Current directions in social cognitive neuroscience
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Social cognitive neuroscience is an emerging discipline that seeks to explain the psychological and neural bases of socioemotional experience and behavior. Although research in some areas is already well developed (e.g. perception of nonverbal social cues) investigation in other areas has only just begun (e.g. social interaction). Current studies are elucidating; the role of the amygdala in a variety of evaluative and social judgment processes, the role of medial prefrontal cortex in mental state attribution, how frontally mediated controlled processes can regulate perception and experience, and the way in which these and other systems are recruited during social interaction. Future progress will depend upon the development of programmatic lines of research that integrate contemporary social cognitive research with cognitive neuroscience theory and methodology.

Introduction
Although interest in the neural bases of human socioemotional behavior dates back over a century, this area of research has truly come into its own in the past five years. This growth and development has been spurred by numerous factors, including increasing availability of methodologies for investigating neural function in normal (i.e. non brain-damaged) adults (such as functional magnetic resonance imaging [fMRI]), increasing recognition of initial studies. Third and finally, many topic-oriented reviews are already available (e.g. [3–12], Jackson and Decety, this volume).

Perception and recognition of social cues
One of the first and most crucial steps in navigating the interpersonal world is the initial perception and recognition of nonverbal cues with socioemotional meaning. Perhaps the most important of these cues is the face, which conveys a wealth of socially relevant information. Early functional imaging and neuropsychological studies suggested that there might be specialized neural systems for processing some facial expressions of emotion, by showing selective amygdala or anterior insula involvement in recognizing expressions of fear and disgust, respectively [13]. Current work has tested the boundaries of these initial findings, and suggests a more complicated picture that has yet to come into crisp focus. For example, studies have found that the amygdala’s response to fearful faces both does [14] and does not [15**] vary with how much attention is paid to the face, and that in some conditions the amygdala and insula might, in fact, respond to multiple expressions of emotion [15**,16**,17,18*].

What might explain these apparent discrepancies? One possibility that can be addressed in future work is that the amygdala has subnuclei with different functions, and that current studies lack the temporal/spatial resolution to detect them. A second possibility is that the amygdala serves the general function of detecting arousing goal-relevant stimuli, and that its responsivity depends upon a stimuli’s relative socioemotional signal value — which isn’t always controlled within or across studies. Consistent with this notion, studies have shown that dynamic changing expressions (which presumably provide a richer signal) activate the amygdala more than do static emotion displays [19,20]. In addition, the amygdala can respond to...
faces depicting disgust, but only when attentional resources are diminished and the goal to detect potential threats is presumably heightened [15**]. It is also possible that discriminating subtle social signals might be a more important goal in everyday life than is identifying expressions of basic emotions (such as fear), which are less commonly expressed in their canonical form than more complex combinations of facial cues that convey feelings like boredom or flirtation. In keeping with this notion, Adolphs et al. [21*] found that amygdala lesions impair perception of social emotions more than perception of basic emotions, even when these emotions were expressed only by the eyes. Indeed, much of the meaning of a facial expression is conveyed by the eyes and the direction of their gaze. Adams et al. [16**] found greater amygdala activation for combinations of fearful or angry expressions and gaze direction that connoted ambiguous threat potential. This suggests that the amygdala is sensitive to the goal relevance, but not direction, of gaze. Consistent with this notion, Hooker et al. [22*] observed heightened amygdala responsivity when participants actively monitored for direct gaze, which is distinct from superior temporal sulcus (STS) responses that were selective for gaze shifts. An important task for future work will be to determine how variations in magnitude of attentional load, goal-relevance, and other factors (see section on appraisal below) could influence the amygdala’s (or other) response to social cues.

Other nonverbal cues also certainly convey important social information. Emotional prosody, or tone of voice, has received comparatively little attention, but a large sample lesions study suggests that it could depend upon tempoparietal and frontal cortical systems important for semantic interpretation [23]. The observation of other people moving in a goal-directed manner might activate neural systems similar to those used if we were to execute those movements ourselves. The importance of such ‘shared representations’ in social perception is discussed in Jackson and Decety, this volume.

Social judgment and attribution

First impressions can tell us that someone seems friendly/approachable or unfriendly/threatening [24], and current work suggests that distinct neural systems might be involved in each kind of evaluation. Whereas perception of attractive faces activates medial orbitofrontal regions implicated in reward processing [25], perception of either unfamiliar unfriendly-looking [18*] or familiar ‘bad’ (e.g. Hitler; [26**]) individuals activates the amygdala. The amygdala response of Caucasian participants to African-American faces in a study by Cunningham et al. [27] suggested that some subjects might perceive individuals from another race as a threat; the magnitude of the amygdala response was predicted by the amount of anti-African-American bias shown on an indirect behavioral measure. An interesting question for future work is whether and how evaluative systems might interact when, for example, when one sees an attractive person expressing a negative emotion, or vice versa.

Beyond recognizing what someone is doing (smiling), and judging their likability (looks friendly), we can ‘get inside their head’ to figure out the reason they’re doing what they’re doing (wants to talk). Understanding the causes of behavior requires attributes about mental states (e.g. beliefs, desires, goals), an ability thought to depend upon a central ‘mentalizing’ capacity (or theory of mind, TOM; [6]). Initial imaging studies showed activation of a network of regions including medial prefrontal cortex (MPFC) during TOM judgments [6]. It is becoming clear that additional regions, such as the STS, are also important for TOM [28], and that MPFC activation occurs when participants infer the intentions of others in a variety of other contexts, including judging whether or not words have social meaning [29,30], evaluating the moral appropriateness of actions [31], hearing your name called or seeing someone looking towards as compared to looking away from you [32]. It isn’t yet clear, however, exactly what attributional computations the MPFC performs. Interestingly, MPFC activation also has been found when participants reflect upon their own mental states, including judging one’s likes and dislikes [33,34], level of arousal [35,36] or personality trait/attributes [37,38*]. The cross-study similarity of these MPFC activations suggests that a single common ‘mentalizing’ ability might underlie the attribution of mental states to self and other [6]. However, this hypothesis has not yet been directly tested using a within-study comparison to determine whether self and other-related activations truly are overlapping or are similar but distinct. Additional work is needed to specify more precisely the computations performed by MPFC and other systems that support social inferences.

Appraisals regulate perception and experience

Although we process them quickly, the socioemotional significance of expressions, actions, and experiences is not fixed, and can hinge upon our cognitive appraisal or construal of their meaning. A punch to the arm, for example, can be construed as either aggressive or playful depending on the way one appraises the puncher’s intentions. Unfortunately, in many studies the effect of construal cannot be evaluated because the nature of appraisal is either held constant or not manipulated. A small but growing number of studies have begun investigating this issue, however, and have found that the cognitive regulation of social perception and emotional experience depends upon interactions between prefrontal systems that implement control processes and evaluative systems that provide initial appraisals of socioemotional significance [39]. For example, Ochsner et al. [40*] found that when participants cognitively reappraised evocative
images in unemotional terms (e.g. judging that a horrific injury was fake) the magnitude of lateral prefrontal activation predicted decreases in amygdala activation normally produced when participants respond emotionally. Beauregard et al. [41] and Levesque et al. [42] obtained similar findings when participants used reappraisal to decrease either sexual arousal or sadness when watching film clips. In a follow-up study, Ochsner et al. [43] found that up- and down-regulating negative emotion recruited similar prefrontal systems, but differentially modulated amygdala activity up or down, respectively.

The conditions under which appraisals might mediate social perception are somewhat less clear. Cunningham et al. [27] found that for subliminal (35 ms) but not supraliminal (525 ms) presentations Caucasian participants showed greater amygdala activation to African-American faces than to Caucasian faces. During supraliminal presentations frontal and amygdala activations were inversely correlated, suggesting that regulation took place via a mechanism similar to that found in the studies described above. However, Winston et al. [18] explicitly manipulated appraisal by asking participants to judge either the gender or the friendliness of faces, and found that amygdala responses to unfriendly faces did not vary with judgment type. The respective consistency and inconsistency for studies of experiential as compared to perceptual regulation highlights the need for future work to determine when regulatory appraisals can and cannot modulate experience and perception and to determine whether or not different regulatory strategies and different types of emotion involve different neural dynamics [39].

Social interaction
People interact in a variety of ways — playfully, competitively, cooperatively — and by their very nature, interactions are more conceptually and methodologically difficult to study than the behavior and experience of a single person. Resources permitting, interaction partners could be simultaneously imaged in two scanners [44]. However, most imaging studies have simply scanned single participants while they played a game with a real or (unbeknownst to the participant) fictitious partner outside the scanner. Using this methodology, a handful of studies have now demonstrated four findings. First, that the MPFC is activated, and presumably intentional inferences are being drawn, only when participants believe they’re playing a game against a human rather than a computer partner [45,46]. Second, that amygdala activation is recorded when participants bluff their partner and presumably fear being found out [47]. Third, that activation of cortical and subcortical reward centers, such as the ventral striatum, is recorded when the participant and their partner cooperate with one another [48]. And fourth, that cortical systems associated in prior work with the experience of either physical pain or disgust are activated when participants are either socially excluded [49] or unfairly treated [50] by their partner.

Although these findings provide initial insight into the mechanisms mediating our feelings of understanding, connection, and disjunction with another person, the brain regions activated in these studies are often associated with more than one behavior or function. This makes it difficult to determine whether, for example, insular activation during unfair exchange is due to a feeling of disgust or due to a sense of response conflict, which has also been associated with this region [51]. To address this issue, future work could compare these behaviors (or social exclusion and pain, bluffing and fear, cooperation and reward) in a single study. The study of neuropsychological populations (i.e. patient groups who have suffered damage to specific regions of the brain due to physical insult, blood flow or oxygen loss, or degenerative disease) might provide converging evidence concerning the function of a given region in social interaction. Although clinical anecdotes of social deficits following brain damage are common, researchers are only just beginning to systematically examine them using well-characterized social psychological interaction paradigms. Beer et al. [52] examined the effects of orbitofrontal cortex (OFC) lesions on the ability to appropriately self-monitor behavior. In keeping with prior work implicating the OFC in response regulation and/or inhibition, lesion patients teased too aggressively and shared overly intimate details of their lives, which suggests a failure to appropriately self-regulate social behavior [52].

Conclusions
As this review might suggest, until now SCN’s growth has been more horizontal than vertical, as researchers have sought to provide initial investigations of a broad array of socioemotional phenomena that heretofore had not been investigated using neuroscience techniques. In part, greater horizontal growth is to be expected for an emerging discipline. Exploratory studies that map neural correlates of phenomena necessarily lay the foundation for theoretically motivated studies that test hypotheses about the role of specific psychological and neural processes in particular behaviors [2]. Over time, however, theoretical advancement will depend crucially on vertical growth, as programmatic experiments build upon one another and systematically discriminate among alternative hypotheses derived from initial studies.

Bridging the gap between initial exploration and programmatic experimentation will be most efficient if SCN researchers attend to and integrate contemporary social cognitive research, which for decades has developed theoretical and methodological approaches to all of the topics covered in this review. Although such integration currently characterizes only a portion of the studies...
discussed above, it is worth noting that an integrative approach has characterized cognitive neuroscience analyses of attention, memory, and mental imagery for over a decade. For each of these topics, researchers have made use of existing cognitive psychological theory and methodology to help guide research. SCN researchers would do well to follow their example.

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References and recommended reading
Papers of particular interest, published within the annual period of review, have been highlighted as:

• of special interest
**of outstanding interest

The authors asked participants to judge whether adjectives could selectively activate when accessing person knowledge distinct from those used to access object knowledge. This suggests that knowledge about people can be qualitatively distinct from other types of knowledge and identifies neural systems that might play an important part in representing social knowledge.


The authors present one of the first studies to examine self-regulation and social cognition in a patient population using contemporary social psychological methods for studying social interaction empirically. In multiple interaction contacts, patients with orbitofrontal lesions experienced alterations in self-conscious emotions (e.g. embarrassment or pride), but not basic emotions (e.g. happiness), which suggests a specific role for the OFC in using affective information to guide social behavior.