

The Role of the Human Prefrontal Cortex in Social Cognition and Moral Judgment*

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Key Words

implicit and explicit social cognitive and moral judgment processing, frontal lobes, neural function, social cognitive neuroscience, structured event complex theory

Abstract

Results from functional magnetic resonance imaging and lesion studies indicate that the prefrontal cortex (PFC) is essential for successful navigation through a complex social world inundated with intricate norms and moral values. This review examines regions of the PFC that are critical for implicit and explicit social cognitive and moral judgment processing. Considerable overlap between regions active when individuals engage in social cognition or assess moral appropriateness of behaviors is evident, underscoring the similarity between social cognitive and moral judgment processes in general. Findings are interpreted within the framework of structured event complex theory, providing a broad organizing perspective for how activity in PFC neural networks facilitates social cognition and moral judgment. We emphasize the dynamic flexibility in neural circuits involved in both implicit and explicit processing and discuss the likelihood that neural regions thought to uniquely underlie both processes heavily interact in response to different contextual primes.

Contents

INTRODUCTION	300
A BRIEF PRIMER ON	
SOCIAL COGNITION	301
Social Perceptual Processes	301
Attributional Processes	301
Social Categorization Processes	302
THE ROLE OF IMPLICIT	
AND EXPLICIT PROCESSES	
IN SOCIAL COGNITION	302
A BRIEF PRIMER ON	
MORAL JUDGMENT	304
Dual Process and Interactionist	
Models of Moral Judgment	304
STRUCTURE AND FUNCTION	
OF THE PFC	306
PFC REGIONS CRITICAL	
FOR SOCIAL COGNITION	
AND MORAL JUDGMENTS	307
The Role of the PFC in Social	
Perceptual Processes	308
The Role of the PFC in	
Attributional Processes	308
The Role of the PFC in Social	
Categorization Processes	309
The PFC's Role in Moral Judgment	
Processes	310
STRUCTURED EVENT COMPLEX	
THEORY DESCRIBES THE	
PFC'S ROLE IN SOCIAL	
COGNITION AND MORAL	
JUDGMENT	311
SECs Are Composed of	
Multiple Dimensions	312
SUMMARY AND	
CONCLUSIONS	314

INTRODUCTION

Take a second to recall a recent interaction you had with someone you met for the first time at a social event. Hopefully the conversation went swimmingly and you devoted most of your attention to the verbal interaction. If probed, however, you could probably recall, in

addition to the information learned verbally, the person's ethnicity, whether he/she was similar to you, and your impressions of which type of person you thought they were in general (and subsequently whether you liked them). You probably even processed all of this information within a few seconds. Thus within a matter of seconds, you encoded identifiable information about the person, predicted what would be best to say to facilitate a pleasant interaction, and formed an impression of him/her, all while your prefrontal cortex (PFC) simultaneously monitored and evaluated neural information from your five modalities, coordinated movements and actions, and kept you focused on adhering to social or personally relevant norms. Yet you likely processed such information with nary a thought, largely because your PFC can engage in most of the aforementioned functions outside of your conscious awareness. With this scenario in mind, you can begin to appreciate the complexity of interactions between multiple cognitive and sensory processes originating from neural regions both within and outside the PFC that provide the foundation for complex social behavior and moral judgment.

The PFC is anatomically organized in a way that allows for information from all five senses to be integrated [see the discussion of Banyas (1999), Fuster (1997) below]. The PFC is also critical for higher order functions such as focusing attention on goal-relevant stimuli and inhibiting distractions (Badre & Wagner 2004, Botvinick et al. 2004, Dolcos et al. 2007, MacDonald et al. 2000, Milham et al. 2001, Miller & D'Esposito 2005), while evaluating and interpreting information within the context of past experiences (Adolphs 1999, Damásio 1994, Rolls & Grabenhorst 2008), storing semantic information about the self and others (Johnson et al. 2002, Kelley et al. 2002, Schmitz et al. 2004), and temporally organizing actions or planned behaviors (A. Barbey, M. Koenigs, and J. Grafman, under review; Fuster 1997, Wager & Smith 2003). Given all the cognitive functions for which the PFC is necessary, it is not surprising that the PFC makes higher-order cognitive functions such as social cognition and

PFC: prefrontal cortex

moral judgment possible. As we describe here, the PFC processes all these functions at varying processing speeds, e.g., impressions and judgments of others and one's surroundings can be reached within milliseconds (termed implicit, fast, or automatic processing) or derived over longer periods of time (termed explicit, slow, or controlled processing).

Below, we review literature linking PFC functions to those of social cognition and moral judgment. We begin with a general overview of social cognition and moral judgment and highlight how the PFC is organized to enable such higher-order cognitive processes and the regions they require most. The existing literature is then interpreted within the framework of the structured event complex theory (Grafman 2002, Wood & Grafman 2003), which offers a broad organizing perspective for how activity in the PFC neural network provides the impetus for social cognition and moral judgment. We highlight how PFC activity underlying the implicit and explicit processes necessary for social cognition and moral judgment varies in different situational contexts, i.e., how situational cues change the way stimuli are processed psychologically and neurologically.

A BRIEF PRIMER ON SOCIAL COGNITION

Social cognition refers to the processes by which we make sense of ourselves, the social environment or culture in which we live, and the people around us (Fiske 1993, Macrae & Bodenhausen 2000). Although the term social cognition can encompass any cognitive process engaged to understand and interpret the self, others, and the self-in-relation-to-others within the social environment, it can be broken down into several primary categories that have both implicit and explicit components. These categories include social perceptual processes, attributional processes, and social categorization processes that use schemas or stereotypes. Research highlighting each category is discussed in turn.

Social Perceptual Processes

Research on social perception includes how one processes and identifies faces and categorical information such as gender and ethnicity, mimics others on a basic level, and interprets others' movements and intentions. Given that humans can process social markers on the order of milliseconds (Cunningham et al. 2004a), engage different neural systems in the processing of inanimate objects compared with people (Mitchell et al. 2002), and appear to be uniquely sensitive to human faces (Kouider et al. 2009), one can presume that humans are innately sensitive to social information (Adolphs 1999, Van Overwalle 2009). Using electroencephalographic (EEG) methodology, research has documented that faces can be consciously distinguished from non-face stimuli by 170 ms, and ethnic in-group and out-group faces are differentiated by 250 ms (Ito et al. 2004). Distinctions between ethnicity and facial recognition can occur as quickly as 30–50 ms postpresentation in neural regions such as the amygdala and middle fusiform gyrus as well (Cunningham et al. 2004a, Kouider et al. 2009). The ability to process social information rapidly and with little other information provides individuals with a perceptual blueprint or schema that allows them to identify and seek out goal-relevant stimuli and avoid potentially dangerous stimuli in a remarkably efficient manner.

Attributional Processes

Attributional processes refer to an innate drive to explain and understand others' actions and behaviors as well as our own (Gilbert & Malone 1995). Attributional processes are highly contingent on the perspective of the perceiver, i.e., whether one is interpreting others' actions from their own perspective or from that of another (Storms 1973). The default mode is for individuals to evaluate others' actions from their own perspective, which typically leads to a fundamental attribution error, i.e., the tendency for people to attribute others' behaviors to trait characteristics and attribute their

own behavior to situational factors (Gilbert & Malone 1995, Ross 1977). Individuals are capable of taking the perspective of others, however (e.g., “walk a mile in another’s shoes”), which has formed the basis for the perspective-taking literature in social psychology and a widely investigated theory in the cognitive neuroscience literature termed theory of mind (TOM). TOM refers to the general ability to infer the thoughts and beliefs of one’s self and others (Carrington & Bailey 2009). Although the mechanisms involved in TOM are still unknown, i.e., whether it occurs via inferring others’ intentions and beliefs on the basis of observed behaviors (the “theory” theory; Gallese & Goldman 1998) or via inferring others’ intentions and beliefs by simulating how the observer might feel in similar situations (simulation theory; Gallese & Goldman 1998, Ramnani & Miall 2004), general consensus indicates that TOM is the fundamental basis for social interactions (for a review, see Carrington & Bailey 2009). As a whole, attributional processes serve as the foundation for developing self-knowledge (e.g., via self-perceptual processes; Bem 1967) in relation to others in our world and rely heavily on executive resources, and subsequently PFC resources, in general (Saxe et al. 2006).

Social Categorization Processes

Another line of social cognitive research examines how categorization processes such as schema and stereotype activation affect individuals’ perception and information processing. In regard to social cognition, schemas represent a cognitive framework for social categories and the associations among them (Fiske & Taylor 1991). Stereotypes, defined as a general belief one has toward different groups or cognitive objects (Allport 1954, Fiske 1998, Macrae et al. 1994), can be considered a specific type of schema. Although schemas and stereotypes make information processing dramatically more efficient (Macrae et al. 1994), they come with a price. For example, research finds that exposure to racial out-group members makes negative stereotypes immediately cognitively

accessible (termed automatic stereotype activation; Devine 1989). Once activated, stereotypes can be cognitively taxing to downregulate or suppress (C. Forbes and T. Schmader, under review; Richeson et al. 2003, Schmader et al. 2008), can bias nonverbal behaviors (Dovidio et al. 2002), and can negatively bias explicit perceptions toward out-group members behaving ambiguously (Rudman & Lee 2002), all seemingly unbeknownst to the perceiver. Thus although stereotypes facilitate the processing of information that is consistent with expectations, they also increase the incidence of judgment errors when information contradicts expectations and biases perceptions to a greater extent than the stereotyping individual assumes.

THE ROLE OF IMPLICIT AND EXPLICIT PROCESSES IN SOCIAL COGNITION

The field of social cognition has devoted much effort to understand better the differential effects of implicit and explicit processes on the aforementioned cognitive processes. Implicit processes unfold rapidly, require little cognitive effort, occur outside individuals’ conscious awareness, and involve posterior cortical and subcortical regions of the brain (Amodio & Devine 2006, Cunningham & Zelazo 2007). In addition to face recognition and stereotype activation, other implicit processes include conditioned, evaluative associations between ideas or categories and stimuli that fit those categories (termed implicit attitudes; Fazio & Olson 2003, Greenwald & Banaji 1995) and self-serving biases. Conversely, explicit processes are deliberative, cognitively taxing, consciously accessible, and largely rely on the PFC (Amodio & Devine 2006, Cunningham & Zelazo 2007). Examples of these processes include deliberative evaluations of objects (termed explicit attitudes; Oskamp & Schultz 2005), introspective perceptions of self and others, and attributions.

Although these processes have historically been treated as distinct from one another, given ambiguities in behavioral findings and the nature of neuroanatomical connections

(e.g., extensive reciprocal connections between PFC and subcortical regions in the brain; see **Figure 1**), recent perspectives argue that implicit and explicit processes may interact at all stages of cognitive processing (Cunningham & Johnson 2007, Devine & Sharp 2009; C. Forbes, C. Cox, T. Schmader, and L. Ryan, under review). Failure to identify a unitary, rapidly unfolding interaction between implicit and explicit processes could be due largely to methodological constraints and the nature of the issue being investigated (Devine & Sharp 2009). Pertaining to the nature of issues being assessed, implicit attitudes can be highly predictive of explicit attitudes, but implicit attitudes can also account for variance that is unexplained by explicit attitudes when researchers assess socially sensitive subjects such as race or gender (Cunningham et al. 2004b, Devine 1989, Greenwald et al. 2009, Nosek et al. 2002).

For instance, women often readily express dislike toward the math domain and can quickly pair negative words with math-related words on an implicit associations test (a common measure used to assess implicit attitudes; Nosek et al. 2002), suggesting they have a negative implicit attitude toward math as well (Nosek et al. 2002). When asking white individuals about their attitudes toward black individuals, however, although they explicitly report positive attitudes toward blacks, they often demonstrate a negative implicit attitude toward them on the implicit associations test (Greenwald et al. 2009, Greenwald & Banaji 1995). These negative implicit associations in turn can predict decreased math effort in women and negative nonverbal behaviors toward blacks during interracial interactions among other things (Dovidio et al. 2002; C. Forbes & T. Schmader, under review).

In the case of women's attitudes toward math, attitudes resulting from implicit and explicit processes appear to represent two ends on a continuum (i.e., faster to slower) that can be generated either rapidly or slowly and result in a unitary attitude. In the example of whites' attitudes toward blacks, attitudes would appear to result from two separate systems (i.e., faster versus slower) that engender two distinct

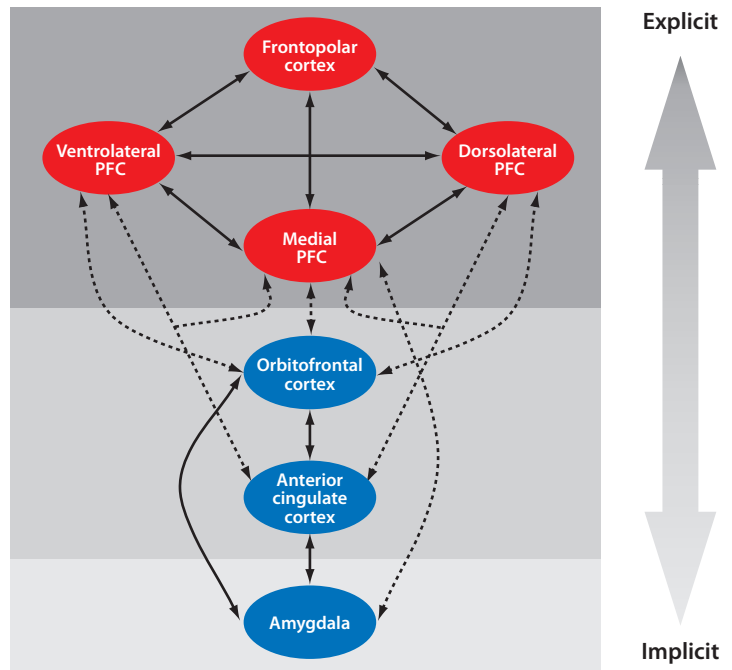


Figure 1

Diagram of direct neural connectivity between regions critical for implicit and explicit social cognitive and moral judgment processes. Solid bidirectional arrows denote direct reciprocal neural connectivity between two regions within a given processing system, i.e., implicit or explicit processing. Dashed bidirectional arrows represent direct reciprocal connectivity between two regions typically involved in either implicit or explicit processing. Blue circles denote neural regions that are typically involved in more implicit cognitive processing. Red circles signify neural regions that are typically involved in more explicit cognitive processing. These regions are not exclusively involved in implicit or explicit processing however. This conjecture is represented by the three shaded boxes and large arrow on the right. The lightest gray box represents neural regions, namely the amygdala here for the sake of simplicity, that are largely involved in implicit processes. Likewise, the darkest gray box highlights neural regions largely involved in explicit processes. The medium shaded box represents regions that are recruited during both implicit and explicit processing. PFC, prefrontal cortex.

attitudes. However, it is also possible that the latter scenario is reflective of an individual's ability to produce a rapid, visceral evaluation of a stimulus that can then be assessed within a given context for appropriateness and be down-regulated, suppressed, or altered accordingly.

This interpretation would suggest that the implicit attitude and explicit attitude are unitary, but situational demands (e.g., the desire to be politically correct in an interaction with a new acquaintance) necessitate alteration of the

fMRI: functional magnetic resonance imaging

overt expression of the explicit attitude, making them appear unique accordingly. In this instance, implicit and explicit processes likely interacted to engender the appearance of two distinct attitudes; however, given that these interactions can reach fruition within 500 ms, one can appreciate the difficulty inherent in examining them effectively [for detailed theoretical examinations of the conditions that may elicit implicit and explicit attitude overlap or differentiation, see Fazio & Olson (2003), Gawronski & Bodenhausen (2006), Petty et al. (2007), Wilson et al. (2000)]. Advances in EEG and functional magnetic resonance imaging (fMRI) methodologies, e.g., combining the exceptional temporal and spatial advantages of each respectively, could soon pave the way for successful assessments of these interactions.

The examination of implicit and explicit processes is not unique to social cognition. Given that visceral, emotional responses to stimuli can also be considered an implicit response, in recent years investigators have devoted much attention to understanding how emotional reactions can bias otherwise rational perceptions when people evaluate the appropriateness of others' behaviors. As you might expect, attributional products of implicit and explicit processes also play a prominent role in our next topic: the field of moral judgment.

A BRIEF PRIMER ON MORAL JUDGMENT

Moral judgments are broadly defined as evaluative judgments of the appropriateness of one's behavior within the context of socialized perceptions of right and wrong (Moll et al. 2005). **Table 1** provides an overview of traditional philosophical dilemmas as well as more recent, real-world examples that have been used to assess moral judgment processes in the literature. The study of morality and subsequent moral judgments has a long history in philosophy and more recently psychology, and as opposed to the fundamental top-down and bottom-up processes the field of social cognition usually tackles, moral judgments have long been thought

to rely solely on controlled, rational, and logical thought processes (Kohlberg 1969, Turiel 1983). Given the likely evolutionary origins of morality and the degree to which it permeates all facets of society and cognition from early childhood on, the idea that moral judgments are only a product of controlled cognitive processing has been convincingly challenged (Haidt 2001, Moll et al. 2005, Schulkin 2000).

More recent research on moral judgments has begun to incorporate the likelihood that moral judgments have an emotional component to them as well. On one end of the spectrum, some researchers have argued that moral judgments are largely direct products of intuitive or implicit emotional processes (Haidt 2001, Nichols 2002, van den Bos 2003). According to Haidt's social intuitionist model (Haidt 2001), moral behavior is predicated largely on implicit moral emotions such as guilt or compassion that compete and interact to guide morality outside of conscious awareness. These moral emotions were likely essential to our survival and evolution as a species and thus influence our perceptions and thoughts at all levels of cognitive processing in the form of "moral intuitions" (Moll et al. 2003). Controlled cognitive processes are likely to play a role in moral judgment only when situational demands necessitate them, e.g., situations that engender moral dilemmas (Moll et al. 2003). Although theories such as Haidt's rightfully identify a critical role for implicit emotional processes, they deemphasize the importance of explicit cognitive processing. As such, it is more difficult to explain findings demonstrating the importance of explicit processes, and the integral role that the PFC appears to play, in moral judgments overall (discussed below).

Dual Process and Interactionist Models of Moral Judgment

To bridge the gap between moral judgments and implicit and explicit processes, other researchers have incorporated the concept of a dual-process theory, positing that moral judgments can be derived via implicit, emotional

Table 1 A sample of traditional philosophically based (numbers 1 and 2; e.g., Greene et al. 2001, Koenigs et al. 2007) and more pragmatic (numbers 3, 4, and 5; Knutson et al. 2010) vignettes used to assess moral judgment processes

Type of moral judgment assessed	Typical examples	Moral judgment
1. Impersonal moral dilemmas	The Standard Trolley dilemma: You are at the wheel of a runaway trolley quickly approaching a fork in the tracks. On the tracks extending to the left is a group of five railway workmen. On the tracks extending to the right is a single railway workman. If you do nothing the trolley will proceed to the left, causing the deaths of the five workmen. The only way to avoid the deaths of these workmen is to hit a switch on your dashboard that will cause the trolley to proceed to the right, causing the death of the single workman.	Is it appropriate for you to hit the switch to avoid the deaths of the five workmen? Note: The decision to hit the switch is considered the utilitarian choice. The decision to not hit the switch is the non-utilitarian or deontological choice.
2. Personal moral dilemmas	The Crying Baby dilemma: Enemy soldiers have taken over your village. They have orders to kill all remaining civilians. You and some of your townspeople have sought refuge in the cellar of a large house. Outside you hear the voices of soldiers who have come to search the house for valuables. Your baby begins to cry loudly. You cover his mouth to block the sound. If you remove your hand from his mouth his crying will summon the attention of the soldiers who will kill you, your child, and the others hiding out in the cellar. To save yourself and the others you must smother your child to death.	Is it appropriate for you to smother your child to save yourself and the other townspeople?
3. Violations of social norms	As I was backing out of a parking lot, I bumped a parked car and left a minor dent. I did not even feel the impact when I hit the car, but it left a little bit of damage. I drove away without leaving a message or trying to contact the person.	Rating the vignette on dimensions of emotional intensity, emotional aversion, harm, self-benefit, other-benefit, premeditation, illegality, social norm violations, the extent to which other individuals were involved in the scenario, likelihood of event occurring in real life, personal familiarity, general familiarity, and moral appropriateness.
4. Social affective/aversive situations	In the late nineties, I got my girlfriend pregnant. She told me she was pregnant and that she wanted me to be there for her. At first, I took her to her appointments and such, until I became nervous and ended the relationship.	Rating the vignette on dimensions of emotional intensity, emotional aversion, harm, self-benefit, other-benefit, premeditation, illegality, social norm violations, the extent to which other individuals were involved in the scenario, likelihood of event occurring in real life, personal familiarity, general familiarity, and moral appropriateness.
5. Intent involved in situations that engender self-benefit	I was taking a statistics class and the professor's instructions were very unclear. So, all the students in the class helped each other on homework assignments and tests. When it came time to take the test we would just give each other the answers.	Rating the vignette on dimensions of emotional intensity, emotional aversion, harm, self-benefit, other-benefit, premeditation, illegality, social norm violations, the extent to which other individuals were involved in the scenario, likelihood of event occurring in real life, personal familiarity, general familiarity, and moral appropriateness.

EFECs: event–feature–emotion complexes

DLPFC: dorsolateral prefrontal cortex

VLPFC: ventrolateral prefrontal cortex

VMPFC: ventromedial prefrontal cortex

OFC: orbitofrontal cortex

routes and explicit, controlled routes (Greene et al. 2001, 2004). Specific to moral dilemmas, Greene and colleagues have argued that emotional and controlled cognitive processes are key components of moral decisions involving utilitarian (e.g., choosing to sacrifice one to save many) and nonutilitarian choices (e.g., choosing to risk detection by enemy soldiers in lieu of smothering one’s crying baby to death; see **Table 1**), and at times can play competitive roles (Greene et al. 2008). Whereas utilitarian judgments require controlled cognitive processing and are thus cognitively demanding, nonutilitarian or deontological judgments are implicit and predicated on emotional responses.

As opposed to implicit and explicit processes competing against each other, other researchers argue that the answer may lie somewhere in between (Moll & de Oliveira-Souza 2007). Moll et al. (2005) suggest that moral processes are products of the integration of social contextual knowledge, social semantic knowledge, and basic motivational and emotional drives. These three component representations interact to produce what Moll et al. term event–feature–emotion complexes (EFECs), which bind together via sequential, temporal, and third-party binding mechanisms and are influenced by one’s situational and cultural context. Through these interactions, the EFEC framework makes specific hypotheses for moral judgments and moral emotions in different contexts. As discussed below, the model proposed by Moll et al. (2005) also makes specific predictions regarding patterns of neural activity in the PFC and subcortical regions engendered by situations that require moral judgments.

In sum, there is much debate regarding how moral judgments are cognitively derived and how they influence overt perceptions of others. Regardless of which theoretical conjecture is most plausible, moral judgments likely arise out of complex interactions between implicit and explicit processes. The field of cognitive neuroscience and the fundamental role the PFC plays in cognition can help shed light on the nature of social cognitive and moral judgment processes. Next we briefly describe the

structure and functions of the PFC that enable social cognition and moral judgments.

STRUCTURE AND FUNCTION OF THE PFC

The PFC can be parsed into dorsolateral (DLPFC), ventrolateral (VLPFC), dorsomedial (DMPFC), ventromedial (VMPFC), and orbitofrontal (OFC) regions. Whereas the VMPFC and OFC regions evolved from subcortical regions in the limbic system, the DLPFC likely evolved much later from motor regions such as the basal ganglia, the premotor cortex, and the supplementary motor area (Banyas 1999, Fuster 1997). Given that the motor areas of the cortex are thought to store motor programs, i.e., representations of well-learned mechanistic procedures, regions of the PFC that evolved more recently may be related to these evolutionarily older regions because they provide a representational basis for goal-directed action (Barbey et al. 2009, Wood & Grafman 2003). By examining the axonal projections distributed by and received by each major region of the PFC, we can learn more about the basic functions in which PFC regions are involved.

The medial and orbitofrontal regions of the PFC are hubs for integrating emotional, viscerally arousing information and relaying that information to the DLPFC (Fuster 1997). Specifically, medial and orbitofrontal regions of the PFC receive direct afferents from the amygdala, from most other limbic structures, from the striatum, and from temporal visual association areas. Medial and orbitofrontal regions also receive indirect afferents from the mesencephalic reticular formation and from the inferior temporal cortex [e.g., the fusiform face area (FFA)] via the magnocellular portion of the mediodorsal nucleus in the thalamus (Fuster 1997). Studies in a variety of animal species, including the monkey, indicate that the medial and orbitofrontal regions of the PFC, in turn, send a multitude of efferents to the DLPFC (Amaral & Price 1984, Ghashghaei & Barbas 2002, Ghashghaei et al. 2007), which

suggests that the medial PFC regions (DMPFC, VMPFC, and OFC) are integral for monitoring individuals' internal states and motivations and for relaying that information to the DLPFC (Elliott & Deakin 2005, Wood & Grafman 2003).

The DLPFC is thought to be involved in the execution of movement and planned behaviors as well as the integration of sensory information (Barbey et al. 2009, Beuregard et al. 2001, MacDonald et al. 2000, Miller & Cohen 2001, Wood & Grafman 2003). This is particularly likely given that the DLPFC is reciprocally connected with the basal ganglia, the premotor cortex, the supplementary motor area, the cingulate cortex, and association areas and receives indirect afferents from the substantia nigra, the cerebellum, and the globus pallidus via mediodorsal and ventrolateral thalamic nuclei (Fuster 1997). Highlighting a fundamental yet pervasive role for the DLPFC in goal-directed behavior, the neural circuit that embodies the reciprocal connections between the DLPFC and anterior cingulate cortex (ACC) has been heavily implicated in the detection of and subsequent correction for behaviors that engender outcomes that differ from expectations (e.g., Cavanagh et al. 2009). Pyramidal cells in the DLPFC also exhibit the potential to fire over extended periods of time (Levy & Goldman-Rakic 2000) and across events (Bodner et al. 1996, Fuster & Alexander 1971), which suggests that the PFC is well suited for representing action and engaging in behaviors that allow humans to execute long-term goals (Barbey et al. 2009).

Overall, the PFC receives direct afferents from most brain regions, including the hypothalamus and hippocampus (at least in the rat, cat, and monkey), and is extensively interconnected with systems within the occipital, parietal, and temporal lobes that are involved in sensory processing for each modality (Fuster 1997). Often considered the "top" of a top-down hierarchically determined architecture, the PFC is critical for setting and achieving long-term goals (Koechlin et al. 2003) and for setting activation thresholds in nonfrontal

brain regions to detect goal-relevant stimuli. As such, in conjunction with subcortical regions, the PFC likely provides the key representations for implicit and explicit social cognitive and moral judgment processing. We next discuss the specific regions involved in said processes and findings supporting these conjectures.

PFC REGIONS CRITICAL FOR SOCIAL COGNITION AND MORAL JUDGMENTS

Many social cognitive processes are uniquely human and, as such, utilize distinct neural processes over and above those involved in memory, executive function, perception, and language in general (Adolphs 1999, Mitchell et al. 2006b, Van Overwalle 2009). Overall, implicit social cognitive and moral judgment processing typically involves the amygdala, insula, hypothalamus, ACC, OFC, and sensory cortex (Cunningham & Zelazo 2007, Moll et al. 2005). Conversely, slower explicit processing typically involves the VMPFC, the DLPFC, the VLPFC, and the anterior most portion of the PFC, termed the frontopolar cortex (FPC) (Cunningham & Zelazo 2007, Moll et al. 2005). Although these regions may be typically involved in implicit or explicit processing, they may not be exclusively involved in one form of processing or the other and, as noted above, likely interact at all levels of processing (see **Figure 1**). For instance, whereas regions such as the amygdala, ACC, and OFC may be typically recruited for implicit social cognitive processes, in the presence of contextual cues that prime different motivational or affective states, these regions may be recruited for, or remain particularly active during, explicit cognitive processing as well and exert influence over PFC regions accordingly (see the discussion of C. Forbes, C. Cox, T. Schmader, & L. Ryan, under review).

Activity in PFC regions associated with social cognition and moral judgment varies on the basis of the situational context and how stimuli are presented. For instance, studies have shown differential neural activity when

ACC: anterior cingulate cortex

FPC: frontopolar cortex

individuals engage in self compared with other processing (Jenkins et al. 2008, Mitchell et al. 2006a, Ochsner et al. 2005), when they are presented with predictable or random patterns of stimuli (Dreher et al. 2002), and whether stimuli are presented for short or long durations (Cunningham et al. 2004a; C. Forbes, C. Cox, T. Schmader, & L. Ryan, under review). Using the primers on social cognition and moral judgments as guides, we review the literature linking brain regions with the social processes outlined in these sections.

The Role of the PFC in Social Perceptual Processes

The social neuroscience literature reveals that social perceptual processes are dynamic and sensitive to basic, even arbitrary distinctions among identifying features of others. Presenting individuals with subliminal faces of out-group members elicits amygdala activation that can be regulated by the ACC, OFC, and DLPFC (Cunningham et al. 2004a; C. Forbes, C. Cox, T. Schmader, & L. Ryan, under review). Van Bavel and colleagues (2008) demonstrated that this typical neural response can be situationally manipulated on the basis of arbitrary social distinctions as well.

Utilizing the minimal group paradigm, a process known to establish novel in-groups and out-groups effectively using arbitrary information (e.g., tossing a coin or selecting a certain painting over another; Tajfel 1982), Van Bavel et al. (2008) randomly assigned white subjects to different arbitrary, mixed-race teams under the assumption that their team would be competing against another team later in the experiment. Subjects were first presented with the supposed faces of their team and the other team (which consisted of equal numbers of white and black faces), were asked to encode them, and then were presented with the faces later during a task that asked them to categorize faces by ethnicity or team membership. After the experiment, subjects provided likeability ratings for the different faces they were presented with throughout the task. Behavioral findings

replicated the basic minimal-group effect: Subjects reported liking members of their team, regardless of ethnicity, more than members of the other team. The neuroimaging results indicated that compared with out-group faces, exposure to in-group faces engendered greater activity in the amygdala, FFA, OFC, and dorsal striatum. Furthermore, activity in the OFC mediated the biased, in-group liking ratings. These findings suggest that the neural networks underlying social perceptual processes are quite sensitive to the malleability of social group membership and self-categorization. A situational shift in self-categorization can alter the way neural networks process and attend to social stimuli, such as an out-group face compared with a teammate's, in spite of otherwise well-learned negative associations linked to out-group members.

The Role of the PFC in Attributional Processes

An abundance of findings in the TOM literature suggests that specific social cognitive neural networks are involved when individuals engage in attributional processes in general (for a recent meta-analysis, see Van Overwalle 2009). Indeed, TOM would not be possible without large contributions from adequately functioning PFC regions and the consistent finding that individuals with autism have particular difficulties with TOM tasks is particularly persuasive. For instance, Castelli and colleagues (2002) asked adults with autism or Asperger syndrome and normal controls to watch animated sequences of triangles engaging in various movements, some of which imply intent. Subjects were asked to describe what was happening in each animation, and sequences that depicted some kind of intent among the triangles led normal controls to "mentalize," or make inferences that implied the triangles had mental states. During this task, autistic subjects demonstrated a lack of mentalizing compared with controls during animated sequences that implied intent; autistic subjects also demonstrated less activity in the medial PFC, the tempoparietal junction, and the temporal poles than did controls.

In addition to findings demonstrating abnormal functioning in autistic individuals' medial PFC during self-related and mentalizing tasks in general (Gilbert et al. 2009), these findings suggest the medial PFC plays a critical role in allowing individuals to identify themselves as unique agents in a social world that, in turn, allows them to infer intent in their behavior and in others'.

The VMPFC seems to be particularly important for perspective taking, TOM, and self and other processing. Research from patient studies supports this conjecture. In addition to the tamping-iron-through-the-medial-PFC-induced curmudgeonry incurred by Phineas Gage, individuals with VMPFC lesions and frontotemporal dementia are known to have particular difficulties with mental tasks such as inferring a person's psychological state by interpreting the directionality and expression of their eyes (i.e., the reading the mind in the eyes test; Baron-Cohen et al. 2001) and faux pas detection (Gregory et al. 2002). Patients with VMPFC as well as OFC lesions are also notorious for inappropriate or irrational social behaviors (Barrash et al. 2000, Beer et al. 2006, Grafman et al. 1996, Koenigs & Tranel 2007). Investigators have also found increased activity in the medial PFC when individuals engage in tasks that are introspective in nature, which suggests that the medial PFC may be a hub for self, other, and self-in-relation-to-other processing in general (Amodio & Frith 2006; Gusnard et al. 2001; Johnson et al. 2002, 2006).

The Role of the PFC in Social Categorization Processes

The medial PFC also plays a critical role in social categorization processes. Individuals with VMPFC lesions have exhibited reduced implicit stereotyping compared with normal controls and those with lesions in the DLPFC (Milne & Grafman 2001), which suggests that this region is important for the representation of social schemas and stereotypes. In light of the functional connectivity between the VMPFC and the DLPFC, stereotype primes likely

engender increased activity in the VMPFC, which then relays information to the DLPFC. Not surprisingly then, many studies suggest the DLPFC is critical for regulating or suppressing stereotype activation in general (Knutson et al. 2007, Payne 2005, Richeson et al. 2003), and studies of patients with primarily VLPFC or VMPFC lesions (Gozzi et al. 2009) support this idea. The latter study also demonstrated that another important component in implicit stereotyping is conceptual social knowledge and that anterior temporal lobe lesions, particularly in the right hemisphere, can compromise this form of social representation.

Highlighting the dynamic flexibility of the neural substrates that underlie these social phenomena, including those involved in implicit and explicit processing, C. Forbes, C. Cox, T. Schmader, & L. Ryan (under review) investigated the effects of priming negative in-group and out-group stereotypes on individuals' motivation to regulate stereotype activation. In this study, white subjects who reported being explicitly nonprejudiced and motivated to remain so were presented with subliminal (30 ms) and supraliminal (525 ms) black and white faces. To prime negative in-group and out-group stereotypes, either a violent death metal or violent rap song, i.e., stimuli that prime negative stereotypes for whites or blacks respectively, was played in the background while subjects were exposed to the novel faces. Results revealed that when negative white stereotypes were primed, the typical amygdala response to subliminal black faces was not evident. When negative stereotypes of blacks were primed, however, amygdala activity was elicited in response to black faces at implicit processing speeds that persisted into explicit processing speeds, i.e. the amygdala response was evident in response to black faces presented at both 30 ms and 525 ms.

Furthermore, functional connectivity analyses revealed that the increased amygdala response to subliminal black faces covaried with increases in OFC and DLPFC activity among other regions. The amygdala response to supraliminal black faces covaried with decreases in ACC activity and again with increases

in DLPFC activity, which suggested that the negative stereotype activation engendered increased processing demands in the DLPFC specifically at implicit and explicit processing speeds. These findings indicate that neural regions involved in implicit and explicit processing may interact at fast and slow cognitive processing speeds and that situational primes can alter how neural networks involved in social cognition perceive and react to social stimuli.

The PFC's Role in Moral Judgment Processes

The basic components of social cognitive and moral judgment processing appear similar, and neural regions involved in these types of processes reflect this. Many key neural regions involved in social cognition overlap with those involved in moral judgment, including the medial PFC and DLPFC. For instance, Greene and colleagues (Greene et al. 2001, Greene & Haidt 2002) suggest that when individuals consider personal moral dilemmas and/or make non-utilitarian judgments, areas involved in emotion processing are likely to exhibit increased activity, and this effect would be mediated by the medial PFC. Conversely, considering impersonal moral dilemmas and/or making utilitarian judgments are more likely to elicit increased activation in regions associated with cognitive control processes and the DLPFC specifically. Again, according to Greene and colleagues, these dual routes to decision making may often compete or create tension.

To test this hypothesis, Greene et al. (2004) asked subjects to read a series of moral dilemmas, ranging from impersonal (e.g., flipping a trolley track switch to save the lives of many compared to one) to personal (e.g., smothering your crying baby to death to avoid being detected by oppositional soldiers who will kill you and others) and indicate which alternative they would choose. Results revealed that personal moral judgments elicited activity in the medial PFC among other regions, replicating previous findings (Greene et al. 2001). In contrast, impersonal moral judgments elicited activity in the

DLPFC, which suggested that individuals engaged in more effortful cognitive, as opposed to emotional, processing in analyzing these moral dilemmas. Increased activity in the DLPFC was also evident when individuals made utilitarian choices on personal moral dilemmas (e.g., indicating they would smother their baby to death to save the lives of many).

One set of findings inconsistent with Greene's dual process theory is that individuals with VMPFC lesions make more emotional choices in an ultimatum game and more utilitarian moral judgments in general compared with normal controls (Koenigs et al. 2007, Koenigs & Tranel 2007, Moll & de Oliveira-Souza 2007). Other important factors to consider when contrasting personal versus impersonal moral decisions include the frequency of exposure to the described scenario. Personal moral decision making as well as more real-world or pragmatic scenarios would be more likely to recruit familiar analogous personal memories, whereas impersonal moral decision making and those dilemmas grounded in traditional philosophy would be less likely to do so on the basis of frequency of experience alone. Controlling for these and other factors that could affect scenario processing is critical, and Knutson and colleagues have now established a normative database of brief, real-world moral scenarios for this purpose (Knutson et al. 2010).

Thus, Moll and colleagues argue for the EFEC framework described above and posit that a network of closely interconnected neural regions is responsible for integrating the diverse functions involved in moral appraisals and judgments. In addition to the VMPFC and DLPFC, other critical regions are the FPC, the anterior temporal cortex, the superior temporal sulcus region, and the limbic structures including the amygdala, the angular gyrus, and the posterior cingulate (Moll et al. 2005, Moll & de Oliveira-Souza 2007, Raine & Yang 2006). Moll and colleagues' EFEC framework (Moll et al. 2005, Moll & de Oliveira-Souza 2007) makes specific hypotheses regarding the neural regions involved in moral judgment, emotions, and values.

Specific to the PFC, the EFEC framework predicts that whereas the anterior PFC is integral for enabling humans to assess the possible long-term consequences of their behavior with respect to others, the DLPFC is integral for predicting outcomes of one's behavior in novel contexts. Consistent with the hypothesized role of the VMPFC in the representation of social knowledge, Moll et al. (2005) argue that the VMPFC plays an important role in allowing one to adhere to social norms and cultural values that individuals derive through the socialization process. Finally, the OFC is likely necessary for comparing social cues in a given context with one's preexisting representations of social knowledge to help one determine appropriate behaviors within a given context. Consistent with one theme of this review, the nature of the presenting stimuli and/or that which individuals are asked to deliberate can differentially activate regions involved in more implicit emotional processing (i.e., the limbic system) or slow explicit processing (e.g., the DLPFC) depending on the context. Although a host of evidence from lesion and experimental studies supports these conjectures, to date no investigators have directly compared the various models of moral judgment and processing in social neuroscience experiments.

Overall, the medial and lateral PFC as well as the ACC and OFC are clearly necessary for social cognitive and moral judgment processing (Figure 2). How these regions interact to facilitate everything from basic social cognitive processes to more complex processes such as moral judgment and in what capacity are still questions that are much debated in the literature. Next, we outline a theory that attempts to answer these questions by providing a framework for the types of information stored in the different regions of the PFC and how they may interact to enable social cognitive and moral judgment processing in general.

STRUCTURED EVENT COMPLEX THEORY DESCRIBES THE PFC'S ROLE IN SOCIAL COGNITION AND MORAL JUDGMENT

As mentioned above, on the basis of the functional connectivity between different PFC and subcortical regions and evolutionary and neurophysiological evidence, the primary role of the PFC is in the representation of action and guidance of behavior (Barbey et al. 2009). Any given behavior can be broken down into a series of recognizable events, which are semantic in nature and of a fixed temporal duration

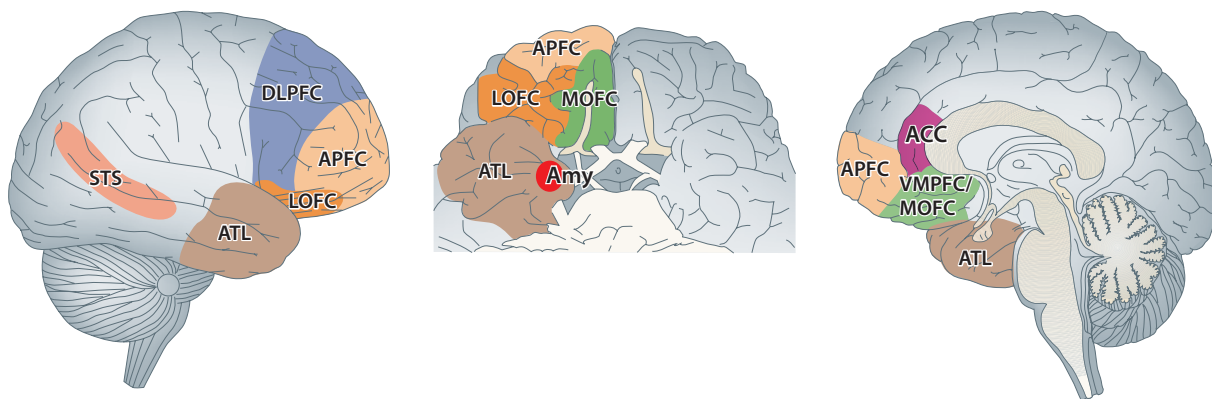


Figure 2

Neural regions identified as critical for social cognitive and moral judgment processing. Neural regions include the anterior prefrontal cortex (APFC), dorsolateral prefrontal cortex (DLPFC), medial and lateral orbitofrontal cortex (MOFC and LOFC), ventromedial regions of the prefrontal cortex (VMPFC), anterior cingulate cortex (ACC), anterior temporal lobes (ATL), amygdala (Amy), and the superior temporal sulcus (STS) region. Modified, with permission, from Moll et al. (2005), figure 1.

(Barbey et al. 2009, Zacks & Tversky 2001). In a given situation, a series of events can be primed and linked together to form a script that guides behavior and allows one to predict how the situation will unfold. The linking of events can, in turn, represent a set of goal-oriented events, one that is sequentially ordered and composed of social norms that guide behavior and perceptions. We refer to this goal-oriented set of events as a structured event complex (SEC) (Barbey et al. 2009, Grafman 2002, Wood & Grafman 2003).

Components of SECs can be semantically independent, but they are encoded and retrieved as an episode using simulation mechanisms or feature maps (Barsalou et al. 2003a,b; Damasio 1989). SECs provide goal-directed actions with semantic and temporal structure and are activated or primed by environmental cues, arming the organism with ammunition to predict how different social scenarios will unfurl. SECs ultimately represent myriad bits of knowledge that can be organized in predictable or unique manners to allow for increasingly complex behaviors and predictions. The type of knowledge a given SEC contains and the format of the behaviors they facilitate can be localized to specific neural regions.

SECs Are Composed of Multiple Dimensions

According to the SEC framework, SECs have multiple dimensions to them, including predictability, complexity, and category specificity, and the nature of the binding process is predicated on the hemisphere in which binding occurs (for a review, see Barbey et al. 2009). Overall, whereas the left PFC is hypothesized to integrate meaning and features between single adjacent events, the right PFC integrates meaning and information across events. In terms of degree of predictability, the medial PFC stores predictable SECs, or those SECs that are engrained in individuals and have structured, familiar goals and behaviors associated with them. Predictable SECs can be thought of as a schema or stereotype in general; e.g., they represent

how different events such as going to a party or a lecture typically unfold, but they are tailored toward the individual's goals. For instance, when going to a party, an introvert is likely to have different goals than an extrovert, and subsequently their SEC for attending a party, while similar, will uniquely vary on the basis of their individual goals for the evening (e.g., stand in a corner like a wall flower versus meet as many new people as possible).

Conversely, the lateral PFC has evolved to store adaptive SECs, which are more flexible in nature and allow for adaptations to unique or ambiguous situations. For instance, when meeting someone new, an individual is likely to activate SECs on the basis of the person's appearance, which allow an individual to predict which behaviors are required for a successful interaction; however, unexpected feedback will stimulate different SECs that, in turn, will update predictions, goals, and ultimately behavior. This conjecture is supported by past research indicating that the VLPFC is particularly active when individuals experience attitude ambivalence, i.e., a situational cue primes both positive and negative information, thus requiring the individual to resolve the ambiguity in a novel manner (Cunningham et al. 2004b).

SECs vary substantially in complexity as well. Given its proximity to phylogenetically older regions of the brain, the posterior PFC stores simple, well-learned SECs that consist of minimal information about event sequences (e.g., see Kruger et al. 2009a,b). This is likely where basic social cognitive SECs, such as neural networks sensitive to different facial expressions or body movements, are stored, which, when activated by a situational cue, in turn activate more complex SECs in the anterior PFC. The most anterior portions of the PFC store the most complex SECs, including long-term goals and integration of multistage event complexes, which is likely why the FPC region is so heavily involved in complex moral judgments (Berthoz et al. 2002; Moll et al. 2001, 2002, 2005).

The VMPFC and DLPFC regions enable categorical specificity in SECs. Specifically, the VMPFC stores SECs specific to social norms

and scripts. In addition to Milne & Grafman's (2001) study demonstrating less stereotype activation by individuals with ventral PFC lesions (Milne & Grafman 2001), fMRI studies have demonstrated that stereotype activation is likely to engender increased activity in the VMPFC specifically (Knutson et al. 2007, Quadflieg et al. 2009). Violations of social norms also elicit activity in the VMPFC (Berthoz et al. 2002), which suggests that this region is upregulated for the purpose of retrieving stored social norms when contextual cues necessitate comparisons between others' behaviors and known norms. Together these findings support the notion that the VMPFC stores SECs specific to general beliefs about various social groups and social norms, which are necessary for one to navigate the social world in an efficient yet moral manner.

Not unlike other theories, the SEC framework posits that the DLPFC is involved in planning and action. The SEC framework specifically hypothesizes that the DLPFC stores event sequences that represent the planning and action necessary to achieve a primed goal state. Based on situational cues, overarching goals dictate how components from SECs activated in other brain regions are integrated and organized to formulate an action plan with a desirable outcome.

One way to assess the mechanisms underlying these assertions would be to examine individual differences between biased and nonbiased individuals interacting with an out-group member. For instance, we might expect interactions with an out-group member to elicit activation in the medial PFC in general, representing stereotypic activation associated with the out-group. We would also expect, however, for DLPFC activity to vary on the basis of an individual's goal to be nonbiased toward the out-group member, by which increased DLPFC activity could represent the manipulation and integration of SECs to allow the individual to actualize an egalitarian goal. One study by Rilling and colleagues (Rilling et al. 2008) provides a format to investigate these questions.

In one study, Rilling et al. (2008) randomly assigned subjects to a red or black team (purportedly based on results from a personality test) and asked them to complete a prisoner's dilemma task with a supposed in-group and out-group partner while brain activity was assessed via fMRI. Participants were classified as discriminators or nondiscriminators post-hoc on the basis of whether they reported feeling different when interacting with the in-group partner compared with the out-group partner. Results indicated that when playing with arbitrarily defined out-group members, both nondiscriminators and discriminators demonstrated increased activity in the medial PFC, suggesting they were activating SECs associated with social norms and perhaps representations of other known out-group members in hopes of predicting their partner's behaviors.

Activity in the DLPFC, however, was modulated by feelings toward the out-group partner. Nondiscriminators elicited greater activity in the DLPFC compared with discriminators. Given that typical minimal group paradigms such as these engender immediate in-group bias and disliking for out-group members (particularly during competitions), increased DLPFC activity in reported nondiscriminators could represent their attempts to organize activated SECs from the medial PFC in a manner consistent with an overarching egalitarian goal. These findings support the conjecture that a given situational cue activates stereotype-related SECs in the medial PFC, but the DLPFC monitors and temporally organizes these SECs within the context of meta-goal states, such as the desire to behave in a morally just way toward others to regulate behavior accordingly.

The SEC framework also provides a means for understanding how different PFC regions contribute to implicit and explicit processes and how these processes differentially affect PFC neural networks. Consistent with the role neural regions along the midline play in implicit processing in general (e.g., the amygdala and the ACC), the medial PFC likely contributes to implicit processes because this region stores predictable SECs associated with habituated

sequences, schemas, and stereotypes (e.g., one cannot have stereotype activation without the stereotype). Likewise, posterior regions of the PFC are likely involved in implicit processing to the extent they store basic features associated with others and others' intentions, which are automatically activated upon encounter. Conversely, the lateral and anterior portions of the PFC are more involved with explicit processing, given that these regions store adaptive and complex SECs involved in explicit planning, action, and detailed sequences.

Any given behavior enacted in a specific context would necessarily involve an interaction between the various SECs that contribute to implicit and explicit processing (see **Table 2**). For example, let's say you run into a friend of a friend at a bar whom you had met a few times before and this second-degree friend is behaving strangely. This behavior prompts you to engage in attributional processing to try and explain your acquaintance's behavior. To do this, simple SECs associated with the individual's features and context, predictable SECs associated with how the individual behaved in the past, and adaptive and complex SECs accounting for the unique situation would all be activated. Your motivation to understand or explain your acquaintance's behavior would in turn dictate whether conclusions would be based more on implicit or on explicit processes. If you do not necessarily like the person, your explicit attributions for their behavior are likely to be more influenced by predictable SECs that reflect your lack of motivation to understand their behavior and your disliking of them in general (e.g., "this person is weird just like I thought"). If the person is someone you want to like, adaptive and complex SECs will dictate explicit attributions as you are motivated to find specific contextual factors that may be influencing their behavior (e.g., "maybe they had a rough day and one drink too many").

Thus the lateral PFC can regulate the medial PFC, i.e. adaptive SECs will be utilized and predictable SECs will be inhibited or restructured within the overarching SEC accordingly, when habituated sequences are not appropri-

ate or desired in light of contextual cues. When motivation is lacking, contributions of the medial PFC to implicit processing will have a greater influence on explicit perceptions, and predictable SECs will be utilized in lieu of adaptive SECs. In both instances, however, the construction of the overarching SEC would be the product of the interaction between multiple SECs varying in complexity associated with contextual primes, norms, values, and current goal states or plans of action.

Overall, the SEC framework provides a rationale for the myriad cognitive processes involved in social cognition and moral judgment, from the heuristic and efficient to the dynamically flexible and cognitively demanding. It also highlights the pivotal role that different neural regions of the PFC play in those processes and the necessity for these neural regions to interact at multiple speeds of cognitive processing (see **Table 2** for a mapping of social processes on to brain regions and SEC components). Together, utilizing knowledge of the phylogenetically hierarchical structure of the PFC in conjunction with physiological properties of the PFC, the SEC framework provides a comprehensive view of how a given social context can activate and integrate SECs throughout the PFC that enable individuals to assess their situations and make predictions that satisfy personal goals in socially and morally appropriate ways either extremely quickly or more deliberately.

SUMMARY AND CONCLUSIONS

The PFC is vital for human social cognitive and moral judgment processing. Because more anterior regions of the PFC serve as the last, integrative stop for all facets of perceptual and emotional processing, regions such as the OFC, the VMPFC, and the DLPFC are likely critical for evaluating current motivational and emotional states and situational cues and for integrating this information within the context of current goal states and past experience. Through interactions among these regions, possibly at both implicit and explicit levels, humans can build immediate impressions of others, infer what

Table 2 A summary of different SECs involved in social cognitive and moral judgment processes, key PFC regions involved, and the tendency for a given process to occur implicitly (fast) or explicitly (deliberative). BA, Brodmann's area; PT, perspective taking; SEC, structured event complex; TOM, theory of mind; labels following a given BA region denote whether fMRI studies (F), lesion studies (L), or transcranial magnetic stimulation (T) provided evidence for that brain region's involvement in the respective social process

	Underlying information processing components	Key PFC regions involved	Implicit or explicit process?
Social perceptual processes			
Other individual identification	Single-event processing: identify basic social features of individual	BA 9 (F), BA 10 (F), BA 11 (F), BA 47 (F)	Implicit
Social mimicry	Single-event processing: sequential dependencies based on partner behaviors that vary by single adjacent event	BA 6 (F), BA 44 (F)	Implicit
Movement intentions	Single-event processing: identify intent and meaning of basic biological movements	BA 9 (F), BA 11 (F)	Implicit
Attributional processes			
Self-related processing	Predictable SECs associated with self-concept; occasional use of adaptive SECs when behaviors contradict perceived self-concept	BA 9 (F), BA 11 (F, L), BA 12 (F, L), BA 32 (F)	Both
Other processing/PT/TOM	Predictable SECs associated with knowledge of others; adaptive SECs to account for ambiguous behaviors; social category-specific SECs bias perceptions based on learned associations of others' group memberships	BA 6 (F), BA 9 (F, L), BA 11 (F, L), BA 12 (F, L), BA 32 (F), BA 46 (T)	Both
Moral judgments	Predictable SECs associated with self-perceived appropriate behaviors; adaptive SECs are applied to morally ambiguous situations; social and nonsocial category-specific SECs consisting of socially and personally acceptable beliefs and norms	BA 9 (F), BA 10 (F), BA 11 (F, L), BA 12 (F, L), BA 32 (F), BA 46 (F), BA 47 (F)	Both
Social categorization processes			
Stereotypes/schemas/scripts	Predictable SECs representing well-learned beliefs toward others and normal courses of behavior in general; social category-specific SECs representing well-learned beliefs, attitudes, and social norms	BA 9 (F), BA 11 (F, L), BA 12 (F, L), BA 46 (F, L), BA 47 (F)	Implicit
Impression formation	Predictable SECs involved with estimating others' intentions based on limited identifying information; social category-specific SECs associated with others' perceived social categorical information	BA 9 (F), BA 11 (F), BA 12 (F)	Implicit

(Continued)

Table 2 (Continued)

	Underlying information processing components	Key PFC regions involved	Implicit or explicit process?
Predictive processes			
Future planning	Long duration SECs involved in planning and action; predictable SECs associated with self-concept	BA 9 (F), BA 10 (F), BA 11 (F), BA 12 (F), BA 46 (F, L)	Explicit
Strategies in novel contexts	Nonsocial category-specific SECs involved in predicting behavior in novel context and planning and action	BA 46 (F), BA 47 (F)	Explicit
Strategies in learned contexts	Social category-specific SECs involved in well-learned social rules and scripts	BA 9 (F), BA 11 (F), BA 12 (F), BA 47 (F)	Implicit

others are thinking, and plan actions that are likely to facilitate a successful interaction with others, all within the context of social norms. These basic behaviors and impressions, in turn, form the foundation for more complex cognitive processes such as evaluating another's behavior in relation to culturally ascribed rules or to function successfully within large social groups.

The SEC framework provides a means to understand how regions within the PFC interact to enable social cognitive and moral judgment processing. Although outside the realm of this article, in light of our understanding of the functional connectivity between the PFC and most other subcortical neural regions, SECs underlying social cognitive and moral judgment processing likely integrate emotional and reward-related responses to contextual stimuli and basic perceptual processes (Wood & Grafman 2003). These SECs, in turn, are influenced by the socialization process and individual differences. The complex interaction between these processes can occur at multiple processing speeds to facilitate sophisticated implicit and explicit social cognition and moral judgment. Moll et al. (2005) posit in their EFEC framework that complex behaviors such as moral judgment likely involve the integration of SECs that represent social norms, basic perceptual features in one's environment such as facial expressions, visceral emotional responses to stimuli, and references to past experience

via autobiographical memory reconstruction, as well as SECs that represent meta or long-term goal states among other things. Such integration would require interplay among neural regions such as the anterior PFC, the DLPFC, the VMPFC, the OFC, the superior temporal sulcus, the anterior temporal lobe, and the limbic system, including the hypothalamus, the septal area, and the amygdala in a matter of milliseconds (**Figure 2**). In line with evolutionary perspectives, the order in which the aforementioned list of critical neural regions are listed may also represent a hierarchical structure that allows for increasingly complex social and moral behaviors.

In attempts to assess such complex neural and social interactions in a scientifically valid manner, social neuroscience experiments have begun to include an increasing array of tasks and problems reflecting the varied social experiences of real life. Social processes are not simply another brain activity worthy of attention but are key brain processes determining such things as outcomes after brain injury, the trajectory of human evolution, and the modulation of human impulses. This review has emphasized the PFC's important role in these behaviors. Whereas some brain regions, such as the ventral axis structures from the brain stem to cortex concerned with reward or limbic structures concerned with emotion and attachment, have been understandably linked to social behaviors, other brain areas, such as regions

within the parietal cortex, which have been implicated (primarily via functional neuroimaging) in social behavior, have not been firmly established yet as being crucial to the examined social process. Although it has become common to attribute social processes to certain regions within the PFC, there is less certainty about how to conceptualize the spatial topography to understand better why certain social processes lie near each other in these brain areas and what might the underlying computational processes be that support these social (and presumably other kinds of cognitive) processes.

The PFC has evolved to represent the most complex aspects of knowledge and information processing. Recent research has shown that some areas within the PFC are part of an increasingly hierarchical system for processing information from single events to the linkage of sets of events. More dorsal regions of the PFC are more likely to process information pertaining to an agent's actions toward external stimuli (e.g., agents acting upon objects), whereas more ventral regions appear more likely to assess the relevance of information to the social agent (e.g., reward value attributed to external stimuli). Hemispheric asymmetries in information processing are also apparent; the left hemisphere codes a dominant meaning or characterization of stimuli, whereas the right hemisphere codes multiple concepts in parallel without committing to one concept or meaning. Although less efficient than left hemisphere processing, particularly when a single solution is optimal, such processing would be superior when more than one solution to a social problem is possible.

This very brief speculative characterization of the PFC's functional roles applies to all kinds of functional domains including the moral and social processes reviewed above. The fact that some of the most prominent deficits that occur following damage to the PFC are social-cognitive suggests that at least certain aspects of social behavior are tightly coupled to the processing constraints of the PFC. In recent reviews, our colleagues offer some examples of how the schema we sketched above is

related to specific social and cognitive processing deficits in patients with lesions to specific areas of the PFC as well as which prefrontal cortical regions might be activated depending on specific processing demands (e.g., Barbey et al. 2009, Krueger et al. 2009a, Moll et al. 2005, Wood & Grafman 2003).

Computational forces within the PFC appear to allow for at least two hierarchical mechanisms to operate. One mechanism involves representational complexity, which links a deep search tree with parallel searches occurring simultaneously. The other mechanism involves temporal coding across events that merges apparently separable events into a single engram, allowing for streamlined forecasting and memory retrieval. These two mechanisms enable more detailed and elaborated conceptions of social behavior to be represented and utilized than would be available from a single event embedded in a stream of events. Although humans may benefit from the development of such elaborated conceptions in our behavior, constraints on resource utilization may bias us to rely more on attitudes, heuristics, and simplified personal vignettes when making decisions about beliefs.

If important aspects of social beliefs are represented in memory in the PFC, how similar is that representation to that which is seen in other forms of representational memory such as semantic memory concerned with the meaning of words and objects? Simpler forms of social representation, such as attitudes, may obey principles similar to that of semantic representations, including being sensitive to frequency of exposure, influenced by context, etc. Little evidence indicates whether the same constraints would apply to more complex beliefs such as religious or political beliefs (e.g., see Kapogiannis et al. 2009, Zamboni et al. 2009). Frequency of event exposure affects the activation site within the medial PFC as does complexity of event information (Krueger et al. 2009a,b). Less frequently exposed information is associated with the complexity of representation and activation of the PFC. This association suggests that more frequently exposed information can lead to sparser cue representation because the behavioral

action sequence would be more predictable and procedurally rigid (also predicting storage sites more posterior within the frontal lobes than FPC), whereas less frequent information would require more complex cuing and deeper representational search and deliberation because outcomes would be less predictable, given less direct personal experience with the event sequence.

This level of complex representation should be slower to process and enact than other forms of representation such as object naming or even social concepts. What kind of advantage does it offer? This form of complex representation would offer an advantage because it could inhibit more impulsive behavior and have a supervening role in decision making. In particular, it would automatically activate potential or certain consequences in the future of an immediate action. Such foresight allows the individual to implement strategic action that is potentially costly in the present but advantageous in the long run and can overcome potential liabilities in physical capabilities or other attributes. In a brain that is built with inherent inhibitory pathways between competitive brain regions, a brain region that was composed of SECs would have the mechanisms to inhibit simple associative behaviors using temporal information encapsulated within engrams stored in the PFC. Compared with other recent evolutionary changes, this particular change would offer substantial advantages in many situations—both social and nonsocial—and could stimulate the evolution or development of other functional brain properties. For example, if our representational memories captured and integrated social information over long time durations, that evolutionary change may have stimulated the development of language content that conveyed the social consequences (e.g., allowing the verbal expression of foresight) associated with one's current actions and motives, thereby facilitating the expansion of language beyond its use for simple object identity and naming.

To make these ideas more concrete, let us take an example of one social event. You are with politically informed friends and are

discussing whom you are going to vote for in the next presidential election. How might your cognitive and neural processes support that social interaction? Because the discussion is within a known social group and it is likely that at least one other person in the group will choose the same candidate as you will, your brain would activate regions within the PFC that are concerned with reading others' intentions, bonding, the heuristics of voting for a party's candidate (if favored, your reward system would also be active), narrative discussion of the candidates' qualifications versus his or her opponent, as well as the overall context of the election. Equal emphasis in information processing is not paid to all aspects of this scenario at any one time, so regions concerned with each of the above social processes are likely to be differentially activated at any one point in time.

Most of the social processes described above are explicit, but other implicit social processes may also be engaged. If you are much more familiar with your own candidate's background, you may be likely to activate stereotypes and biases about his opponent (who may be classified as being a candidate from an out-group, from your perspective). Expectation of how the conversation will go allows priming of future narratives to occur and also taxes cognitive structures concerned with foresight and action planning. Similar conversations with less informed people could wind up taxing more primitive and implicit cognitive and social representations and typically evoke more emotional, and less rationale, discourse. The dynamics of such discussions cause many regions and social processes to be simultaneously primed in preparation for retrieval of information (relevant or irrelevant).

It is difficult to capture the above scenario within a laboratory setting, and even compartmentalizing such a dynamic situation is challenging. Investigators have tended to isolate the major social process contributors to simple responses with various kinds of probes. What differentiates us from other species that have their own social structures is the human ability to use solutions and ideas that do not depend on the surface features of the subjects (e.g., size,

attractiveness, progeny) nor their physical capabilities (e.g., strength, aggressive tendency). Despite these differences, under certain circumstances with unknown individuals, the selection of the person who is judged to be the most popular or whom you might vote for often corresponds with the physical features of the face, and a significant association exists between those attractive features and the candidate's likelihood to win an election (Spezio et al. 2008, Todorov et al. 2005). So although human social complexity has distanced us from related species, e.g., chimpanzees or gorillas, they are not out of view.

In this article, we have emphasized functional neuroanatomy and have not discussed the chemical and genetic features of human social behavior. Quantifying the anatomic, chemical, genetic, and behavioral components of social behavior in combination will allow researchers to account for as much variance in behavior as is possible in open societies. Social neuroscience will play a key role in this effort.

The social interactions and judgments of humans have been based on evolutionary pressures and environmental and social contingencies. They will continue to evolve in parallel with technological changes. The widespread use of devices that can provide almost instant information (e.g., face recognition and identification) and feedback (e.g., eliciting pleasurable sensations via individually tailored visual stimuli on Web sites) as well as the emergence of social networks based simply on user-provided input will change the way we interact with others and the way the brain evolves or devolves in the future. In addition, introducing such sophisticated technology at a young age may affect development and enhance brain systems concerned with more immediate results and gratification. Public discussion of these issues will become more important as we judiciously manage the benefits of new technology in balance with its effects on social behavior and on the development of the social brain.

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Contents

Attention, Intention, and Priority in the Parietal Lobe <i>James W. Bisley and Michael E. Goldberg</i>	1
The Subplate and Early Cortical Circuits <i>Patrick O. Kanold and Heiko J. Luhmann</i>	23
Fly Motion Vision <i>Alexander Borst, Juergen Haag, and Dierk F. Reiff</i>	49
Molecular Pathways of Frontotemporal Lobar Degeneration <i>Kristel Slegers, Marc Cruts, and Christine Van Broeckhoven</i>	71
Error Correction, Sensory Prediction, and Adaptation in Motor Control <i>Reza Shadmehr, Maurice A. Smith, and John W. Krakauer</i>	89
How Does Neuroscience Affect Our Conception of Volition? <i>Adina L. Roskies</i>	109
Watching Synaptogenesis in the Adult Brain <i>Wolfgang Kelsch, Shuyin Sim, and Carlos Lois</i>	131
Neurological Channelopathies <i>Dimitri M. Kullmann</i>	151
Emotion, Cognition, and Mental State Representation in Amygdala and Prefrontal Cortex <i>C. Daniel Salzman and Stefano Fusi</i>	173
Category Learning in the Brain <i>Carol A. Seger and Earl K. Miller</i>	203
Molecular and Cellular Mechanisms of Learning Disabilities: A Focus on NF1 <i>C. Shilyansky, Y.S. Lee, and A.J. Silva</i>	221
Wallerian Degeneration, Wld ^S , and Nmnat <i>Michael P. Coleman and Marc R. Freeman</i>	245

Neural Mechanisms for Interacting with a World Full of Action Choices <i>Paul Cisek and John F. Kalaska</i>	269
The Role of the Human Prefrontal Cortex in Social Cognition and Moral Judgment <i>Chad E. Forbes and Jordan Grafman</i>	299
Sodium Channels in Normal and Pathological Pain <i>Sulayman D. Dib-Hajj, Theodore R. Cummins, Joel A. Black, and Stephen G. Waxman</i>	325
Mechanisms of Synapse and Dendrite Maintenance and Their Disruption in Psychiatric and Neurodegenerative Disorders <i>Yu-Chih Lin and Anthony J. Koleske</i>	349
Connecting Vascular and Nervous System Development: Angiogenesis and the Blood-Brain Barrier <i>Stephen J. Tam and Ryan J. Watts</i>	379
Motor Neuron Diversity in Development and Disease <i>Kevin C. Kanning, Artem Kaplan, and Christopher E. Henderson</i>	409
The Genomic, Biochemical, and Cellular Responses of the Retina in Inherited Photoreceptor Degenerations and Prospects for the Treatment of These Disorders <i>Alexa N. Bramall, Alan F. Wright, Samuel G. Jacobson, and Roderick R. McInnes</i> ...	441
Genetics and Cell Biology of Building Specific Synaptic Connectivity <i>Kang Shen and Peter Scheiffele</i>	473
Indexes	
Cumulative Index of Contributing Authors, Volumes 24–33	509
Cumulative Index of Chapter Titles, Volumes 24–33	513

Errata

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