Macrae, & Banaji, 2004). If the process of person perception is truly located in the mPFC, then the data imply that subjects engage more strongly in person perception during baseline periods (i.e., viewing a fixation cross) than when they are explicitly engaged in the person perception process. This explanation assumes that people naturally reflect on others when at rest (presumably while also thinking about the self; but see Csikszentmihalyi & Figurski, 1982). As with interpretations of the mPFC as reflecting activation of the self, this issue complicates the idea that the mPFC is the neural substrate of person perception.

Other researchers have proposed that this region serves a domain-general process of coordinating one’s responses with complex (e.g., externally guided) plans (Amodio & Frith, 2006; Amodio et al., 2006), such as when a research subject prepares for an upcoming trial during intertrial intervals (when mPFC activity is usually highest). This interpretation of mPFC function helps to account for the broad range of findings involving this region.

Although the potential contribution of mapping abstract constructs like “the self” and “social cognition” to theories of social-personality psychology has yet to be established, fMRI research on mentalizing, person perception, and the self has inspired interesting debates about the processes through which a person judges another’s thoughts or intentions. For example, “simulation” theory posits that people consider how they would respond in the other person’s situation and then respond to that person accordingly. “Theory” theory posits that people have an implicit theory of how a person would respond in a particular situation and, rather than reflecting on the self, form their perceptions based on this theory. As evidence for “theory” theory, some researchers have noted that brain activity associated with self and other judgments is related to different regions of the mPFC, implying that people do not activate representations of the self when considering the responses of others (Saxe, 2005). Other researchers have argued in favor of simulation theory, based on the observation that judgments of similar or familiar others activate a region close to areas activated by self-reflection, (Mitchell, 2005). Although a lively debate, these interpretations are tentative because they have relied primarily on reverse inferences about the function of brain areas (cf. Poldrack, 2006), assuming that these regions of the mPFC truly represent the “self” and “social cognition”. Indeed, the strongest evidence in such debates comes from behavioral studies, which provide more clearly interpretable data (Saxe, 2005).

Empathy

Empathy is broadly defined as concern for another’s welfare (Batson, 1991). By some definitions, empathy involves experiencing another’s perspective and affective response (Lamm, Batson, & Decety, 2007; see also Castano, chapter 17, this volume). As with mentalizing and theory of mind, empathy is complex and involves a broad set of neural and psychological processes associated with affect, perception, social cognition, self-regulation, mimicry, and action (Decety, 2010). Building on neuroscience studies of mentalizing, research on the neural substrates of empathy have focused primarily on the role of the mPFC (Decety, 2010; Rameson & Lieberman, 2009). Many studies have examined empathy by measuring brain activity while a subject views another person experiencing pain. For example, Singer et al. (2004) used fMRI to measure brain activity while participants experienced a painful stimulus or viewed a loved one receiving the same stimulus. A set of structures, including the rostral ACC and anterior insula, were active in both conditions, relative to baseline. Rostral ACC activity was greater in response to observing a loved one’s pain among subjects with higher scores on a trait empathy scale. Other research has found similar brain regions to be more strongly activated when participants observed racial ingroups experiencing pain than racial outgroups (Xu, Zuo, Wang, & Han, 2009). There are also suggestive findings from lesion patient studies, in which damage to the ventromedial PFC and ACC are associated with impaired empathy (Shamay-Tsoory, Tomer, Berger, & Aharon-Peretz, 2003). Given that the ACC is involved in a wide range of processes involving expectancy violation, these findings may reflect some aspect of expectancy violation or concern when either the self or another person is subjected to pain, rather than suggesting that empathy is related to the experience of pain per se. Overall, this body of research has focused primarily on the brain mapping of empathic processes.
Related to work on empathy, a “mirror neuron” system has been proposed as a brain network devoted to understanding other people through their actions (Iacoboni & Dapretto, 2006). The mirror neuron idea originated from single-unit recording in the macaque premotor cortex, in which the same neuron fired when the monkey moved its arm toward the reward and when it watched an experimenter move its arm toward the reward (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996).

“Mirror neuron” is not a literal term, in the sense that no single neuron can be described as providing a mirroring function. Rather, “mirror neurons” refer loosely to areas of the brain that are activated both when an individual observes the behavior of another person, and when one performs the same behavior. Brain regions implicated in the “mirror neuron” network include premotor cortex, inferior frontal cortex, superior temporal sulcus, anterior insula, and the amygdala (Iacoboni & Dapretto, 2006; Rizzolatti & Sinigaglia, 2010), although the patterns and locations of activity in these regions vary considerably from study to study. Although the notion that we relate to other people by representing their actions and mental states in the same way we represent our own actions and states has intuitive appeal, more recent theoretical analyses have questioned the plausibility of mirror neurons as mechanisms of action understanding (Decety, 2010; Hickock, 2009; Saxe, 2005; Vivona, 2009). Aside from questions about the neural substrates, the fact that so many social interactions often require complementary responses (e.g., when conversing or dancing), rather than mimicry, calls into question the idea that human social behavior is rooted in a mirroring system. Hence, more research will be needed to assess the utility of the mirror neuron idea.

Humanization

Humanization refers to the process of seeing another person as possessing the characteristics unique to the human species, including the human rights associated with being a member of society. Hence, dehumanization refers to the process of denying a person these qualities (Haslam, 2006). High status groups and members of one’s ingroup are typically perceived as possessing these qualities; low-status individuals and members of the outgroup are often seen as lacking these qualities (Leyens et al., 2001; Leyens et al., 2003). The process of “humanization” is also associated with empathy and mentalizing, but whereas humanization processes typically apply only to people, empathy and mentalizing may also relate to nonhumans and inanimate objects, as a form of anthropomorphism (Epley, Waytz, & Cacioppo, 2007). Research on dehumanization has connected the neuroscience work on mentalizing and the mPFC to the topic of intergroup relations (Harris & Fiske, 2009). For example, a study by Harris and Fiske (2006) demonstrated that mPFC activity was greater when participants viewed pictures of valued others (e.g., members of the ingroup, people of high social status) compared with “dehumanized” individuals, such as drug abusers and homeless people.

Why the mPFC?

What is the significance of the mPFC as it relates to the self, person perception, and mentalizing? Mitchell argued (2009) that the fact that these “social” processes all activate the same general brain region indicates that social psychology is a “natural kind,” meaning that social psychological processes have a unique and privileged place in neural activity. Taking a different approach to this issue, Amodio and Frith (2006) considered the neuroanatomical properties of the mPFC in its relation to social cognition. They noted that the mPFC is a highly interconnected region of brain uniquely situated to integrate information about internal processes (e.g., motor responses, visceral states) and higher-level representations of goals, reward contingencies, and complex expectancies. In their analysis, the mPFC is thought to be involved in any processes that involve a complex interplay of internal states and the tracking of abstract external contingencies for one’s response—a type of process exemplified by social cognition. According to this view, the mPFC is not the neural instantiation of the self or social cognition, and “social psychology” is not a natural kind in the brain. Rather, thinking about the self and others is most likely to involve the neural and cognitive processes supported by this region. More research is needed to understand the significance of the mPFC for social cognition.

To date, social neuroscience research on social-cognitive processes, as has those reviewed above, has primarily focused on brain mapping. In this way, it has been primarily exploratory and used to elucidate the understanding of neural function. How has this research informed social-personality psychology? Neuroscience studies of cognitive control have informed social psychological theories by delineating different components of the self-regulatory process.
Similarly, neuroscience research on learning and memory systems has provided a useful framework for understanding automatic and implicit forms of social cognition (Amodio, 2008; Amodio & Ratner, 2011b). By contrast, the contribution of extant brain-mapping studies of the self and person perception for theories of social-personality psychology remains less clear.

Attitudes

The attitude is a foundational construct in the field of social psychology (Thurstone, 1928; see also Ajzen, chapter 15 this volume), and attitudes were the subject of the earliest psychophysiological studies of social psychological processes. Rankin and Campbell (1955) measured changes in skin conductance levels (i.e., galvanic skin response) while White participants in their study interacted with White and Black experimenters. Skin conductance responses, which reflect activity of the sympathetic nervous system, were interpreted as instances of heightened anxiety. Although participants in their study reported similar liking for the two experimenters, they exhibited larger skin conductance responses to Black than White experimenters on average. The authors interpreted the results as evidence for negative attitudes toward African Americans—the first evidence of implicit racial bias.

The attitude construct is complex, and although it is often defined simply as liking/disliking, the psychological and physiological processes that give rise to an attitude are very complicated. The classic tripartite model of attitudes includes cognitive, affective, and behavioral components. However, at the physiological level of analysis, an attitude likely corresponds to several other processes, such as motivational tendencies, action representations, changes in attention, and basic motor tendencies, among others. For this reason, it is very difficult—and perhaps inadvisable—to map the high-level construct of an attitude onto specific physiological systems. Indeed, there are ongoing debates on whether an “attitude” is properly conceptualized as an abstract appraisal or a psychological mechanism (Fazio, 2007; Harmon-Jones, Harmon-Jones, Amodio, & Gable, in press; Schwarz, 2007). To the extent that an attitude is not defined as a mechanism, a neuroscience analysis of attitudes may not be useful. If a researcher is simply interested in assessing a subject’s affective response to an object, peripheral physiological responses may provide more useful indicators.

The use of physiological methods to examine attitudes was developed significantly by the research of Cacioppo and his colleagues. These methods allowed researchers to assess changes in a participants’ response unobtrusively and often unconsciously, using a range of physiological indicators including skin conductance (Cacioppo & Sandman, 1978), heart rate (Cacioppo, Sandman, & Walker, 1978), facial EMG (Cacioppo & Petty, 1979), EEG spectral power (Cacioppo, Petty, & Snyder, 1979), and ERPs, among others. This early social psychophysiology research on attitudes focused on the psychological processes involved in persuasion, which leads to attitude change. Of special interest was the role of information processing. For example, Cacioppo and colleagues focused on asymmetries in parietal cortical activity associated with semantic versus nonsemantic processing of a stimulus (e.g., Cacioppo, Petty, & Quintanar, 1982). This focus contrasts with other researchers’ focus on hemispheric asymmetries in frontal cortical brain regions that were associated with emotion and motivation (Davidson & Fox, 1982). Other research examined subtle and implicit affective responses to pro- versus counterattitudinal messages by measuring subtle changes in facial expressions during message processing (Cacioppo & Petty, 1979). Cacioppo and Petty’s early use of psychophysiological methods to study attitudes and persuasion blazed the trail for future neuroscience approaches in social and personality psychology.

Peripheral physiological measures have been especially useful for assessing the affective component of attitudes, by way of assessing arousal (e.g., Rankin & Campbell, 1955). However, skin conductance measures are limited because they cannot distinguish between positive versus negative responses. In order to draw stronger inferences about the valence of a physiological response, facial EMG may be used to measure activity in muscle groups associated with different facial expressions linked to emotion (Dimberg, 1982; Cacioppo & Petty, 1979). Activity of the corrugator supercili muscle, located just above and running parallel to the brow, is commonly described as brow-furrowing, and it is associated with many forms of negative affect, including anger and disgust. Activity of the zygomaticus major muscle, which runs across the cheek from the corners of the mouth to the cheekbones, is related to smiling, and it is associated with many forms of positive affect. Thus, EMG provides information about an emotional expression, from which researchers may infer valence.
approach/withdrawal orientation, or any other psycho-
ological process linked to a facial expression.

Although emotional expressions can usually be
observed directly, EMG allows researchers to quant-
tify their activity with precision, providing continu-
onous online assessments of affective response without
requiring an overt response from the participant.
Facial EMG has also been shown to be sensitive to
microexpressions—changes in facial muscle activity
that are imperceptible to the naked eye (Cacioppo,
1965). This ERP component was named the P300,
a positive-going ERP response approximately 300–
400 ms following the stimulus (Sutton, Braren, Zubin, & John,
1965). This ERP component was named the P300,
for its positive polarity and its approximate peak at
300 ms. However, given that the latency of its peak
varies considerably across tasks, it is often referred
to as the P3 (because it is the third positive-going
peak following the stimulus) or late positive potential
(LPP). The P3 was interpreted as reflecting the
engagement of attention, associated with a surprise
response, and the updating of one’s mental set
(Donchin, 1981). More recent research has linked
the LPP to activity of norepinephrine systems in
response to an unexpected event (Nieuwenhuis,
Aston-Jones, & Cohen, 2005), suggesting the LPP
reflects a complex set of processes associated with
attention and arousal.

Cacioppo, Crites, Berntson, and Coles (1993)
noted that the LPP component, in conjunction
with the oddball task, could be used to assess indi-
viduals’ evaluations of attitude objects. For example,
the authors found that a negative “oddball” stimu-
lus that appeared within a series of positive objects
elicited an LPP response, much like a high-pitched
tone amongst a series of low-pitched tones. Other
research showed that the magnitude of the evaluative
oddball effect varied as a function of its evaluative
extremity, such that extremely negative trait
words elicited larger LPP amplitudes than moder-
ately negative trait words, when they were embed-
ded within a series of positive words (Cacioppo,
Crites, Gardner, & Berntson, 1994; Crites &
Cacioppo, 1996; Ito, Larsen, Smith, & Cacioppo,
1998). These LPP effects were also found to be sen-
titive to individual differences in attitudes, such that
they were responsive to subjects’ ideographically
liked versus disliked objects (Crites & Cacioppo,
1996). The LPP/oddball method of attitude assess-
ment has even been shown to reveal people’s true
attitudes when they attempted to misreport the atti-
itude (Crites, Cacioppo, Gardner, & Berntson,
1995) or when implicit evaluations differed from
explicit task instructions (Ito & Cacioppo, 2000).
This technique of examining attitudes by measuring
the LPP during the oddball task has since been used
to assess a variety of attitudes, including intergroup
attitudes (as described below).

Hemispheric asymmetries in ERP responses have
also been related to attitudes. In one study, Cunning-
ham, Espinet, DeYoung, and Zelazo (2005) mea-
sured the LPP while participants made evaluative
(good vs. bad) and nonevaluative (abstract vs. con-
crete) judgments about socially relevant concepts.

The concepts were then rated for goodness and bad-
ness. Concepts rated as “bad” caused greater LPPs
over the right frontal hemisphere, while concepts
rated “good” caused greater LPPs over the left
frontal hemisphere. Similarly, van de Laar, Licht,
Emotion and Motivation

Affect and emotion range from relatively low-level aspects of reward and punishment; to discrete basic emotions, such as joy, anger, and fear; to highly complex emotion processes such as guilt, jealousy, compassion, and schadenfreude (see Clore & Robinson, chapter 13, this volume), and they are almost always intertwined with motivation.

Although some research has attempted to study brain activations unique to complex emotional responses (e.g., Moll, Zahn, Oliveira-Souza, Krueger, & Graffman, 2005), interpretation of such findings is difficult (Barrett & Wager, 2006). Indeed, a meta-analysis of brain activations in response to manipulations of different emotional states failed to reveal clear patterns of activity for specific emotional states (Phan, Wager, Taylor, & Liberzon, 2002).

Although one could interpret this finding as evidence against mechanistic distinctions among different emotions, this pattern of null results likely reflects the limitations of trying to assess fine-grained processes using comparatively coarse measures (e.g., fMRI) and methods (e.g., meta-analysis).

Like attitudes, emotion constructs correspond to a complex set of more basic processes at the neurophysiological level of analysis and, therefore, common distinctions in the subjective experience of emotions should not cleanly map onto the organization of the brain and physiology. For this reason, most progress has been made in studying the neural processes associated with lower-level emotion processes, such as motivational, attentional, and autonomic processes, and basic mechanisms underlying fear and reward responses.

At the physiological level of analysis, emotional processes overlap substantially with motivational processes. In the affective neuroscience literature, it is generally assumed that approach motivation and responses to rewards involve a positive affective system, whereas avoidance motivation and responses to punishments involve a negative affective system.

Indeed, motivational dispositions toward approach and withdrawal are often associated with emotions. However, an emotion is not a single “thing,” but the learning and coordination of motor plans linked to reward-driven actions (Alexander, DeLong, & Strick, 1986). This line of research on evaluations is useful because it links evaluation processes more directly to goals and behavior, whereas contemporary social psychology research on attitudes focuses on the representation of attitudes in cognition, with less emphasis on links to behavior.
rather a multicomponent process made up of basic processes such as feelings of pleasure or displeasure, facial/body expressions, particular appraisals, and particular action plans and activation states (Frijda, 1993). Moreover, these components are not perfectly correlated with one another (Lang, 1995).

Approach and withdrawal motivational processes likely involve neural systems rather than specific brain structures. However, a systems-level analysis of approach-withdrawal motivation has yet to be thoroughly investigated due to the empirical difficulties of mapping the precise timecourse of these microprocesses. In addition, much of the research on the neuroscience of emotion and motivation has proceeded under a “brain mapping” approach rather than a “hypothesis testing” approach, as defined earlier. Consequently, this review will focus on brain regions that have received the most research attention. These are the amygdala, nucleus accumbens/ventral striatum, the orbitofrontal cortex, and the prefrontal cortex. While considering the reviewed research, it is important to keep in mind the difficulty of making one-to-one associations between psychological processes and physiological processes. For example, if fMRI data indicate amygdala activity in response to viewing a face, it is almost impossible to claim that this activation reflects a certain psychological variable like fear, given that different subnuclei of the amygdala support a wide range of psychological variables, including uncertainty (Whalen, 1998), positive affect (Anderson et al., 2003), and motivational relevance (Cunningham, Van Bavel, & Johnsen, 2008).

Perception of Motivational Relevance

Many of the stimuli that arouse motivation are perceived via the visual or auditory system. Novel and significant events attract our attention and engage the orienting response, and they are typically associated with approach and avoidance behavior (Thorndike, 1911) or the emotion evoked by an event (Bradley, 2009; Maltzman, 1979). The processes of orienting and attending have been posited to “stem from the activation of defensive and appetitive motivational systems that evolved to protect and sustain the life of the individual” (Bradley, 2009, p. 1). In this way, attention, emotion, and motivation are inextricably linked. Emotion is often theoretically defined, fundamentally, as a disposition to act, or to behave effectively to events that threaten or promote life (Frijda, 1986; Lang, 1985). The associated motivational tendencies are realized in general systems of approach and avoidance, with approach processes often acting to promote survival and avoidance processes often acting to prevent threats to well-being. Some theorists suggest that judgments of positivity reflect approach motivation, judgments of negativity reflect avoidance motivation, and judgments of arousal index the intensity of activation or motivation (Bradley, 2009). Although this may often be the case, the relationship between emotional valence and motivational direction (i.e., approach motivation is positive) is not always so direct. For instance, anger, a negatively valenced emotion, is often associated with approach motivation (Carver & Harmon-Jones, 2009). We return to this point later.

Fear Processing

As noted above, human neuroimaging research has converged with the animal research to reveal that the amygdala is important for processing fear. For instance, the amygdala region is more activated by a neutral stimulus paired with an aversive event (conditioned stimulus) compared to another neutral stimulus that does not predict an aversive event (LaBar et al., 1998). Moreover, amygdala activation correlates with the degree of skin conductance response (an indication of arousal) to the conditioned stimulus (LaBar et al., 1998). Going beyond these correlations, research has revealed that patients with lesions of the right, left, or bilateral amygdala do not demonstrate a conditioned response as measured by skin conductance, even though they respond normally to the unconditioned (aversive) stimulus (Bechara et al., 1995). These results fit well with the animal research demonstrating that the amygdala—specifically, the central nucleus of the amygdala—plays a critical role in fear conditioning.

Interestingly, although the amygdala is important for the acquisition of fear, as measured implicitly by skin conductance to fear-conditioned stimuli, it does not appear to be important for the acquisition of fear learning measured explicitly. Individuals who suffer bilateral amygdala damage acquire explicit knowledge about the relationship between the conditioned stimulus and the aversive unconditioned stimulus (Gazzaniga, Ivry, & Mangun, 2002). This type of explicit knowledge is associated with the hippocampus (Squire & Zola-Morgan, 1991). Individuals with a damaged hippocampus but intact amygdala show normal skin conductance response to conditioned stimuli but no explicit knowledge of the relationship between the conditioned stimulus and unconditioned stimulus (Bechara et al., 1995).
More recent human neuroimaging research has revealed that the amygdala becomes activated in response to a variety of emotive stimuli in addition to fear-provoking ones (Whalen, 1998). For instance, experiments have revealed that positive stimuli also evoke greater amygdala activity than neutral stimuli (Breiter et al., 1996). Other studies have independently manipulated valence and intensity and found that amygdala activity is more associated with processing affective intensity than with processing any specific valence (Anderson et al., 2003). Consistent with results obtained from these studies, Whalen (1998) observed that the amygdala is generally associated with vigilance to motivationally relevant stimuli (see also Anderson & Phelps, 2001; Cunningham et al., 2008). Although these findings appear to contradict the fear conditioning literature, they likely reflect the role of a different part of the amygdala—the basal nucleus—which supports the initiation of appetitive and goal-driven responses to stimuli, such as rewards (Holland & Gallagher, 1999; LeDoux, 2000). Contemporary fMRI methods lack the resolution to sufficiently discern the subnuclei in the amygdala, and this sometimes leads to confusion over interpretations of the amygdala as relating to motivational and emotional responses such as fear (e.g., freezing), withdrawal, and approach.

Along these lines, research has revealed that extraversion is correlated directly with amygdala activation to positive (relative to negative) emotional pictures and that neuroticism is correlated directly with amygdala activation to negative (relative to positive) emotional pictures (Canli et al., 2001). Extraversion has also been found to correlate directly with amygdala activation to happy (relative to fearful) faces (Canli, Sivers, Whitfield, Gotlib, & Gabrieli, 2002). Similarly, individual differences in promotion focus (sensitivity to gains) is associated with amygdala activation to positive (relative to negative) word stimuli, whereas individual differences in prevention focus (sensitivity to losses) is associated with amygdala activation to negative (relative to positive) word stimuli (Cunningham, Raye, & Johnson, 2005). These findings demonstrate that the amygdala is responsive to both appetitive and aversive stimuli, although this pattern likely reflects the roles of different subnuclei of the amygdala.

**Reward Processing**

In humans, fMRI research has linked the anticipation of rewards to activity in regions of the basal ganglia, such as the nucleus accumbens. For instance, Knutson, Wimmer, Kuhnen, and Winkielman (2008) found that anticipation of viewing rewarding stimuli (e.g., erotic female nudes, viewed by heterosexual men) increased nucleus accumbens activity and financial risk taking. Nucleus accumbens activity also increased in anticipation of making a risky decision, that is, a relatively high-risk ($1.00) as compared to a low-risk ($0.10) financial gamble. Moreover, the risk taking was partially mediated by increases in nucleus accumbens activation.

Research on dopamine and the nucleus accumbens have revealed differential mechanisms associated with the “wanting” and “liking” of a reward. Specific subregions of the nucleus accumbens, in combination with specific neurotransmitters, are involved in “liking” or postgoal positive affect. For instance, microinjection of morphine, which activates opioid receptors, into posterior and medial regions of the accumbens shell increases positive affective reactions to sweet tastes (Peciña & Berridge, 2000). Other research has revealed that the nucleus accumbens is critical in regulating effort-related functions, such that lever pressing schedules that require minimal work are unaffected by accumbens dopamine depletions, whereas lever-pressing schedules that require greater work are impaired by accumbens dopamine depletions (Salamone, 2007).

The orbital frontal cortex (figure 6.1; OFC) is another brain region that is widely implicated in studies of reward contingencies, such as in reversal learning (Schoenbaum, Setlow, & Ramus, 2003), and in the self-monitoring of emotional responses. In reversal learning, an animal is taught that responding to one cue produces reward, whereas acting similarly to another cue produces nonreward or punishment. After the animal learns to respond correctly, the experimenter switches the cue-outcome associations, and the animal must learn to change its behavior. During cue-outcome learning across reversals, the OFC is activated (O’Doherty, Critchley, Deichmann, & Dolan, 2003).

The reversal-learning function of the OFC relates to the process of self-monitoring in humans. Self-monitoring is defined as the ability to evaluate one’s behavior in the moment in reference to higher-order goals or the reactions of other people (Prigatano, 1991; Stuss, 1991; Stuss & Benson, 1984). This is the process “by which individuals evaluate their behavior in the moment to make sure that the behavior is consistent with how they want to behave and how other people expect them to
behavior” (Beer, John, Scabini, & Knight, 2006, p. 872). Individuals with OFC damage have an impaired ability to prioritize solutions to interpersonal problems (Saver & Damasio, 1991), a tendency to greet strangers in an overly familiar manner (Rolls, Hornak, Wade, & McGrath, 1994), and to behave with disruptive manners in hospital settings (Blair & Cipolotti, 2000). They also tease strangers inappropriately and are more likely to disclose unnecessary or inappropriate personal information when answering questions (Beer, Heerey, Keltner, Scabini, & Knight, 2003; Kaczmarek, 1984). This self-monitoring perspective on OFC is consistent with the previously reviewed research on the emotional functions of this region when functional accounts of emotion are considered.

PFC Asymmetries Associated with Emotion and Motivation

The asymmetric involvement of prefrontal cortical regions in positive affect (or approach motivation) and negative affect (or withdrawal motivation) was suggested over 70 years ago by observations of persons who had suffered damage to the right or left anterior cortex (Goldstein, 1939). Later research supported these observations using the Wada test, which involves injecting amytal, a barbiturate derivative, into one of the internal carotid arteries, suppressing the activity of one hemisphere. Amytal injections in the left side were found to produce depressed affect, whereas injections in the right side produced euphoria (Alema, Rosadini, & Rossi, 1961; Perria, Rosadini, & Rossi, 1961; Rossi & Rosadini, 1967; Terzian & Cecotto, 1959). These effects were interpreted as reflecting the release of one hemisphere from contralateral inhibitory influences. According to this view, activation in the right hemisphere, when not inhibited by the left hemisphere, caused depression; and disinhibited left hemisphere caused euphoria.

Subsequent studies appeared to confirm these results, finding that persons who had suffered left hemisphere damage or lesions tended to show depressive symptoms (Black, 1975; Gasparini, Satz, Heilman, & Coolidge, 1978; Gainotti, 1972; Robinson & Price, 1982), whereas persons who had suffered right hemisphere lesions tended to show manic symptoms (Gainotti, 1972; Robinson & Price, 1982; Sackeim et al., 1982). Other research has revealed asymmetries underlying appetitive and avoidant behaviors in nonhuman animals, in species ranging from great apes and reptiles (Deckel, Lillaney, Ronan, & Summers, 1998; Hopkins, Bennett, Bales, Lee, & Ward, 1993) to chicks (Güntürkün et al., 2000), amphibians (Rogers, 2002), and spiders (Ades & Ramires, 2002).

More recent research suggests that in humans these affect-related asymmetric activations are often specific to the frontal cortex. This research often uses asymmetric activation in right versus left frontal cortical areas as a dependent variable, usually assessed by EEG recordings. Frontal cortical asymmetry is assessed by comparing activation levels between homologous areas on the left and right sides. Difference scores are widely used in this research, and their use is consistent with the amytal and lesion research described above that suggests that asymmetry may be the key variable, with one side dominating the other hemisphere. Evidence has been obtained with EEG measures of brain activity, or more specifically, power (root mean square of the voltage amplitude) of activity within the alpha frequency band (8-13 Hz) of the EEG. Research has revealed that alpha power is inversely related to regional brain activity using hemodynamic measures (Cook, O’Hara, Uijtdewege, Mandellkern, & Leuchter, 1998) and behavioral tasks (Davidson, Chapman, Chapman, & Henriques, 1990). Source localization of EEG signals (Pizzagalli, Sherwood, Henriques, & Davidson, 2005) and fMRI results (Berkman & Lieberman, 2010) obtained in emotion-frontal asymmetry studies converge in suggesting that the dorsolateral PFC (figure 6.3) is responsible for these alpha asymmetry effects. These findings are further corroborated by evidence from studies of transcranial magnetic stimulation, discussed later (Schutter, 2009; Schutter, van Honk, d’Alfonso, Postma, & de Haan, 2001).

Trait Affective Styles and Resting Frontal Cortical Asymmetry

Depression has been found to relate to resting frontal asymmetric activity, with depressed individuals showing relatively less left than right frontal brain activity (Jacobs & Snyder, 1996; Schaffer, Davidson, & Saron, 1983), even when in remission status (Henriques & Davidson, 1990). Other research has revealed that trait positive affect in healthy subjects is associated with greater left than right frontal cortical activity, whereas trait negative affect is associated with greater right than left frontal activity (Tomarken, Davidson, Wheeler, & Doss, 1992).

Subsequent studies observed that trait behavioral activation, construed as approach motivation (Carver & White, 1994), was related to greater
left than right frontal activity at resting baseline (Amodio, Master, et al., 2008; Harmon-Jones & Allen, 1997; Sutton & Davidson, 1997). These studies suggested that asymmetric frontal cortical activity could be associated with motivational direction instead of affective valence. However, avoidance and approach motivation are mostly associated with negative and positive affect, respectively (Carver & White, 1994), and consequently, the interpretation is clouded. Similarly, the finding that promotion (versus prevention) forms of regulatory focus are associated with greater relative left (versus right) frontal activation at baseline (Amodio et al., 2004) could be interpreted from either the motivational direction or affective valence view. The distinction between emotional valence and motivation has been somewhat ambiguous given the methods used in past research, and researchers have tended to interpret relatively greater left than right frontal cortical activity as reflecting greater approach motivation and positive affect, and relatively greater right than left frontal cortical activity as reflecting greater withdrawal motivation and negative affect. Although these claims fit well into dominant emotion theories, our positive affect with approach motivation, and affect with withdrawal motivation (Lang, 1997; Watson, 2000), they do not fit so well with known physiological structure and function, as discussed below.

State Affect and Asymmetric Frontal Activity

Research has also demonstrated that asymmetric frontal brain activity is associated with state emotional responses. For instance, Davidson and Fox (1982) found that 10-month-old infants exhibited increased left frontal activation in response to a film clip of an actress generating a happy facial expression as compared to a sad facial expression. Frontal brain activity has been found to relate to facial expressions of positive and negative emotions, as well. For example, Ekman and Davidson (1993) found increased left frontal activation during voluntary facial expressions of smiles of enjoyment. Coan, Allen, and Harmon-Jones (2001) found that voluntary facial expressions of fear produced relatively less left frontal activity. Some positive affects are lower in approach motivation, whereas others are higher in approach motivation. An important question remains regarding the findings relating affective valence to asymmetric frontal cortical activity: Do positive affects of any approach motivational intensity cause increases in relative left frontal activation? An experiment by Harmon-Jones, Harmon-Jones, Fearn, Sigelman, and Johnson (2008) addressed this issue by manipulating positive affect and approach motivation independently while measuring frontal EEG. Participants who wrote about positive/high approach and positive/low approach events both reported elevated positive affect, but only the positive/high approach manipulation produced an increase in left-frontal EEG. These results support the hypothesis that it is the approach motivational component of positive affective experiences, and not the positive valence per se, that causes greater relative left frontal cortical activation (as measured by EEG).

Anger and Asymmetric Frontal Cortical Activity

The experiment by Harmon-Jones et al. (2008), described above, suggests that approach motivation and positive affect are not perfectly associated with each other. More convincing evidence for the dissociation of affective valence and motivational direction (e.g., positive affect = approach motivation) comes from research on anger. Anger is a negatively valenced emotion that evokes behavioral tendencies of approach (e.g., Darwin, 1872; Ekman & Friesen, 1975; Plutchik, 1980; Young, 1943). Anger is associated with attack, particularly offensive aggression (e.g., Berkowitz, 1993; Blanchard & Blanchard, 1984; Lagerspetz, 1969). Offensive aggression can be distinguished from defensive aggression, which is associated with fear. Other research also suggested that anger was associated with approach motivation (e.g., Izard, 1991; Lewis, Alessandri, & Sullivan, 1990; Lewis, Sullivan, Ramsay, & Alessandri, 1992). More recent studies examined whether trait behavioral approach or behavioral approach sensitivity (BAS) related to anger-related responses. Several studies have found that trait BAS, as assessed by Carver and White’s (1994) scale, is positively related to state and trait anger (Carver, 2004; Harmon-Jones, 2003; Smits & Kuppens, 2005). Therefore, the emotion of anger provides a critical test case to disentangle interpretations of frontal cortical asymmetry as relating to valence or motivational direction.

In an initial test of this hypothesis, Harmon-Jones and Allen (1998) assessed trait anger using the Buss and Perry (1992) questionnaire and assessed asymmetric frontal activity by examining baseline, resting EEG activity. In this study of adolescents, trait anger related to higher left frontal activity and lower right frontal activity at baseline. Asymmetric
activity in other brain regions did not relate to anger, a finding that has been observed in all subsequent observations of this effect. Replications have revealed that these results were not due to anger being evaluated as a positive feeling (Harmon-Jones, in press), and this general effect has been replicated in other laboratories (e.g., Hewig, Hagemann, Seifert, Naumann, & Bartussek, 2004; Rybak, Crayton, Young, Herba, & Konopka, 2006). Other research has manipulated asymmetrical frontal cortical activity using transcranial magnetic stimulation and found that the disruption of right PFC increased approach responses to angry faces compared with disruption of the left PFC (d’Alfonso, van Honk, Hermans, Postma, & de Haan, 2000; van Honk & Schutter, 2006).

Researchers have also tested the motivational direction model of frontal cortical asymmetry by manipulating state anger. Harmon-Jones and Sigelman (2001) found that individuals who were insulted evidenced greater relative left frontal activity than individuals who were not insulted. Additional analyses revealed that within the insult condition, reported anger and aggression were positively correlated with relative left frontal activity. Neither of these correlations was significant in the no-insult condition. Harmon-Jones, Peterson, and Harris (2009) conceptually replicated the above research and extended it by showing that anger and jealousy in responses to social rejection caused increased relative left frontal activity. The state anger and approach motivation conceptual model, as well as (e.g., Jensen-Campbell, Knack, Waldrip, & Campbell, 2007; Verona, Sadeh, & Curtin, 2009).

Considered as a whole, EEG asymmetry studies of emotion and motivation have provided a critical test of how emotions are organized in the brain. Although the subjective appraisal of emotion is usually described in terms of valence (e.g., pleasant vs. unpleasant), this large body of research demonstrates that at the neural and physiological level of analysis, emotional responses are organized in terms of their approach versus withdrawal motivational orientation (Harmon-Jones et al., in press).

**Emotion Regulation**

The idea that people often seek to regulate their emotional response dates back to classic theories of Freud and Descartes, who suggested that reason is needed to overcome passion (in Freud’s terms, the ego must adjudicate the sway of the id). Contemporary views on emotion regulation have similarly focused on the role of cognitive control in modulating lower-level emotional processes (Davidson, Jackson, & Kalin, 2000). In social cognitive neuroscience, researchers have focused on regions of the PFC as the neural substrate of control and on regions of the sub cortex, such as the amygdala, as the substrate of emotion, particularly negative emotion (Ochsner & Gross, 2005). For example, in many emotion regulation studies, subjects view aversive (vs. neutral) images during an fMRI scan. On some trials, subjects are instructed to simply view the image. On other trials, subjects may be instructed to decrease their affective response to the image. In one study using this method, Ochsner, Bunge, and Gabrieli (2002) found that the simple viewing of aversive images was associated with increased activity in the amygdala. When subjects attempted to reduce their affective response, activations in lateral prefrontal cortex (PFC, figure 6.3) were observed and interpreted as reflecting the engagement of control, whereas amygdala activity on such trials did not differ from baseline (Ochsner et al., 2002). Several other studies have observed similar effects (e.g., Banks, Eddy, Angstadt, Nathan, & Phan, 2007; Cunningham et al., 2004; Ochsner et al., 2002; Lieberman, Hariri, Jarcho, Eisenberger, & Bookheimer, 2005; Lieberman et al., 2007; Phan et al., 2005; Ury et al., 2006).

As more direct evidence for the down-regulation hypothesis, researchers have observed a negative correlation between activity in the lateral PFC during emotion regulation trials and amygdala activity during baseline (no-regulation) trials (e.g., Hariri, Mattay, Tessitore, Fera, & Weinberger, 2003; Ochsner et al., 2002). This negative correlation is typically interpreted as demonstrating the direct “down-regulation” of emotion, in the direction of the PFC acting on the amygdala. There are problems with this interpretation, however. Despite observed correlations between regions of lateral PFC and the amygdala, these regions share very few anatomical connections, and of these, most run from the amygdala to the PFC (Ghashghaei & Barbas, 2002). Thus, the idea that the PFC “down-regulates” emotion may be incorrect, or at least inconsistent with neuroanatomy.

If the PFC does not directly down-regulate emotion, how might it otherwise play a role? One recent study suggests that PFC activity interpreted as controlling emotion may actually reflect the control of eye gaze (van Reekum et al., 2007). The authors found that, when instructed to reduce one’s affective...
response to aversive images, subjects’ gaze avoided the most aversive parts of the image, as measured by eye-tracking sensors. Interestingly, increases in PFC activity (and decreases in amygdala activity) associated with the voluntary reduction of negative affect were statistically explained by these changes in eye gaze. This important finding suggests that PFC activations previously interpreted as reflecting the direct down-regulation of affect may actually reflect an indirect mechanism, whereby the control of attention away from the aversive stimulus lessens the emotional impact. The notion of an indirect pathway for emotion regulation is consistent with previous physiological studies (Gross & Levenson, 1993, 1997).

Neuroscience research on emotion regulation highlights the idea that psychological conceptions of emotion do not map cleanly onto specific underlying neural structures (Amadio, 2008; Cacioppo et al., 2003). Rather, psychological constructs of emotions (e.g., subjective feelings) more likely reflect a summary appraisal of several interacting physiological mechanisms that function in concert to promote adaptive responses to an emotion-eliciting situation. If so, then questions about the neural correlates of emotion and emotion regulation may need to be reconsidered and perhaps replaced by questions about more basic processes of motivation, attention, arousal, and action that support the adaptive functions associated with subjective experiences of emotion.

**Intergroup Processes**

One of the most active areas in the field of social neuroscience examines prejudice, stereotyping, and intergroup relations (for a review, see Amadio, 2008). The area has provided fertile ground for social neuroscience research because it concerns the confluence of multiple psychological processes across multiple levels of analysis. That is, researchers can simultaneously examine issues of automaticity and control, emotion and cognition, motivation, attitudes, and a range of individual differences, all within the context of social cognition and social behavior, and with broad societal implications (see also Tropp & Molina, chapter 22, this volume).

**Seeing Groups**

How early is a person's social category perceived in the person perception process? Several studies have examined this question by testing whether faces of ingroup and outgroup members are perceived differently in basic visual processes. A study by Golby, Eberhardt, Chiao, and Gabrieli (2001) observed greater activity in the fusiform gyrus in response to ingroup than outgroup faces, and this difference predicted later recognition of the faces. Several studies have also examined this question using the N170 component of the ERP while participants viewed faces of Black and White people in the context of various tasks. However, the findings have been mixed, with some studies observing no differences (Caldara, Rossion, Bovet, & Hauert, 2004; Caldara et al., 2003; Wiese, Stahl, & Schweinberger, 2009), some finding larger effects of visual processing for the ingroup (Ito & Urland, 2005) and others for the outgroup (Walker, Silvert, Hewstone, & Nobre, 2008). These inconsistent findings are likely due to task differences. Also, few extant studies have controlled for important low-level visual factors (e.g., luminance and contrast) in their stimuli, and therefore more research is needed to understand what aspects of group membership might contribute to N170 effects.

In an effort to address these methodological issues, Ofan, Rubin, and Amadio (in press) presented White participants with "two-tone" faces of Black and White people. These two-tone faces were created by transforming grayscale images into images consisting only of pure white or black pixels. Images of White and Black faces were then equated for luminance and contrast by equating the proportion of black and white pixels in each face. In addition, the authors proposed that differences in face processing might relate to participants’ degree of implicit racial bias. Participants with stronger pro-White bias, as assessed using a sequential evaluative priming task, may perceive Black outgroup faces as less normative compared with White ingroup faces. Given past work showing that N170 amplitudes are larger in response to non-normative faces (e.g., Halit, de Haan, & Johnson, 2000), the authors predicted that participants with stronger pro-White implicit bias would exhibit larger N170s to Black faces than to White faces. Indeed, this pattern was found (Ofan et al., in press). These results suggest that social group differences are indeed registered at the earliest stages of visual face processing, but that the effect of group differences on these processes varies as a function of the context and the perceiver’s goals and attitudes.

**Brain Mapping of Racial Bias**

Physiological research on responses to race provided the first evidence that implicit forms of racial bias may differ from explicit self-reports (Rankin &
Campbell, 1955; Vanman, Paul, Ito, & Miller, 1997). The earliest neuroscience studies of intergroup bias attempted to map this implicit response to the brain. At the time of these early neuroimaging studies, new findings were emerging from the study of fear conditioning in human animals that inferential neural structure involved in the amygdala may be involved in implicit responses to race. By suggesting a neural correlate of implicit bias, these studies provided a foothold for future research to consider how mechanisms of learning and memory associated with the amygdala might be involved in implicit intergroup processes.

Social-Personality Research on Intergroup Bias and the Brain

From a social psychological perspective, identifying a neural substrate of implicit racial bias was interesting because it could offer new clues as to how implicit racial biases are learned, activated, expressed in behavior, and potentially altered or extinguished. Furthermore, such research could help to clarify important individual differences in people’s abilities to respond without prejudice. For example, it could help us understand whether egalitarians respond without prejudice because they are very effective in regulating their responses or because they do not have biased responses in the first place. To address these questions, Amadio et al. (2003) conducted a study in which they used the startle-eyeblink method to examine fear-related amygdala responses to race.

Amadio et al.'s (2003) study was designed to address multiple goals. First, the authors sought to identify a uniquely affective form of implicit racial bias. Previous theories assumed that implicit bias reflected associations between a target group and related attributes within a semantic network (Fazio et al., 1995; Greenwald & Banaji, 1995). This type of theory explained observations of priming between target groups and judgments of stereotypic and evaluative words. Interestingly, priming effects for evaluative word associations were frequently interpreted as an affective form of bias. However, it is difficult to make this claim based on a measure of semantically based word associations. Amadio et al. (2003) noted that although the amygdala is associated with fear-related affective responses, it is not able to process semantic information (see also Amadio & Devine, 2006). Therefore evidence for differences in amygdala activity to Black versus White faces using the startle-eyeblink measure would provide strong evidence for an affective basis of implicit bias. By using a startle-eyeblink index of amygdala activity, the authors could also assess rapid changes in amygdala activity in response to
an ingroup versus outgroup face, which would strengthen the interpretation that the amygdala response reflects “automatic” processing. Furthermore, the startle eyeblink method assesses activity of the amygdala’s central nucleus—the region specifically involved in the learned fear response. By contrast, fMRI measures of amygdala activity cannot distinguish activity in the central nucleus from other regions that are not associated with fear. Thus, the startle eyeblink method provided the best method for linking implicit racial bias to fear and threat-related affect.

Amodio et al.’s (2003) second goal was to understand why some people with sincere low-prejudice attitudes nevertheless show anti-Black bias on implicit measures, whereas other low-prejudice people do not. Previous research had shown that among people with strong internal motivations to respond without prejudice, those who were also very worried about appearing prejudiced in front of others exhibited high levels of implicit racial bias (e.g., on the IAT), whereas those who were not worried about social pressures exhibited low levels of implicit bias (Devine, Plant, Amodio, Harmon-Jones, Vance, 2002). Thus, Amodio et al. (2003) asked whether the subset of low-prejudice people who did not show implicit affective bias in behavior either (1) did not have a bias in the first place or (2) were biased but were very effective in regulating their bias.

To address these questions, participants viewed pictures of White, Black, and Asian faces. Some trials included a startle probe at 400 ms following picture onset, which assessed amygdala responses prior to the opportunity for controlled processing, and other trials included a startle probe at 4000 ms, assessing amygdala activity after an opportunity for controlled processing. At 400 ms, startle-eyeblink responses revealed greater amygdala activity to Black than White faces, but only among people with low internal motivation to respond without prejudice (i.e., high-prejudice subjects). At 4000 ms, there was greater amygdala activity to Black versus White faces for people with low internal motivations, as well as those with high internal motivation who were also very concerned about external social pressures. Subjects with strong internal motivations who did not worry about external social pressures—the ones who showed low implicit bias in other research—did not show a different startle response to Black versus White faces. These data suggested that indeed, some low-prejudice people did not show any signs of implicit affective bias to begin with, which might explain why they often do not show bias on behavioral measures such as the IAT (Devine et al., 2002).

Although other low-prejudice people, who worry about external pressures, do show signs of bias in their amygdala activity, a second study found that they are effective at controlling their expression of bias in more deliberative behaviors (Amodio et al., 2003, Study 2). Thus, this research was the first to show significant differences in amygdala activity to Black versus White faces, and this effect was moderated by individual differences. This research also provided evidence for a uniquely affective form of implicit bias, and it suggested that some low-prejudice people possess implicit negative affective association with racial outgroups, whereas other low-prejudice people do not.

By linking the amygdala to implicit affective racial associations in several studies, this body of research suggested that affective racial bias may reflect a form of fear conditioning. Therefore, knowledge about how fear responses are learned, expressed, and potentially unlearned could be applied to the topic of implicit affective intergroup bias. For example, fear-conditioned responses are learned rapidly, often after a single experience, and they are expressed primarily in autonomic responses and nonverbal behaviors (such as freezing and avoidance). Such associations are also very difficult and perhaps impossible to extinguish (Bouton, 1994; Schiller, Freeman, Mitchell, Uleman, & Phelps, 2009)—instead of being unlearned, new learning is needed to override the effects of older fear-conditioned associations. Interestingly, most theories of implicit social cognition suggest that implicit associations are learned slowly, only after repeated exposure (e.g., Smith & DeCoster, 2000)—an idea that is inconsistent with fear conditioning. Nevertheless, behavioral studies have shown that measures of implicit evaluative bias predict nonverbal behaviors linked with freezing and avoidance (Amodio & Devine, 2006; Dovidio, Kawakami, Johnson, Johnson, & Howard, 1997; Fazio et al., 1995), consistent with the models of amygdala-based learning. Finally, the fact that evaluative biases are so difficult to extinguish is also consistent with research suggesting that fear-conditioned associations are relatively permanent.

Since these initial studies, several event-related fMRI studies have observed that amygdala activity is greater to outgroup than ingroup faces under some conditions but not others, and that these effects are typically subtle (Cunningham et al., 2004; Lieberman et al., 2005; Wheeler & Fiske, 2005).
Ronquillo et al., 2007). That is, differences in amygdala activity to Black versus White faces tend to emerge only in the absence of a minimally demanding task. As tasks become more demanding, such as when searching for a “dot” on the image, when imagining whether the target likes a particular vegetable, or when attempting to match the face to written group labels, amygdala activations tend not to be found (Liberman et al., 2005; Wheeler & Fiske, 2005). Other research suggests that amygdala effects are lessen when the outgroup face is not looking directly at the subject (i.e., has averted gaze; Richeson, Todd, Trawalter, & Baird, 2008).

It is also notable that amygdala activity to Black versus White faces may reflect participants’ concern about appearing prejudiced in such studies. That is, participants are usually aware that a task concerns reactions to race after a few trials of viewing Black and White faces. To the extent that a participant is worried about showing prejudice toward Black faces, each Black face serves as a threat stimulus—that is, a trial on which the subject may reveal bias, either to others or to the self. Thus, it is possible that amygdala responses to race are due to this anxiety, rather than to previously learned affective associations. Other research has shown that the amygdala responds to motivationally relevant stimuli, such as to rewarding stimuli (Holland & Gallagher, 1999) or to one’s ingroup members (e.g., in the context of an implied competition; Van Bavel, Packer, & Cunningham, 2008), although these responses may reflect the basal nucleus rather than the central nucleus of the amygdala. These findings suggest some alternative explanations for observations of amygdala activity associated with responses to race, highlighting the complexity of these processes and the need for careful interpretations and additional research.

Stereotyping

Whereas much research has examined the neural correlates of race-related affect and evaluation, very little has investigated social stereotypes. Stereotypes are believed to represent cognitive structures stored in memory that represent a set of attributes associated with a social group (Devine, 1989). Amadio and Devine (2006; see also Amadio, 2008; Amadio & Mendoza, 2010) noted that stereotypes are rooted in mechanisms of semantic memory and selection, which are associated with neural activity in the temporal lobes and lateral posterior PFC (e.g., Brodmann areas 45 and 47). Behavioral and neuroscience research on semantic learning systems has uncovered the dynamics of how such associations are learned and expressed in behavior, and by accessing this literature, researchers can apply findings from the memory literature to understand stereotyping processes (Amadio, 2008; Amadio & Ratner, 2011b). For example, whereas affective associations are learned quickly and are relatively indelible, semantic associations may be learned and unlearned through a process of repeated pairings and nonpairings. Semantic learning systems are more likely to be expressed in trait impressions, goal representations, and goal-driven behaviors, and thus they are more likely to emerge in verbal responses (Amadio & Devine, 2006).

Some fMRI studies have examined neural activity associated with the completion of stereotyping tasks (Knutson, Mah, Manly, & Grafman, 2007; Mitchell, Ames, Jenkins, & Banaji, 2009; Quadflieg et al., 2009), but these studies have not explored the mechanisms of stereotypes per se. Rather, these studies have focused on brain activity associated with more general aspects of task completion, such as response conflict and inhibition, or face perception. In a brain lesion study, patients with mPFC damage did not show bias on a male versus female IAT (Milne & Grafman, 2001). However, it is likely that this mPFC damage interfered with the general process of response conflict that drives the IAT effect, rather than representations of stereotype knowledge (a function typically ascribed to the PFC and temporal lobes). Thus, the neural mechanisms of stereotyping remain largely unstudied, although researchers have already applied findings from the broader cognitive neuroscience literature on semantic selection and representation to help understanding the representation and functions of stereotypes (Amadio, 2008; Amadio & Ratner, 2011b).

Control and the Regulation of Intergroup Bias

Given that racial stereotypes and implicit evaluations may be automatically activated, regulatory processes are needed to reduce their expression in behavior. Social-personality psychologists have begun to apply findings from neuroscience studies of cognitive control to understand how expressions of intergroup bias may be regulated (Amadio, Devine, & Harmon-Jones, 2007; Amadio & Devine, 2010). Amadio et al. (2003; see also Richeson et al., 2003) proposed that PFC regions were likely involved in the control of behavioral responses to race, but that control operated on behavior rather than the putative source of bias in...
the amygdala (indeed, behavioral expressions of bias were reduced despite sustained amygdala responses to race). Indeed, Amodio et al. (2003) found that participants who are highly motivated to respond without prejudice are generally unable to control the activation of affective responses to race directly, but rather are highly effective at controlled behavioral expression of bias. This finding suggests that the mechanisms of control are complex, and that research was needed to understand the different ways in which control functions to guide intergroup behavior.

Detecting the Need for Control

Despite holding nonprejudiced beliefs, many self-avowed egalitarians still often express stereotypes and affective biases in their behavior. In light of recent neuroscience models positing that control involves two major components, conflict monitoring and regulative control (Botvinick et al., 2001), Amodio et al. (2004) wondered whether such “slips” might reflect a failure to detect the need for control by the conflict monitoring system, or rather a failure to implement control once its need has been detected. The authors measured EEG in low-prejudice participants while they completed the weapons identification task—a sequential priming task that requires enhanced control on some trials to override the influence of automatic stereotypes. The use of a behavioral “control” task was critical because it (1) clearly manipulated the engagement of controlled processing and (2) provided behavioral indicators of both automatic bias and the degree of successful control—both of which are needed to interpret associated brain activity as being involved in control.

Amodio et al. (2004) focused on two ERP measures of ACC activity—the error-related negativity component and the N2 component associated with successful control—and found that both were more strongly activated on trials where control over stereotypes was needed (see also Bartholow et al., 2006; Correll, Urland, & Ito, 2006). Importantly, heightened ACC activity was observed both when control succeeded and when it failed. In the case of failure, the finding suggested that when low-prejudice people respond with unwanted stereotypes, it is the result of failing to implement a controlled response rather than a failure to detect that control is needed. A conceptually related ERP study by Bartholow et al. (2006) found that alcohol administration selectively impaired the regulative component of control without affecting the conflict monitoring component in the process of stereotyping inhibition, providing further support for the distinction between these two components of control in the regulation of intergroup bias.

Amodio, Harmon-Jones, and Devine (2008) conducted a follow-up study to address why some low-prejudice people—those who have strong internal motivation to respond without prejudice but are also very concerned about external social pressures—are especially prone to unintended expressions of bias. The authors asked whether these individuals were less sensitive to conflicts between activated stereotypes and egalitarian response goals. Consistent with this hypothesis, these high-internal/high-external motivation subjects showed lower levels of ACC activity on task trials that required control over automatic stereotypes, similar to subjects reporting high-prejudice beliefs. By contrast, participants who were highly internally motivated and unconcerned about external pressures showed strong ACC responses when stereotype control was needed. A second study showed that these groups did not differ in domain-general forms of control and that the observed differences were specific to racial stereotypes (as expected, given that groups were determined by their motivations to respond without prejudice). Other research suggests that mechanisms for engaging control in response to external cues (e.g., cues from other people) involve more rostral regions of the ACC and mPFC, in contrast to ACC-related mechanisms involved in control based on internal cues (Amodio et al., 2006). This finding suggests that when controlling responses according to external social cues, people rely on mentalizing and social cognition processes associated with the mPFC in other research (Amodio & Frith, 2006; Mitchell et al., 2006).

Implementing Control

Many theories in social and cognitive psychology posit that, once the need for control is detected, other mechanisms are engaged to implement a controlled response (Devine, 1989; Shiffrin & Schneider, 1977). Neuroscience research has implicated the PFC in this function (Botvinick et al., 2001; Kerns et al., 2004; Badre & Wagner, 2007). However, the specific target of control is not always clear—it could be the emotional response, the stereotype itself, the expressed behavior, the way a person is perceived, or some other process. Neuroscience can help clarify this issue, as an analysis of the neuronal circuitry of the PFC provides clues about the targets of control. In particular, this
circuitry suggests that the PFC modulates goal-directed action processes as well as the modulation of sensory input and perceptual processing (Miller & Cohen, 2001). By contrast, the PFC has few connections to the amygdala, and to the extent that the amygdala is the source of implicit affective bias, it is unlikely to be a direct target of control.

Several studies have observed patterns of PFC activity associated with responses to race, but their role in response control has not been clear. In the earliest example, Richeson et al. (2003) found that subjects who showed greater PFC activity when viewing Black versus White faces in one experimental session were more likely, in a subsequent experimental session, to perform more poorly on a cognitive control task following a stressful interracial interaction. The authors reasoned that subjects who spontaneously engaged control when viewing faces were more likely to engage control during an interracial interaction, which in turn interfered with their performance on the Stroop task. A study by Cunningham et al. (2004) measured brain activity to faces of Black and White people using fMRI. Participants simply indicated whether faces appeared on the right or left side of the visual field. Like Richeson et al. (2003), Cunningham et al. (2004) assumed that people spontaneously engage some form of control during passive face viewing. Indeed, the ACC and several regions of the PFC were more active to Black faces than White faces, although some PFC regions were more active to White faces than Black faces. Similarly, a study by Lieberman et al. (2005) found a reduction in amygdala activity and an increase in some PFC regions (e.g., the right ventrolateral PFC, figure 6.3) when participants viewed Black versus White faces and were instructed to match the faces to written labels.

Taken together, these studies are provocative, suggesting a possible role of the PFC in the control of racial bias. However, without the manipulation of response control or a behavioral measure of control, interpretations of these studies are unclear.

That is, the PFC is involved in a wide range of functions, and therefore one cannot necessarily infer the engagement of “control” from the observation of PFC activity alone, as this would be a poorly supported reverse inference. A second issue is that researchers often assume that the target of control is the amygdala (i.e., the putative source of implicit bias). Indeed, Cunningham et al. (2004) and Lieberman et al. (2005) each found a region of lateral PFC (a different region in each paper) that was inversely correlated with an index of amygdala activity to Black versus White faces. These authors interpreted this correlation as evidence for a neural mechanism of prejudice control. However, these regions of lateral PFC are known to have few, if any, anatomical connections to the amygdala (Ghashghaei & Barbas, 2002), and therefore the interpretation of this “down-regulatory” effect is likely to be incorrect. For example, it is possible that observed PFC activations were associated with task demands and changes in attention that were indirectly associated with a reduction in amygdala responses (as in Wheeler & Fiske, 2005).

Other research has examined the role of the PFC in modulating behavioral intentions and the perceptual processing of race in a way that is more consistent with PFC anatomy. Previous work by Amodio et al. (2003) observed that controlled processes operated on behavior, but not directly on amygdala activity. In a later study, Amodio et al. (2007) demonstrated that increases in PFC activity were associated with the behavioral measure of prejudice-reducing behaviors. More recently, Amodio (2010a) proposed that mechanisms of control promote intentional behavior by modulating attention to and perception of cues that control is needed. For example, Monteith’s (1993) self-regulation model posits that, once the goal to control intergroup responses is formed, an individual becomes vigilant to cues that control is needed, such as the presence of an outgroup member (see also Richeson & Trawalter, 2008). Amodio (2009) predicted that control-related PFC activity would serve to allocate greater attentional resources to the perception of outgroup faces, which in turn would facilitate better response control (i.e., more accurate responding despite any biasing effects of racial stereotypes). Indeed, while White participants in the study by Amodio (2010a) completed the weapons identification task, greater left PFC activity throughout the task predicted larger attentional ERP responses to Black versus White face primes just 180 ms after a face appeared, as well as greater response control. Furthermore, the effect of PFC activity on response control was mediated by attentional ERP responses to Black faces, among low-prejudice participants. These findings are consistent with anatomical models of the PFC, as well as behavioral research showing that people are effective at controlling their actions and perceptual attention, but ineffective at directly controlling their thoughts or emotions (Gross & Levenson, 1993; Wegner, Schneider, Carter, & White, 1987).
1 **Intergroup Emotion and the Brain**

Research on intergroup emotion examines responses such as love, hate, threat, disgust, and guilt in an intergroup context, and their implications for social interactions and discrimination (Mackie & Smith, 1998; Fiske, Cuddy, Glick, & Xu, 2002; Devine, Monteith, Zuwerink, & Elliot, 1991). Other research has focused on the role of intergroup anxiety in interracial interactions (Stephan & Stephan, 1985). Several social neuroscience studies have been conducted to probe these processes further. However, as noted above, the study of emotion (and affect) at the neural level of analysis is challenging because emotions and affect typically describe psychological states rather than mechanisms. When one begins to describe mechanisms associated with an emotion, a lower level of analysis that involves motivational, attentional, and/or autonomic functions is often necessary. Thus, social neuroscience research on intergroup emotion often focuses on these lower-level mechanisms.

Several studies have examined the physiological correlates of intergroup emotional responses within a social interaction. Early physiological studies showed that despite reports of liking for outgroup members, White participants revealed heightened skin conductance levels and facial EMG patterns indicating negative emotion in response to outgroup members (Rankin & Cambell, 1955; Vanman et al., 1997; Vrana & Rollock, 1998). As noted above, initial cognitive neuroscience studies of intergroup emotion focused on the amygdala as a key substrate, on the basis of animal research linking the amygdala to the learning and expression of fear (e.g., Amodio et al., 2003; Hart et al., 2000; Phelps et al., 2000). However, a simple mapping of implicit bias to the amygdala is not informative about the emotional quality of implicit bias per se. Rather, it links the construct of implicit bias to a set of mechanisms involved in the response to a learned threat, such as the activation of the autonomic nervous system, heightened attention and perceptual vigilance, behavioral inhibition and the preparation for “fight or flight” behaviors (Amodio, 2008). This research suggests a mechanism underlying implicit bias, which in turn suggests new ideas for how implicit bias might relate to behavior, learning, and other low-level psychological functions. In general, though, relatively few studies have examined the role of the brain in intergroup emotional processes. Here we note a few examples.

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2 **Role of Self-Directed Negative Affect**

Guilt is an important intergroup emotion experienced among egalitarians after responding unintentionally with prejudice, and it is associated with new goals to regulate one’s prejudices in future situations (Monteith, 1993; Monteith, Ashburn-Nardo, Voils, & Czopp, 2002). Amodio et al. (2007) showed that guilt resulting from the unintentional expression of prejudice is associated with a decrease in left PFC activity, relative to baseline, and a reduction in approach motivation. Other negative emotions, such as shame, sadness, and anxiety, were not associated with changes in PFC activity in this situation.

Importantly, when an opportunity to reduce future prejudice arose, subjects’ degree of guilt predicted a shift toward greater left PFC activity, which was associated with stronger approach motivation toward behaviors designed to reduce prejudice. Thus, this research used EEG measures of brain activity to show that guilt is a complex intergroup emotion that coordinates shifts from inhibition to approach-motivated responses to promote prosocial behavior.

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3 **Intergroup Anxiety**

In actual intergroup situations, anxiety is often a factor. Using cardiovascular assessments of threat versus challenge appraisals, Mendes, Blascovich, Lickel, and Hunter (2002) observed stronger threat responses during interactions with outgroup members on the basis of race or socioeconomic status, compared with ingroup members. Based on earlier research suggesting that anxiety can interfere with performance and controlled processing (e.g., Easterbrook, 1959; Baumeister & Shener, 1986), prejudice researchers have proposed that intergroup anxiety might undermine attempts to control implicit racial bias, leading to greater expressions of prejudice (Lambert et al., 2003; Richeson & Trawalter, 2005). However, the mechanism through which anxiety might interfere with control has been unclear, particularly because self-report assessments of anxiety are typically uncorrelated with changes in behavioral control.

Taking a neuroscience perspective on this issue, Amodio (2009) proposed that anxiety might affect the control of intergroup responses through a neural pathway that operates independently of subjective emotional responses. That is, he noted that social threats are typically associated with the release of norepinephrine within the brain, which has been shown to modulate ACC activity and conflict
monitoring processes (Aston-Jones & Cohen, 2005). According to this model, high norepinephrine signaling to the ACC sensitizes the conflict monitoring processes, such that vigilance to conflict is very high, but the ability to implement an intended response becomes impaired. Through this pathway, high anxiety should impair the control of automatic stereotyping effects on behavior. Although one cannot measure brain norepinephrine during an interracial interaction, one of its downstream effects is the release of the hormone cortisol in the bloodstream, which can be measured in saliva. Thus, Amodio (2009) measured salivary cortisol changes in response to an interracial versus same-race interaction. As part of the interaction, participants completed a stereotype inhibition task that assessed response control. Interaction-related increases in cortisol predicted worse control during the interracial interaction. This effect was not observed during the same-race interaction. Also, although participants reported greater subjective anxiety in the interracial interaction condition, self-reported anxiety was unrelated to cortisol levels or behavior. This research applied a neuroscience model to propose a specific mechanism through which intergroup anxiety might enhance some aspects of control (e.g., vigilance) but impair other aspects (e.g., response implementation) during an intergroup interaction.

Personality and Individual Differences

Personality is the study of enduring psychological dispositions and their influence on thought, emotion, and behavior (see Flesson, chapter 3, this volume). For researchers interested in personality processes, physiological processes that operate on a longer timescale, such as genes and hormones, are of special interest. Some research in this area has examined direct correlations between personality traits, such as those comprised by the “Big Five.” Increasingly, however, researchers have used neural and physiological models of continuity and change to help understand the complexities of personality processes and individual differences. In this section, we describe just a few examples of this growing area of research.

Affective Style

Research by Davidson and colleagues suggested that enduring affective styles, associated broadly with depression and anxiety, relate to different patterns of neural function (Davidson & Irwin, 1999). Specifically, these styles relate to differences in frontal cortical asymmetries, as described in previous sections, which are also associated with differential approach versus withdrawal tendencies (Davidson, 1998; see also Heller, Nitschke, & Miller, 1998). Although much research has examined state changes in frontal EEG asymmetry to study emotion and motivation, more stable, trait-like components of the asymmetry (e.g., at rest or baseline) have been taken to reflect a substrate of affective personality style. These trait-like patterns have been observed in adults, children, and nonhuman primates using a range of measures, and individual differences in these styles have been linked to various assessments of mental and biological health (Kern et al., 2008; Rosenkranz et al., 2003). More recently, trait-like patterns of activity in other brain regions, including the amygdala and regions of the basal ganglia have been included in an expanded framework of affective style (e.g., Fox, Shelton, Oakes, Davidson, & Kalin, 2008).

Role of Genes in Personality and Social Psychology

Psychologists have long suspected that many personality traits are substantially heritable, with longitudinal studies showing strong continuity in temperament from childhood to adulthood (Casp, 2003; Cramer & Block, 1998). Over the past several decades, research on heritability using twin designs has supported this view (Casp, Roberts, & Shiner, 2005; Plomin, DeFries, McClearn, & Rutter, 1997). Across the “Big Five” personality dimensions, a review of heritability estimates suggests that these traits are approximately 50% due to genetic similarities (Bouchard & Loehlin, 2001). The traits neuroticism and extraversion tend to show the largest heritability estimates, consistent with theory and research suggesting that these factors are dominant over other traits (Eaves, Eysenck, Martin, 1989; Tellegen et al., 1988). Significant heritability has also been observed for attitudes, such as toward social policy (e.g., the death penalty, immigration), racial beliefs, and hobbies (e.g., doing crossword puzzles) (Olson, Vernon, Harris, & Lang, 2001).

More recently, researchers have used a molecular genetics approach to explore the relationships between particular gene polymorphisms found in DNA with personality traits (Plomin & Caspi, 1999). The best known example of this candidate-gene approach is the effort to associate differences in emotional processing with variations in the
serotonin transporter gene—a gene that codes for proteins involved in the reuptake of serotonin from the synapse (Hariri & Holmes, 2006; Canli & Lesch, 2007). Lesch et al. (1996) found that trait neuroticism was associated with individual differences (i.e., polymorphisms) in this gene. Other research has observed suggestive associations between gene polymorphisms related to dopamine function and traits of extraversion and sensation seeking (Smillie, Cooper, Proitsi, Powell, & Pickering, 2010), although a meta-analysis suggests that evidence for these relationships is mixed across studies (Munafo, Yalcin, Willis-Owen, Flint, 2008).

Another method for garnering convergent insight into the genetic and neurotransmitter systems involved in social processes is the experimental administration of various drug challenges. These studies provide insight into the molecular involvement in aspects of personality and various behaviors, such as extraversion and economic decision-making (DePue, Luciana, Arbisi, Collins, & Leon, 1994; Crockett, Clark, Tabibnia, Lieberman, & Robbins, 2008). A growing body of evidence suggests that environmental experiences can directly and indirectly modulate the expression of DNA (Caspi et al., 2003; Champagne & Curley, 2005; Way & Gurbaxani, 2008), consistent with psychological theories that highlight the importance of both personal and environmental factors. Although this approach has generated much excitement, it is notable that effects in this literature have been difficult to replicate (Caspi et al., 2005; Munafo et al. 2003).

It is likely that the extreme complexity involved in traversing such distal levels of analysis—from DNA to complex behaviors, traits, and mental states—remains beyond the grasp of extant theoretical models. Therefore, much of the current work in this area continues to explore gene-behavior associations in an effort to incrementally constrain our understanding of their causal relationship, slowly progressing toward a coherent genetic account of personality and behavior.

**Hormones and Psychological Dispositions**

Although genes provide a close analog to the concept of personality as an enduring trait, the role of hormones in individual differences and social behavior has received much more attention. Hormones are characterized as providing a broader “organizational” function, in that they help to orchestrate the coordinated response of multiple physiological and brain mechanisms. By comparison, specific neural activations are typically interpreted as reflecting very specific, low-level aspects of a psychological response. Furthermore, whereas neural processes typically relate to specific state-related responses, the effects of hormones on behavior are slower, ranging from a few seconds, in the case of hormonal responses to specific events, to the course of a lifetime, in the case of baseline hormonal function. Hormonal influences in early development can set the stage for enduring dispositions in biological and mental processes. For example, prenatal exposure to sex hormones has been shown to have long-term implications for gender development and adult sexual behavior (Singh, Vidaurri, Zambarano, & Dabbs, 1999).

As with gene effects, hormone effects can vary substantially as a function of the situation. For example, testosterone levels may vary with changes in power and social status (Josephs, Sellers, Newman, & Mehta, 2006; Mazur & Booth, 1998), and individual differences in the testosterone response following a competition predict who chooses to seek a rematch (Mehta & Josephs, 2006). Experimental administration of testosterone can also increase attention to potential social threats, such as angry faces (van Honk et al., 1999). More recent research suggests that testosterone plays a larger role in orchestrating social behavior, such that it may promote greater cooperation in reciprocal social exchanges (Eisenegger et al., 2010).

Another steroidal hormone, cortisol, is widely studied as a physiological response to stress (Dickerson & Kemeny, 2004). Cortisol is produced by the adrenal glands following activation along the hypothalamic-pituitary-adrenal axis, and it functions broadly to regulate metabolism and arousal in dispositional (i.e., baseline) diurnal processes and also in response to specific arousing events. Cortisol secreted into the blood can be detected in saliva, and thus salivary cortisol concentrations may be measured non-invasively and with relatively low cost in the typical psychological laboratory (Schulthess & Stanton, 2009).

Cortisol reactivity in response to a stressor coordinates an adaptive response (e.g., fight or flight), but after chronic exposure, heightened levels of cortisol become maladaptive (McEwen, 1998; Sapolsky, Romero, & Munck, 2000). For example, higher baseline cortisol levels have been associated with unhealthy profiles, including perceived stress, anxiety, depression, and cardiovascular stress (Cohen et al., 2006; Gallagher, Reid, & Ferrier, 2009). Although cortisol reactivity in response to a stressful
event has been examined in different contexts, a
meta-analysis by Dickerson and Kemeny (2004)
suggests that it is especially sensitive to socioevalua-
tive stressors, such as when a subject must give an
extemporaneous speech to a panel of disapproving
peer judges. Thus, cortisol research has highlighted
the primacy of social interactions in human motiv-
ation and stress responses. As an outcome measure,
cortisol provides a useful assessment of the stress
response that does not rely on self-report. Further-
more, the connection between psychological distress
and biological responses highlights connections
between the mind and body, and it underlines the
important effects that social and dispositional fac-
tors have on physical health. Research on immune
variables, such as proinflammatory cytokines, pro-
vides a similar link that pertains even more directly
to healing and illness processes (Maier & Watkins,
1998; Segerstrom & Miller, 2004).

It is notable that the greatest power of the social
neuroscience approach lies in its ability to probe
mechanism, and researchers have recently begun to
conceptualize hormones and immune variables as
mechanism variables. For example, Amodio (2009)
measured salivary cortisol as a downstream correlate
of within-brain norepinephrine activity to test a
mechanism through which intergroup anxiety
affects the control of racial stereotypes. Maier and
Watkins (1998) provided a detailed analysis of how
changes in cytokines and other associated immune
and endocrine variables can act as mechanisms to
alter cognition, emotion, and behavior, and to pro-
mote an organism’s health. These examples suggest
that endocrine and immune approaches will increas-
ingly be used to understand psychobiological mech-
anism associated with social and personality
processes in future research.

The Future of Social Neuroscience in
Social-Personality Psychology

Over the past decade, physiological approaches have
reemerged as an important facet of social-personal-
ity research, now augmented by advances in neural,
pharmacological, endocrinological, immunological,
and genetic approaches. This time, we think neuro-
sience is here to stay. Recently a novelty in social-
personality circles, the neuroscience perspective is
now woven into the natural discourse of social-per-
sonality inquiry. Neuroscience data are increasingly
integrated into the literature reviews of mainstream
social-personality manuscripts, and psychophysio-
logical methods complement the traditional tools of
behavioral psychology, now without the fanfare of a
novelty act. Social neuroscience is also becoming
more prevalent in the training of new social-personal-
ity psychologists. These are healthy developments
for the field.

The purpose of this volume is to highlight the
interplay of personality and social psychological
approaches. It is interesting to consider this aim
from the perspective of social neuroscience, a field
in which traditional boundaries between the person
and the situation are reinterpreted as complex,
dynamic, and inherently multilevel interactions.
For example, neuroscientific models reveal how our
perception of a situation is influenced by disposi-
tional factors, such as personality, goals, and mental
sets (following ideas from the New Look move-
ment). At the same time, research on genetics shows
that even our DNA may be influenced by situational
factors at the time of conception, and that gene
expression—often held to be the purest expression
of personality—is strongly influenced by the situa-
tion. Thus, from the social neuroscience perspec-
tive, a dynamic interplay of personal and situational
influences operates at every level of analysis.

In this regard, the social neuroscience approach
is helping to build connections between the fields of
social and personality psychology in two ways. The
first way is through its influence on theory and
research. As noted above, social neuroscience
research reveals the dynamic symbiosis between sit-
utional and personal factors that exists across levels
of analysis, in line with the interactionist view that
the effects of personality and the situation can
only genuinely be studied in the context of each
other. The second way is by bringing together
researchers from different disciplines to lend their
respective expertise to integrative research questions,
and by promoting education and training in inter-
disciplinary approaches used in social neuroscience
research.

Conclusion

Although neuroscience has reemerged on the social-
personality scene, it still needs to establish itself as a
substantive contributor to social and personality
psychology theory. Success in this endeavor will
depend on researchers’ ability to ground their social
neuroscience research in rigorous methodology and
to relate it to central questions and theories of social
and personality psychology. Researchers in the field
are clearly rising to this challenge. As we described
in this chapter, neuroscience theories and methods
have begun to shed new light on the mechanisms
of person perception, emotion, stereotyping and
prejudice, and some aspects of personality processes. Once the functions of specific neural structures, and their associated networks, are better understood, the contributions of linking social-personality processes to the brain will be increasingly realized. We look forward to new contributions from the social neuroscience approach in years to come.

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