

and language that promote complex and coordinated collective actions are commonly thought to be among those that are important.

Given their evolutionary heritage and daily currency, there is little wonder that both emotional and social processes are biologically rooted and culturally molded. Evidence of both biological and sociocultural contributions to emotions is now so plentiful that few would doubt this assertion, and evidence for biological and emotional contributions to social processes is rapidly accumulating. Altruistic reward and punishment, for instance, are thought to have been crucial for the evolution of a level of cooperation in human societies that is unparalleled (e.g., Boyd, Gintis, Bowles, & Richerson, 2003; Fehr & Gächter, 2002).

The past decade has even seen a virtual explosion of research on the neural networks underlying human emotions and, for the most part quite separately, on the neural substrates underlying social perception, reasoning, and behavior. Surprisingly little attention has been devoted to the relationship *between* these neural systems, however, despite the essential role that emotions play in social development and discourse. Our focus in this chapter is on this latter question. We begin by considering the adaptive significance of emotional and social stimuli, as well as the inherent links between them, as many emotion elicitors are social in nature and emotions are critical for the formation and maintenance of social relationships. Furthermore, we argue that social processes may have co-opted existing neural networks for affective processing to promote interactive and synergistic processing. Finally, we consider the importance of the social context for interpreting the intentions of conspecifics and for the culturally appropriate expression and experience of emotion.

EMOTIONS AS ADAPTIVE NEUROBEHAVIORAL ORGANIZATIONS

From 1831 to 1836, Charles Darwin sailed on the naval survey ship *HMS Beagle*, invited as company for Robert FitzRoy, the ship's captain whose rank precluded his socializing with anyone but another gentleman. The observations and specimens with which Darwin returned led to the realization that all organisms compete for resources and that those that had some advantage in a habitat would be more likely to transmit this advantage to future generations via their offspring. Following the publication of *Origin of the Species* (Darwin, 1859), Darwin turned his attention to explaining the evolution of behavior. For example, pondering the nature of facial expressions, he wrote: "No doubt as long as man and all other animals are viewed as independent creations, an effectual stop is put to our natural desire to investigate as far as possible the causes of Expression" (Darwin, 1872, p. 12). Thus, Darwin observed that to understand the expression of emotion, humans must be understood as falling on a continuum of species;

observing the behavior of other animals, therefore, could shed light on the expression and function of emotion for humans.

The evolutionary approach to studying emotions has given rise to the notion of emotions as response packages, as predispositions to respond in specific, adaptive ways to environmental stimuli. Emotion theorists disagree about the number of emotions, the structure of emotions, the primacy of emotions, and the relationship between feelings and emotions, but there is general agreement that emotions have adaptive utility. Whether fleeing from a potentially harmful stimulus, such as a snarling bear giving chase, or pursuing something beneficial, such as food or a caring partner, emotions promote adaptive responses and future guidance regarding approach and avoidance behavior. Fear and disgust provide clear illustrations of the value of emotional experience—without these two emotions, an individual (whether human or a nonhuman animal) is unlikely to survive long in most environments. Both fear and disgust are emotional responses to threatening stimuli that often result in avoidance; whereas fear promotes avoidance of predators and potentially harmful encounters, the adaptive utility of disgust includes the avoidance of poisons, rancid foodstuffs, and materials that may promote disease (Curtis, Anger, & Rabie, 2004).

Many contemporary theorists have approached the study of emotion from a cognitive but equally adaptive perspective, arguing that emotions serve as signals that provide information regarding pursuit of current goals. Positive emotions (e.g., joy, contentment, pride) are experienced when progress is made toward a goal; whereas negative emotions (e.g., fear, sadness, anger) indicate the potential or confirmed loss of a goal or otherwise thwarted efforts toward goal attainment (e.g., Carver & Scheier, 1990; Stein & Trabasso, 1992). Others have emphasized the continuity across the neuraxis of the partially separable substrates for positive and negative affect, including a focus on differences in the stimuli that trigger positivity and negativity, the behavioral responses that each guides, and the hierarchical control of these substrates (for reviews, see Berntson, Boysen, & Cacioppo, 1993; Berridge, 2004). Regardless of the different perspectives of current emotion researchers, agreement on the fundamentally adaptive nature of emotion is ubiquitous.

Views of the evolutionary advantage of emotions often focus on the benefit of an emotional response for an individual; for example, being frightened and consequently avoiding a poisonous snake has immediate benefits for the potential victim but does not necessarily affect anyone else. However, *Homo sapiens* are characteristically social beings, and emotions may therefore have adaptive significance not only for an individual but also for the social group to which an individual belongs. To this end, recent research has tested hypotheses regarding altruistic punishment, the costly punishment of social defectors in the service of the public good. Fehr and Gächter (2002) argue that when some group members fail to cooperate (e.g., by keeping all resources to themselves rather than sharing reciprocally

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HUMANS ARE

Although emotion (as Darwin origin are fundamentally promote coopera are a major sour institutions. Soci throughout the li duction, vigilanc tory and significa ensure affiliation (Bowlby, 1969/1

and fairly, a behavior referred to as *defecting*), other members may, at a personal cost, punish such “defectors” to encourage socially responsible behavior in the future. Importantly, altruistic punishment occurs even when punishers can expect no benefit to themselves (i.e., they have no future encounters with defectors and cannot gain a reputation as no communication between group members is possible) and when punishment is costly for them. In a recent study using positron emission tomography (PET) to study the neural basis of altruistic punishment, de Quervain and her colleagues (2004) suggest that the anticipation of a pleasant emotional response following the punishment of a defector may motivate punishers. Consistent with this reasoning, they found activation of the caudate nucleus (a neural structure implicated in reward processing) correlated with degree of punishment levied. In other words, emotions may serve to encourage individual behaviors that promote collective over self-interests.

The question remains as to whether the evolution of behaviors that benefit the group at the expense of personal gains is viable. To address this question, Boyd and colleagues (2003) developed a set of simulation models in which the frequency of cooperation within a group over many time periods (2,000 years) was measured as a function of the presence or absence of altruistic punishment, in addition to other factors such as group size and rate of intergroup conflict. Results indicated that models of group selection in which altruistic punishment was present were more effective in maintaining high frequency of cooperation across all group sizes, suggesting that altruistic punishment is a viable solution to the evolutionary puzzle of social cooperation. In sum, research on altruistic punishment indicates that in the case of *Homo sapiens*, emotions evolved not only to protect the individual from predators and to encourage the pursuit of appetitive stimuli but also to promote reciprocity, cooperation, communication, and collective action, which allowed for the creation of organizations, institutions, and cultures in their wake.

HUMANS ARE SOCIAL ANIMALS

Although emotions have adaptive utility for humans as well as for animals (as Darwin originally suggested), it is important to note that human beings are fundamentally social creatures. And as emotions may have evolved to promote cooperation and communication in a social group, conspecifics are a major source of adaptive emotions in these groups, societies, and institutions. Social information is highly valued and critical for survival throughout the lifespan, as it contributes to successful attachment, reproduction, vigilance toward threatening encounters, and protection of territory and significant others. From birth, we engage in behaviors intended to ensure affiliation with other members of the species, especially caregivers (Bowlby, 1969/1982). Quality of social interactions in infancy, including

of intentions, emotions, gender, relationships, and personality to the three shapes. Heberlein and Adolphs (2004) have recently argued that these spontaneous social attributions rely on the functioning of an intact amygdala, based on evidence that S.M., a patient with bilateral damage to the amygdala, failed to spontaneously provide a social interpretation of the film. Interestingly, S.M. performed normally on direct questions regarding the film that relied on social attributions (e.g., "What was the large triangle like?"), suggesting that her impairment lies in automatically inferring social meaning from a nonsocial stimulus and that the amygdala may play an important role in these social inferences. The tendency to spontaneously make social attributions about stimuli or events may be an adaptive mechanism for a highly social species.

SOCIAL STIMULI POSSESS INHERENT ADAPTIVE SIGNIFICANCE

Research on emotion often focuses on responses to nonsocial stimuli, such as dangerous creatures (e.g., snakes, spiders, bears) and primary rewards (e.g., food) and, in addition, tends to treat social and nonsocial stimuli as comparable; however, most emotion elicitors in life are social. Facial expressions provide both social and emotional information, conspecifics often generate and reciprocate our own emotional reactions, and social fears (e.g., speaking in public) and triumphs (e.g., a home team victory) dominate our emotional lives. In their social-functional account of emotion, Keltner and Kring (1998) argue that emotions serve a set of functions that are critical for coordinating social interactions. A conspecific can serve either as an emotional stimulus (e.g., encountering an unknown person on a dark street late at night) or as a cue to an emotionally relevant stimulus present in the environment (e.g., a fearful individual may indicate the presence of a dangerous stimulus, such as a snake). In addition, our perception of others' emotions can elicit emotional states that are either reflective (e.g., empathy) or complementary (e.g., fear of an unknown individual expressing anger), thus providing information regarding the relationship and promoting adaptive behaviors in the context of social interactions.

Because of the inherent connections between and the relative importance of social and emotional information, we have argued that social and emotional processes may interact, as well as share some basic neural mechanisms (Norris, Chen, Zhu, Small, & Cacioppo, 2004). Specifically, we proposed that social and emotional information is interactively processed in order to produce adaptive behavior and serve regulatory functions for an individual embedded in a social environment. We suggest that because social stimuli are strong elicitors of emotion, they have the same adaptive utility as emotional stimuli and may possess inherent, latent emotional significance.

The adaptive advantage of discerning social signals and organizing flexible behavioral responses may have been achieved in part by co-opting and building on selected neural systems that evolved originally for dealing with hedonic events (threats, appetitive stimuli). This would mean that social stimuli can be processed quickly by neural regions implicated in motivational processes (e.g., medial orbitofrontal cortex) and in generating (e.g., amygdala, insula, motor cortex) and regulating (e.g., ventrolateral and medial prefrontal cortex) an emotional response.

A recent study using functional magnetic resonance imaging (fMRI) provides an appropriate illustration of this co-option hypothesis. Eisenberger, Lieberman, and Williams (2003) reported neural activation in a dorsal portion of the anterior cingulate cortex (ACC) implicated in the affective component of the pain response when participants were excluded from a social situation (i.e., a ball-tossing game). The authors argue that the similarity in activation of the dorsal ACC to physical pain (e.g., Rainville, Duncan, Price, Carrier, & Bushnell, 1997) and to social pain suggests that the experiences of physical and social pain may share a common neuroanatomical basis. Furthermore, Eisenberger and her colleagues suggest that "Because of the adaptive value of mammalian social bonds, the social attachment system . . . may have piggybacked onto the physical pain system to promote survival" (p. 291). The co-option of neural systems for purposes other than their primary function is potentially a flexible, conservative answer to challenges presented over the course of evolution.

Additional evidence for the hypothesis that the neural mechanisms contributing to the detection of social cues may have co-opted and built on existing emotion networks is provided by data implicating certain brain regions in processing both social and emotional stimuli. The amygdala, a limbic structure occasionally referred to oversimplistically as the emotional brain, is clearly involved in social behavior, as well as emotional experience. Kluver and Bucy (1939/1997) first reported disturbances in the social behavior of primates with extensive amygdala damage; research by Heberlein and Adolphs (2004) using the Heider and Simmel (1944) paradigm discussed earlier provides convergent evidence for the role of the amygdala in making social inferences in humans. Much of the research on amygdala function has focused on judgments and responses to facial displays of emotion, either using fMRI to investigate patterns of neural activity in nondamaged individuals or examining the behavior of people with amygdala damage. These studies suggest that the amygdala is involved in processing emotional expression, particularly fear (cf. Adolphs, Tranel, Damasio, & Damasio, 1994; Breiter et al., 1996); in making judgments regarding the trustworthiness of unknown individuals (Adolphs, Tranel, & Damasio, 1998; Winston, Strange, O'Doherty, & Dolan, 2002); and in the attribution of internal states, beliefs, and desires to other people (Baron-Cohen et al., 2000). However, it is important to note that each of these studies confounds social and emotional processes; for example, as deter-

mining the emotion expressed by information from a social context the other.

One recent study has attention response to faces and scenes in regions implicated in processing only faces (e.g., faces) or whether amygdala emotional stimuli as well. Hariri (2002) used fMRI to measure response to fearful and threatening emotional stimuli. Importantly, none of the IAPS faces included natural threats (i.e., guns, car accidents). Hariri et al. report that the amygdala shows greater activation to social stimuli; however, activation of the amygdala when participants viewed fearful faces. Results suggest that the amygdala is more active to social and emotional stimuli, consistent with the hypothesis that it has co-opted existing neural networks.

The study conducted by Hariri et al. has design features that limit its interpretation. Differences in complexity across conditions could potentially account for the activation for faces and scenes (Hariri et al., 2002). Furthermore, the study does not directly address the question of whether the amygdala is more active to social and emotional stimuli or to neutral stimuli, as in the study by Hariri et al. (2002).

We recently conducted an experiment to test the independent effects of social and emotional information which we controlled for the complexity of the stimuli (Hariri, 2002) and included neutral stimuli (Norris et al., 2004). The stimuli varied in two dimensions, social and emotional (pleasant or unpleasant). Participants viewed one or more faces or scenes, objects). Animals were excluded. The stimuli were matched on complexity and arousal. Results for the amygdala indicated two main effects, such as greater activation to social than for neutral stimuli (Norris et al., 2004; see also Hariri et al., 2002). The amygdala is clearly implicated in social cognition.

mining the emotion expressed by a conspecific requires distilling emotional information from a social context, an impairment in one necessarily affects the other.

One recent study has attempted to compare amygdalar activation in response to faces and scenes in order to examine whether the amygdala is implicated in processing only emotional stimuli that contain social cues (e.g., faces) or whether amygdalar activation generalizes to other kinds of emotional stimuli as well. Hariri, Tessitore, Mattay, Fera, and Weinberger (2002) used fMRI to measure amygdalar activation while participants viewed fearful and threatening faces and 'scenes' taken from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 1999). Importantly, none of the IAPS pictures contained human faces, but rather included natural threats (i.e., dogs, snakes, spiders, sharks) and other threats (i.e., guns, car accidents, plane crashes, explosions). The authors report that the amygdala showed significant activation to both types of stimuli; however, activation of the right amygdala was significantly greater when participants viewed fearful and threatening faces than scenes. These results suggest that the amygdala is involved in processing both emotional and social stimuli, consistent with the hypothesis that social cognition may have co-opted existing neural networks underlying hedonic processes.

The study conducted by Hariri et al. (2002) contained a number of design features that limit its interpretation. For instance, the authors suggest that differences in complexity, arousal, or similarity of the stimuli across conditions could potentially account for observed differences in activation for faces and scenes (Hariri et al., 2002); none of these explanations can be ruled out. Furthermore, the study by Hariri et al. (2002) does not directly address the question of whether the amygdala is involved in processing emotional stimuli or whether activation would be observed in response to neutral stimuli, as well.

We recently conducted an fMRI study to investigate the interactive and independent effects of social and emotional processes in the brain in which we controlled for the confounding factors in the Hariri et al. study (2002) and included neutral stimuli to allow a test of effects due to emotionality (Norris et al., 2004). Participants viewed a set of IAPS pictures that varied in two dimensions, such that each picture was either neutral or emotional (pleasant or unpleasant stimuli) and was either social (i.e., contained one or more faces or bodies of conspecifics) or nonsocial (i.e., scenes, objects). Animals were excluded from the design; all four groups of stimuli were matched on complexity; and social and nonsocial stimuli were equally arousing. Results for the amygdala, one of our regions of interest, indicated two main effects, such that amygdalar activation was greater for emotional than for neutral stimuli and greater for social than for nonsocial stimuli (Norris et al., 2004; see Figure 5.1). Thus the amygdala, a central component of many neuroanatomically based theories of emotion, is also clearly implicated in social cognition. These findings suggest that the

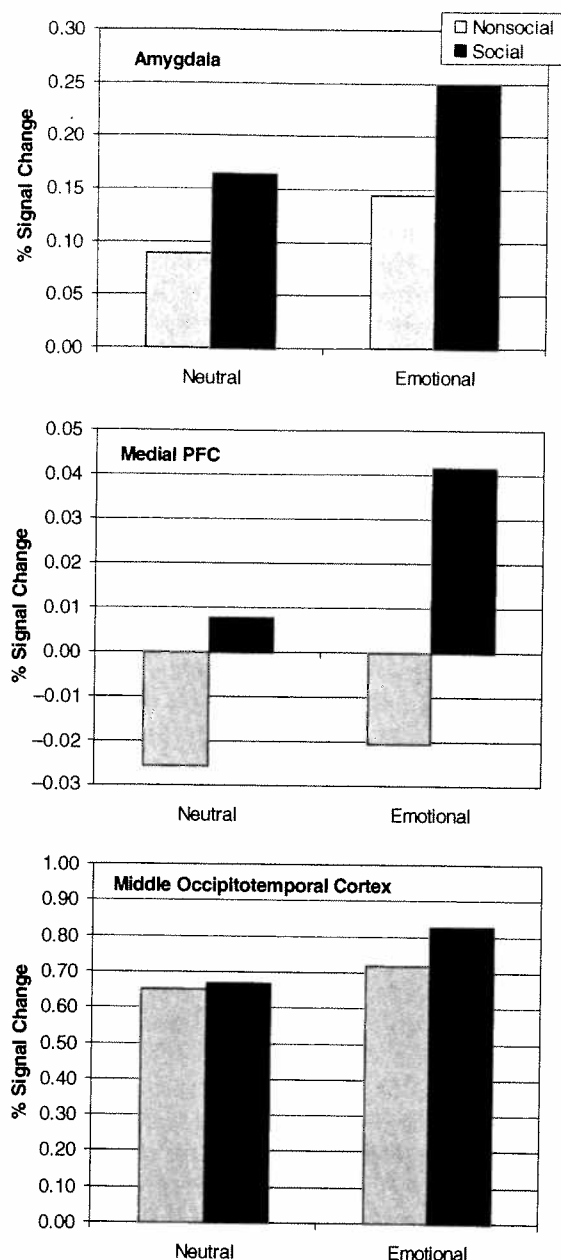


FIGURE 5.1. Patterns of neutral activation in the amygdala (top), medial prefrontal cortex (middle), and middle occipitotemporal cortex (bottom) during viewing of pictures that vary in social and emotional content. Bars represent the mean percent signal change for the peak of the hemodynamic response in a priori regions of interest. Based on Chen, Zhu, Small, and Cacioppo (2004).

amygdala may be involved in both emotional (negative and p motivational significance. How motivational significance throu *sapiens* and their inherently soc babies, snakes, diseased things) of amygdalar activation to em that social cognition may have cessing stimuli with hedonic va

The hypothesis that socia organizations that are involved in line with our finding that th by social stimuli. Norris et al. (mPFC) and the middle occip cortex), neural regions often re tures, were also more active depicted conspecifics than thos Taylor, and Liberzon's (2002) commonly activated in studie to be active during experiences gust, regardless of whether el through guided recall. Althou processes has yet to be specifi also to be more active to social ity, arousal, visual complexity, over, a good deal of research su tal cortex are more active to er neutral, unarousing stimuli (cf 1999; Lang et al. 1998). We re middle occipitotemporal corte nonsocial stimuli (Norris et al. social information garner att

Interestingly, complement: plicated in social cognition (e motion, face perception and r content. One of the first stud study conducted by Geday, Gj participants viewed a set of pic from low (e.g., faces) to high valence (positive, negative, ne cerebral blood flow (rCBF) in ously implicated in face perce 1997), was not only greater wh less complex social stimuli but emotional (i.e., positive and ne

amygdala may be involved in more general motivational processes, with both emotional (negative and positive) and social stimuli possessing strong motivational significance. However, social stimuli have arguably acquired motivational significance through the process of the evolution of *Homo sapiens* and their inherently social nature; whereas emotional stimuli (e.g., babies, snakes, diseased things) may be more primary motivators. Patterns of amygdalar activation to emotional and social stimuli therefore suggest that social cognition may have co-opted existing neural networks for processing stimuli with hedonic value.

The hypothesis that social information processing co-opted neural organizations that are involved in emotional information processing is also in line with our finding that the amygdala was not alone in being affected by social stimuli. Norris et al. (2004) found the medial prefrontal cortex (mPFC) and the middle occipitotemporal cortex (i.e., visual association cortex), neural regions often reported as being activated by emotional pictures, were also more active when participants viewed pictures that depicted conspecifics than those that did not (see Figure 5.1). Phan, Wager, Taylor, and Liberzon's (2002) meta-analysis indicated that the mPFC is commonly activated in studies of emotion. Specifically, they found mPFC to be active during experiences of happiness, fear, anger, sadness, and disgust, regardless of whether elicitation occurred visually, auditorially, or through guided recall. Although the specific role of mPFC in emotional processes has yet to be specified, it is noteworthy that the mPFC appears also to be more active to social than nonsocial stimuli matched for extremity, arousal, visual complexity, and luminance (Norris et al., 2004). Moreover, a good deal of research supports the claim that portions of the occipital cortex are more active to emotionally arousing pictorial stimuli than to neutral, unarousing stimuli (cf. Phan et al., 2002; Lane, Chua, & Dolan, 1999; Lang et al. 1998). We replicated this effect and further found that the middle occipitotemporal cortex was also more active to social than to nonsocial stimuli (Norris et al., 2004), suggesting that both emotional and social information garner attentional resources.

Interestingly, complementary findings suggest that neural regions implicated in social cognition (e.g., gaze pursuit, perception of biological motion, face perception and recognition) are also sensitive to emotional content. One of the first studies to demonstrate this pattern was a PET study conducted by Geday, Gjedde, Boldsen, and Kupers (2003) in which participants viewed a set of pictures that varied both in social complexity, from low (e.g., faces) to high (e.g., social situations), and in emotional valence (positive, negative, neutral). Results demonstrated that regional cerebral blood flow (rCBF) in the fusiform gyrus, a neural region previously implicated in face perception (cf. Kanwisher, McDermott, & Chun, 1997), was not only greater when participants viewed more complex versus less complex social stimuli but was also greater when participants viewed emotional (i.e., positive and negative) as compared with neutral stimuli (see

also Dolan et al., 1996; Vuilleumier, Armony, Driver, & Dolan, 2001). In other words, neural structures involved in processing social signals, such as eye gaze, faces, and biological motion, may have evolved to also be sensitive to emotional content based on the fact that social stimuli have inherent emotional value for human beings and other social species.

We recently replicated the finding that the fusiform gyrus is more active to emotional than to neutral stimuli; furthermore, this pattern was driven by activation to social stimuli, consistent with the proposed role of the fusiform in social cognition (Norris et al., 2004). In addition, our results indicated that two other neural regions implicated in processing social information were also sensitive to emotional content: the superior temporal sulcus (STS) and the inferior frontal gyrus (IFG). Although the STS is most often considered to be involved in the perception of biological motion (cf. Puce & Perrett, 2003; Grossman & Blake, 2001), a growing literature supports the conclusion that the STS is also sensitive to emotional content. Narumoto, Okada, Sadato, Fukui, & Yonekura (2001) showed that selective attention to emotional expression versus to the face itself enhanced activation of the right STS. In a study examining the neural correlates of basic and moral emotions, Moll et al. (2002) reported that the STS was recruited by viewing scenes evocative of moral emotions. Kilts, Egan, Gideon, Ely, and Hoffman (2003) demonstrated that whereas dynamic emotional displays of anger expressions elicit greater activation of the STS than do static emotional displays of anger, this finding does not generalize to expressions of happiness. Thus the STS is not just activated by dynamic (i.e., moving) stimuli but is also selectively responsive to different emotional content, and particularly to emotional stimuli that may have stronger motivational significance for the observer (anger vs. happiness).

The IFG has also been implicated in social cognition, particularly face processing, as evidenced by studies examining visual imagery of famous faces (Ishai, Haxby, & Ungerleider, 2002), integration of visual faces and names (Campanella et al., 2001), viewing of unfamiliar faces (McDermott, Buckner, Petersen, Kelley, & Sanders, 1999), and performing a face-matching task (Haxby, et al., 1994). In addition, regions of the IFG in the left hemisphere are critically important for speech perception and potentially for the integration of heard speech and speech read from a moving face (Calvert & Campbell, 2003). Rizzolatti and his colleagues (cf. Rizzolatti, Fadiga, Gallese, & Fogassi, 1996) have argued that the human IFG may correspond to area F5 of the monkey premotor cortex, which contains *mirror neurons* that discharge both when an action is performed and when it is observed (cf. Rizzolatti, Fogassi, & Gallese, 2001; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Koski et al., 2002). These findings, taken together, have led some researchers to suggest that the IFG is involved in empathy, an emotion that derives its meaning from the social context and that may function through imitative mechanisms (cf. Carr, Iacoboni, Dubeau, Mazziotta & Lenzi, 2003; Meltzoff & Decety, 2003).

In sum, converging evidence involved in social information processing, biological motion, are also involved in the fusiform gyrus, the STS, and the IFG have shown that individuals process social stimuli differently than non-social stimuli.

Finally, it is also possible that social and emotional information may be interactively processed in the brain. Recent evidence has depicted or implicate conspecifics that are sensitive to either social or emotional stimuli (cf. Gauthier et al., 2004), three neural regions involved in the processing of social and emotional information: the superior temporal cortex, and the STS and the IFG. These structures that were emotional in nature showed greater activation than those that were neutral. Importantly, these three neural regions interacted in a stream, suggesting that emotion processing may require greater attentional resources. They appear to interact at very early stages of processing, indicating the stationary significance of social information.

ET TU, BRUTE: THEORY C

As exemplified by perhaps the most famous example, Caesar by Brutus, his fellow statesman did not read correctly the motives of his fellow statesmen not only cooperators but also defectors. This suggests that when altruistic behavior benefits the individual, natural selection may lead to an asymmetric strategy where individuals make high levels of cooperative behavior (Doebeli, Hauert, & Killingback, 2004). This state in a cooperative environment is not stable for individuals. However, this is not necessarily a benefit from such a mixed strategy. The perception of the motives of others and the ability to navigate these skills necessary for navigating a complex social environment.

Although every social species has the ability to perceive social cues (e.g., facial expressions), humans are unique in their ability to understand the motives of conspecifics. Recent evidence suggests that humans are sensitive to these high-level social cues not on reacting to simple stimuli but on considering motives, context, and social information into consideration motives, context, and social information. This is particularly true for

In sum, converging evidence supports the notion that neural structures involved in social information processing, such as perception of faces and biological motion, are also involved in emotional processing. The fusiform gyrus, the STS, and the IFG have all been shown to be recruited both when individuals process social stimuli and when stimuli have emotional significance.

Finally, it is also possible that social and emotional information may be interactively processed in the brain such that emotional stimuli that depict or implicate conspecifics may elicit much stronger activation than either social or emotional stimuli alone. In our recent fMRI study (Norris et al., 2004), three neural regions showed evidence of the interactive processing of social and emotional information: the thalamus, the middle occipitotemporal cortex, and the STS all exhibited the same pattern, such that pictures that were emotional in nature and that contained social cues elicited greater activation than those that were either emotional, social, or neither. Importantly, these three neural regions are relatively early in the processing stream, suggesting that emotional stimuli depicting conspecifics may garner greater attentional resources. Thus emotional and social information appear to interact at very early stages of processing, consistent with the evolutionary significance of social and emotional stimuli.

ET TU, BRUTE: THEORY OF MIND

As exemplified by perhaps the most famous betrayal in history—that of Caesar by Brutus, his fellow statesman and confidante—it can be dangerous not to read correctly the motives and intentions of others. Conspecifics can be not only cooperators but also defectors; in fact, a recent article suggests that, when altruistic behavior benefits not only the group but also the contributor, selection may lead to an asymmetric stable state, in which some individuals make high levels of cooperative investment and others invest little or nothing (Doebeli, Hauert, & Killingback, 2004). Thus the achievement of a steady state in a cooperative environment may require the presence of both types of individuals. However, this is not to say that interpersonal interactions necessarily benefit from such a mixed society of givers and takers. Accurate evaluation of the motives of others and decryption of their current emotional states are skills necessary for navigating our social world.

Although every social species may possess specialized systems for the perception of social cues (e.g., biological motion, eye gaze), humans appear unique in their ability to empathize with and infer the intentions of conspecifics. Recent evidence supports the existence of neural mechanisms for these high-level social computations. Much of our emotional life relies not on reacting to simple stimuli but on sophisticated calculations that take into consideration motives, context, past experience, and relationship history. This is particularly true for emotion elicitors that are social, such as

intentions of others, including the STS and temporoparietal junction (TPJ; Saxe & Kanwisher, 2003), as well as the mPFC and anterior paracingulate (Gallagher, Jack, Roepstorff, & Frith, 2002). Accurate assessment of conspecifics' intentions, beliefs, and motivations is critical for adaptive emotional responses in a social environment. Thus we might predict that neural regions implicated in ToM will show some evidence of an interaction between social and emotional processes. Indeed, the STS and mPFC are sensitive to both the emotional and social content of pictures; both regions also appear to interactively process social and emotional information, such that emotional stimuli depicting conspecifics recruit greater neural resources (Norris et al., 2004).

Further evidence for the influence of social context on emotional processes comes from research on autism, a neurodevelopmental syndrome thought to result in the selective impairment of theory of mind abilities. Autistic individuals show deficits in social functioning, as well as in emotion perception (Abdi & Sharma, 2004), empathy (Baron-Cohen, 2004), perception of biological motion (Blake, Turner, Smoski, Pozdol, & Stone, 2003), face processing (Dawson et al., 2002; Grelotti, Gauthier, & Schultz, 2002), gaze pursuit (Emery, 2000), and spontaneous mimicry of emotional expressions (McIntosh, Riechmann-Decker, Winkielman, & Wilbarger, in press). In addition, studies using a wide range of methods, including functional neuroimaging, postmortem measurements, and behavioral studies, have begun to examine the neuroanatomical correlates of autism. Many researchers have focused on the amygdala as a potential neural mediator of autism (Baron-Cohen, 2004; Baron-Cohen et al., 2000; Howard et al., 2000). Di Martino and Castellanos (2003) reviewed the neuroimaging literature and suggest that autism is associated with decreased neural activation in ventromedial PFC, the TPJ, and extended amygdala and with increased activation in primary sensory cortices. All of this research is consistent with a deficit in ToM that potentially has downstream consequences for emotional processes that are dependent on the social context (e.g., facial expressions, empathy). Furthermore, autistic children do not differ from normally developing children in patterns of emotional modulation of the startle response, a task that relies heavily on basic emotional responses and does not require modulation by the social context (Salmond, de Haan, Friston, Gadian, & Vargha-Khadem, 2003); and it has been argued that basic responses to emotional expressions remain intact in autism, whereas the true deficit lies in an impaired ability to represent the individual displaying the emotion (Blair, 2003). In sum, although autism is characterized by impairments in spontaneous "socio-emotional" processing, such as a lack of spontaneous activation of premotor cortex to action observation (McIntosh et al., in press), additional impairments are evident in the modulation of emotional responses as a function of interpretations of and judgments about the social context, that is, of the ability of the social context to influence emotional processes.

SOCIAL MODULATION OF EMOTIONAL PROCESSES

The immediate social context can not only provide many clues as to a conspecific's goals and intentions as intimated by theory of mind research but can also affect the emotional meaning of an event, and therefore it needs to be considered when determining an adaptive response in any environment. In other words, the emotional meaning of an event can be influenced by social context and culture. Take, for example, a standard practice on reality television programs such as *Survivor* and *The Apprentice* that involves mixing teams over the course of the competition. A victory by a single contestant can be experienced either as a triumph (if he or she is a teammate) or a defeat (if he or she is an opponent); in addition, one contestant's emotional response to another's victory can change over the course of the season as contestants are shuffled among teams. In sum, the social context of an event can modulate our emotional experience to produce even polar-opposite reactions to the same event (see Englis, Vaughan, & Lanzetta, 1982).

The social context can also modulate how one responds to the event. Appropriate emotional displays and responses in different social contexts are prescribed by display rules (e.g., cultural prescriptions for displays of emotion), which are acquired through social learning. Failure to regulate emotional expressions in the socially prescribed fashion can have significant and immediate effects. In the first presidential debate of the 2004 campaign between President George W. Bush and Senator John Kerry, President Bush was observed showing a range of unpleasant facial expressions when Senator Kerry was speaking. President Bush's immediate decline in the voter polls has been partially attributed to his inappropriate emotion displays.

In contrast to the "emotion expression view" of facial displays, which suggests that expressions of emotion are simply "readouts" of a person's internal emotional state (e.g., Buck, 1994), Fridlund (1991, 1994) has proposed that facial expressions are social signals and, as such, can be modified by the social context (the "behavioral ecology view" of emotional expression). Although the two views are clearly not mutually exclusive (cf. Cacioppo, Bush, & Tassinari, 1992) because facial expression may serve both purposes, Fridlund's research illustrates the point that emotional expression can be influenced by the social context. In one such study, degree of smiling to a pleasant film varied as a function of the social context, such that participants smiled more when a friend was present in the same room than when they were alone and had not arrived with a friend; importantly, self-reported feelings did not differ across contexts (i.e., the social environment did not simply increase enjoyment of the film; Fridlund, 1991). This finding clearly suggests that the presence or absence of a close friend can influence facial displays of happiness. However, a similar study investigating responses to sad films found that participants expressed less

sadness when in the presence of a friend (Fridlund & Fischer, 2001). Although this research suggests that facial expressions are socially learned, it suggests that some emotions are not often appropriate or common in certain contexts (e.g., crying) to either close friends or in public. This is a socially learned attempt to regulate emotional expression.

The idea that emotional expression is modulated by social context, and specifically by social norms, poses theoretical and practical questions. Mesquita and Frijda (1992) discuss cross-cultural literature on emotion and the interpretation of events (e.g., death and grief responses and facial expressions) and how they relate to emotional experience (e.g., guilt vs. shame). Research on the development of emotion regulation and facial acts (Meltzoff & Decety, 1993; Cole, Martin, & Dennis, 2000) suggests that the regulation of empathy and emotion regulation is a complex process. Damasio, Tranel, and Damasio (1990) suggest that the prefrontal cortex (PFC) may be involved in the development of emotion regulation and rules regarding emotion regulation. They provide detailed case studies on two individuals with lesions in the ventral PFC during the first half of their lives. The behavior with that of patients with lesions in the ventral PFC in life. Major differences in behavior were observed and late acquisition of ventral PFC functions in learned social norms regarding emotion regulation. That those who acquire lesions in the PFC have impaired responses.

Finally, there exist a small number of studies that show both the immediate social context and the "social emotions" include guilt and shame (Barrett & Nelson-Goens, 1999). These studies uphold cultural norms of behavior and discourage behaviors while discouraging behaviors. Pride and admiration may be used to attain culturally mandated standards and punishments for inappropriate, poor behavior. Guilt plays an important role in determining when emotions are experienced, in a social context (e.g., guilt in the United States). These studies serve as an illustration of how social norms and processes. Recently, Adolphs, Baetens, and colleagues (2002) study investigating the role of

sadness when in the presence of a friend or a stranger (Jakobs, Manstead, & Fischer, 2001). Although this finding may seem contrary to the hypothesis that facial expressions are social signals that promote behaviors in others, it suggests that some emotions are regulated in certain social contexts; it is not often appropriate or comfortable to show signs of extreme sadness (e.g., crying) to either close friends or strangers. Thus context can also promote socially learned attempts at regulation of emotion expression.

The idea that emotional expression can be modulated by the social context, and specifically by socially learned display rules and appropriate regulation of responses, poses the question of how individuals acquire these norms. Mesquita and Frijda (1992) provide an excellent review of the cross-cultural literature on emotion, from emotion antecedents and interpretation of events (e.g., death as a loss vs. a gain) to physiological responses and facial expressions to appropriate, culturally dependent emotional experience (e.g., guilt vs. shame; acceptance of anger). New research on the development of emotion regulation suggests that infant imitation of facial acts (Meltzoff & Decety, 2003) and early caregiver relationships (Cole, Martin, & Dennis, 2004) are critical for appropriate development of empathy and emotion regulation. Furthermore, Anderson, Bechara, Damasio, Tranel, and Damasio (1999) have shown that the ventromedial prefrontal cortex (PFC) may be required for the learning of social norms and rules regarding emotion regulation and display. The authors performed detailed case studies on two individuals who had acquired large lesions of the ventral PFC during the first few months of life and compared their behavior with that of patients who acquired comparable lesions much later in life. Major differences in behavior observed between patients with early and late acquisition of ventral PFC lesions appear to stem from a difference in learned social norms regarding behavior and emotional expression, such that those who acquire lesions early in life fail to learn socially appropriate responses.

Finally, there exist a small subset of emotions that depend heavily on both the immediate social context and on acquired cultural norms; such "social emotions" include guilt, shame, pride, embarrassment, and others (Barrett & Nelson-Goens, 1997). The social emotions serve to protect and uphold cultural norms of behavior, as they promote socially acceptable behaviors while discouraging behaviors that would be harmful for the society. Pride and admiration may function as rewards for individuals who attain culturally mandated standards of excellence; guilt and shame as punishments for inappropriate, potentially detrimental behaviors. Thus culture plays an important role in determining the conditions under which social emotions are experienced, in addition to which social emotions are prominent (e.g., guilt in the United States; shame in Japan). Clearly, social emotions serve as an illustration of the interaction of social and emotional processes. Recently, Adolphs, Baron-Cohen, and Tranel (2002) conducted a study investigating the role of the amygdala, a structure implicated in both

social and emotional processes, in the recognition of social emotions. Individuals with amygdala damage were impaired in recognizing social emotions, more so than in recognizing basic emotions (e.g., happiness, anger). The authors suggest that the amygdala may be involved in processing complex social stimuli. Furthermore, they suggest that, as people with autism also are impaired in the recognition of social emotions, the deficits observed in social cognitive abilities in autism may be due to dysfunction of the amygdala.

SUMMARY

Interest in the overlap and influences between social and emotional information processes as illuminated by a neuroscience perspective, although relatively recent, is leading to new findings and insights on a weekly basis. Both emotional and social stimuli have adaptive utility for humans. To promote flexible, accurate, and efficient responding, we have suggested that social information processing may have co-opted existing structures specialized for affective processing and that neural regions that have evolved to serve social information processing may also be involved in a variety of emotional processes (Norris et al., 2004; Eisenberger et al., 2003). Emotion is critical for our social relationships (e.g., Keltner & Kring, 1998), and relationships are important for our and the collective emotional well-being (Cacioppo & Hawkley, 2005). We, therefore, reviewed evidence that social and emotional stimuli can have additive and synergistic effects on neural substrates in cortical and limbic regions, as well as evidence that social stimuli can also modulate the experience and expression of emotions.

ACKNOWLEDGMENT

This work was supported by National Institute of Mental Health Grant No. P50 MH52384-01A1.

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