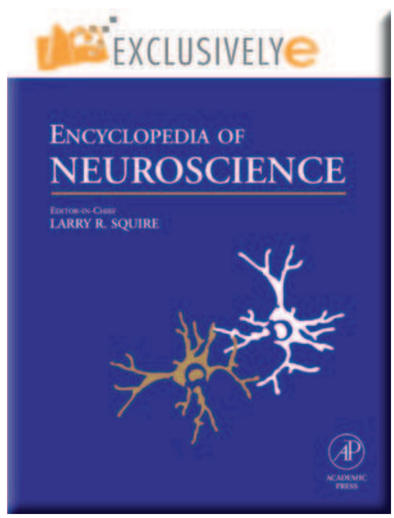

Heatherton T F and Krendl A C (2009) Social Emotion: Neuroimaging. In: Squire LR (ed.) Encyclopedia of Neuroscience, volume 9, pp. 35-39.
Oxford: Academic Press.

Social Emotion: Neuroimaging

T F Heatherton and A C Krendl, Dartmouth College, Hanover, NH, USA

Humans are social beings who live in groups. Dependency on group living is not unique to humans, but the nature of relations among and between in-group and out-group members is especially complex in human societies. Decades of research in psychology has established the central role of emotional processes in facilitating social relationships and guiding group behavior. 'Social emotions,' which are complex subjective experiences (e.g., pride, admiration, jealousy, envy, irritation, and flirtatiousness), serve many important social functions that promote long-term relationships and group stability. From a functional perspective, social emotions enable people to be good group members, thereby avoiding rejection and enhancing their survival and reproduction. Thus, social emotions are essential to human social life.

Social emotions facilitate successful social relationships through two primary pathways: they provide incentives to engage in social interactions (e.g., affection, love, feelings of pride, or admiration for those with whom we interact), and they increase the likelihood that people will adhere to societal norms that are necessary for group living. When such norms are violated, people experience negative social emotions (e.g., feelings of guilt, embarrassment, or shame) that subsequently encourage them to act within the bounds of socially acceptable conduct, thereby reducing the risk of social exclusion and promoting positive social interactions. Moreover, long-lasting social emotions (such as remembering an embarrassing moment from adolescence) reduce the likelihood of repeat violations.

Although it is possible that nonhuman animals experience emotional states that modulate behavior, it is apparent to most researchers that complex social emotions are particularly characteristic of humans and some are possibly uniquely human. An open question, however, is whether social emotions are innate or learned behaviors. From an evolutionary perspective, social emotions serve the adaptive function of fostering social relationships within groups. Thus, it is possible that people have evolved dedicated neural circuits for social emotions, much as has been argued for the more basic emotions, such as fear. At the same time, some evidence suggests that many social emotions are influenced more by socialization than by genes, indicating that important aspects of social emotions develop within a social context. Indeed, research suggests that the influence of the shared environment on feelings of guilt increases over time, whereas the influence of genes disappears. Nonetheless, for most people, social emotions play a powerful and prominent role in their interactions with other people. Extensive evidence from patient research, as well as recent efforts using the methods of neuroscience to study human social emotions (i.e., neuroimaging), have started to provide important insights into the factors that produce and maintain social emotions.

Neuropsychological Evidence for Discrete Neural Networks in Social Emotions

Extensive evidence from patient research suggests that there are two primary neural regions involved in perceiving social emotions. The first (the amygdala) contributes to the identification of the social emotion, whereas the second (discrete regions of the prefrontal cortex) translates those emotions into information that can be used to facilitate social interactions. The process of garnering socially relevant information from social emotions involves three critical components. First, social emotions require people to be aware of their behavior, so as to gauge it against societal or group norms. Second, people need to understand how others are reacting to their behavior so as to predict how others will respond to them. To do so requires them to be able to make attributions about the mental states of others, a capacity often called 'theory of mind' (ToM). Finally, there need to be mechanisms for detecting discrepancies between self-knowledge and social expectations of norms, thereby motivating behavior to resolve any conflict that exists.

The first evidence that regions of the prefrontal cortex plays a critical role in social emotions came from the case of Phineas Gage, who suffered profound frontal lobe damage when a railroad tamping rod misfired into his head. Formerly described by friends as dependable, polite, and hardworking, Gage became capricious, volatile, and lewd after the accident, showing no evidence of embarrassment or remorse at his socially inappropriate behavior. Gage's radical personality change after his injury provided convincing evidence that the prefrontal cortex plays a crucial role in the social emotions that regulate behavior (e.g., guilt, embarrassment, and remorse). Since Gage's accident, abundant evidence from patient research, and more recently neuroimaging studies, has further identified discrete neural networks involved in both identifying and using social emotions.

Neuroimaging and Patient Research on Self-Awareness

Social emotions require that people be aware of the effects of their behavior on others, which necessitates self-awareness. That is, when people commit a *faux pas*, they must be able to recognize that the behavior they performed is inappropriate and that the feelings they are experiencing are embarrassment at having committed the *faux pas*. Self-awareness occurs when people themselves are the objects of their attention, such as when they think about themselves or process other information in a personal manner. Many years of research in psychology has revealed that information processed with reference to self seems to be treated 'specially.' For instance, people show a robust enhancement in memory for material that has personal meaning. This self-reference memory enhancement effect has been observed in many contexts, such as when people remember information processed with reference to self better than information processed with reference to other people (i.e., friends and politicians). The use of functional neuroimaging has provided key insights into the brain regions that support self-awareness.

A series of functional magnetic resonance imaging (fMRI) studies conducted over the past 10 years have indicated that the medial region of the prefrontal cortex (MPFC) plays a vital role in self-awareness. This region is more active, for example, when people report on their personality traits, make self-relevant judgments about pictures, or retrieve autobiographical memories of past events. Recent research indicates that regions of the ventral anterior cingulate cortex (ACC) may work in conjunction with MPFC to reflect the valence of self-relevant information. Interestingly, the MPFC has also been identified as part of a 'default network,' which also includes the posterior cingulate gyrus and precuneus. This network is active when the brain is at rest (i.e., not engaged in an overt cognitive task). An abundance of positron emission tomography (PET) and fMRI data suggest that the default network plays a dominant role in self-awareness. As such, the default network supports important components of social emotions.

It is interesting to note that converging evidence from patient research indicates that frontal lobe lesions, particularly to the MPFC and adjacent structures, have a deleterious effect on personality, mood, motivation, and self-awareness. Patients with frontal lobe lesions show dramatic deficits in recognizing their own limbs, engaging in self-reflection and introspection, identifying a *faux pas* as being socially inappropriate, and even reflecting on personal knowledge. Indeed, frontal lobe patients are particularly impaired in social emotions, such as feeling embarrassed in appropriate contexts. The convergence of patient and imaging data support the conclusion that MPFC plays a prominent role in self-awareness, a necessary and critical contributor to the experience of social emotions.

ToM and the MPFC

In addition to recognizing our own mental states, social emotions require that we are able to accurately interpret the emotional states of others. For instance, to feel guilty about hurting a loved one, people need to understand that other people have feelings. Indeed, all social emotions related to empathy require the capacity to attribute specific mental states to others. Similarly, at the core of many social emotions is the belief that one is being evaluated by others (thereby giving rise to emotions such as embarrassment and social anxiety), which means recognizing that other people make evaluative judgments. The ability to infer the mental states of others is commonly referred to as mentalizing, or having the capacity for ToM. ToM enables the ability to empathize and cooperate with others, accurately interpret other people's behavior, and even deceive others when necessary. The rapidly emerging neuroimaging literature on ToM has consistently implicated MPFC as a central component of the neural systems that support mentalizing. Patient research in this area primarily focuses on people who have syndromes that involve impaired ToM (i.e., Asperger's or autism). This line of research indicates that such people have decreased neural activity and cerebral blood flow to the MPFC during ToM tasks. Such findings suggest that the MPFC plays a vital role in mentalizing tasks.

It is interesting to note that the ability to mentalize relies heavily on similar neural networks engaged in processing self-relevant information, notably MPFC. However, this region of MPFC tends to be more dorsal in ToM studies than in self-reference studies, although overlap in activity has been observed. In a typical neuroimaging study of ToM, participants are required to make judgments about other people's mental states after reading scripted scenarios or observing pictures of people with differing facial expressions. For instance, early investigations compared neural activity observed during trials in which participants were asked to judge the motivations of an actor's behavior (e.g., "he turned himself into the police because they knew he had committed a crime") with that observed during nonmentalizing tasks, such as judging a person's physical actions, and revealed MPFC activation in the mentalizing task only. MPFC activation can also be observed when participants are asked to determine the underlying motivation of an actor as depicted by pictures that convey specific social behavior (i.e., stealing, sharing). This region is also engaged when perceivers are asked to infer the mental states of targets that are most similar to them. This latter finding suggests that self-reflection is possibly engaged in mentalizing tasks, illustrating perhaps a common role that MPFC is playing for both self-awareness and ToM. Indeed, deficits in this brain region are associated with a reduction in ToM, reinforcing the importance of MPFC in ToM tasks. Although activity in other brain regions has been observed during ToM tasks, notably the superior temporal sulcus (STS), the temporoparietal junction, and less often the amygdala, MPFC appears to play a central role in the ability to make mental state attributions about other people. This ability is critical for social emotions because it enables us to modify our behavior in order to promote smooth social interactions.

Social Emotions and the Amygdala

In addition to MPFC, a distributed network of brain regions has been implicated in selecting and processing social emotions. One such region is the amygdala. For decades, the amygdala was considered most often in the context of fear learning and attention tasks. More recently, however, amygdala activation has been observed in making social judgments, such as evaluating stigmatized individuals. Not surprisingly, then, evidence has emerged from patient and neuroimaging research to implicate the amygdala in perceiving social emotions. For instance, patients with unilateral or bilateral amygdala damage have been shown to be impaired at recognizing specific social emotions from facial expressions (e.g., arrogance, guilt, admiration, and flirtatiousness). Interestingly, this deficit appears to be limited to social emotions, and does not extend to other emotions, suggesting that the amygdala plays a central role in recognizing social emotions.

Neuroimaging studies have also demonstrated an important role for the amygdala in processing a variety of social emotions. For instance, when participants are asked to choose the appropriate reaction (from varying perspectives) to sentences that represented different social emotions (e.g., embarrassment, pride, shame, guilt, admiration, irritated, and impressed), as compared to sentences conveying nonsocial emotions, heightened amygdala activation is observed, regardless of perspective taken during the task. Interestingly, when participants are asked to examine intentional violations of social norms through stories (e.g., "You are invited for dinner at your friend's house") that have one of three endings: one that was descriptive of normal social behavior (e.g., "You have a bite of the first course and like it, congratulate your friend for her good cooking"); one that described an embarrassing conclusion (e.g., "You have a bite of the first course, you choke and spit out the food while you are coughing"); or one in which the protagonist violated a social norm (e.g., "You have a bite of the first course, but do not like it and spit the food back onto your plate"), a similar pattern of activation is observed. When taking their own perspective, participants showed greater amygdala activation in response to intentional violations of social norms. These results suggest that the amygdala is indeed involved in processing social emotions.

Based on the extant literature on the amygdala, it is not surprising that this area may be involved in processing social emotions. It has long been argued that the primary role of the amygdala is to automatically respond to arousing emotional stimuli, particularly fear-inducing or aversive items. From this perspective, the role of the amygdala in processing social emotions may simply be to respond to the highly arousing nature of the unique conditions that produce social emotions. More recently, however, this region also has been implicated in drawing attention to novel stimuli that have biological relevance. Under this argument, it is plausible that the amygdala plays a role in processing social emotions because they have direct relevance in maintaining long-term social relations, which is a fundamental biological need. Regardless, the role of the amygdala in processing social emotions suggests that an automatic response network exists in the brain for distilling social emotions.

Social Emotions and the ACC

In addition to the MPFC and amygdala, patient research and neuroimaging have also implicated the ACC in processing social emotions. Although the ACC is anatomically part of the prefrontal cortex, a wealth of evidence from patient and neuroimaging research illustrates that ACC activity is functionally distinct from MPFC regions involved in self-awareness and ToM. Evidence from patient studies suggests that the ACC is involved in integrating cognitive and affective information to guide behavior appropriately. For instance, imaging research has implicated the ACC in resolving cognitive conflicts. With respect to social emotions, the anterior cingulate appears to be engaged in social interactions that provide conflicting social feedback, thereby eliciting conflicting emotions.

Although emerging evidence from neuroimaging research has yielded disparate results as to the roles of discrete regions of the ACC in processing social feedback, it has provided a working framework for understanding the ACC. Rejection, for instance, is a social emotion that results from a violation of the expectancy that people believe they are valued. Some neuroimaging research has found that a region of the dorsal ACC (dACC) is responsive during tasks designed to elicit social rejection, such as when virtual interaction partners suddenly and surprisingly stop cooperating with research participants. It is possible, however, that the dACC activity observed in these types of tasks indicates cognitive conflict more than social pain resulting from rejection, *per se*. Indeed, being rejected may violate the fundamental expectancy of social inclusion. Other research has indicated that a more ventral region of the ACC (vACC) is important for the social emotion of feeling rejected. Interestingly, interpersonal distress, such as feeling unloved, is often involved in depression, and abnormalities in vACC activity have been observed in unipolar depression. For instance, imaging research has found differential patterns of vACC activity to emotional facial expressions between depressed and nondepressed subjects. Thus, one possible role for vACC reflects its involvement in general affective state, thereby affecting social emotions indirectly.

Another possible role for ACC in social emotions is its involvement in detecting and attempting to resolve cognitive conflict. Thus, information that conflicts with pre-established knowledge signals errors that must be resolved, a situation that produces ACC activity. From this perspective, then, the ACC may be involved in processing social emotions by detecting conflict between actions and outcomes. For instance, when a social norm is violated, the ACC may play a role in identifying this error because it detects differences between the expectation (social norm) and action (violation). The detection of errors in social behavior may produce social emotions that guide future appropriate behaviors.

Self-Conscious Emotions

An important distinction that emerges in the psychological literature is the subcategory of 'self-conscious emotions' from the more general social emotions. Self-conscious emotions, including embarrassment, guilt, and shame, occur when the emotional experience reflects an evaluation of the self. People feel embarrassed when they believe that others are evaluating them negatively, and ashamed when they do it to themselves. Either way, the self is implicated in a way that is more specific than emotions such as jealousy, admiration, or flirtatiousness. The primary adaptive value of self-conscious emotions is that they provide a clear disincentive for people to act in a socially inappropriate manner. Although, neuroimaging research on self-conscious emotions is still in its infancy, patient studies and a handful of imaging studies shed light on the neural networks involved in this specific category of social emotions.

Patient research has provided compelling evidence that damage to the orbitofrontal cortex, a region adjacent to the medial prefrontal cortex, severely impairs self-conscious emotions. Patients with lesions to this area exhibit extremely socially inappropriate behavior (e.g., making inappropriate jokes, kissing or hugging strangers, disclosing intimate information about themselves to strangers). Imaging studies of self-conscious emotions such as guilt and embarrassment implicate additional brain regions, including anterior cingulate gyrus, MPFC, STS, and insula. For example, asking people to recall the most guilt they ever experienced produces greater activity in these regions than does recalling events when they did not feel guilty. In research comparing guilt and embarrassment, both self-conscious emotions elicited MPFC activation, but guilt apparently does so more than embarrassment. Robust MPFC activity in self-conscious emotions may reflect the unique circumstances under which people mentalize about how others are evaluating them.

Imaging Moral Emotions

Another category of social emotions, namely, moral emotions, dictate what is ethically 'right' or 'wrong' in a given situation. As might be expected by the foregoing discussion, when participants are asked to resolve various moral dilemmas during imaging, MPFC activation is observed. Specifically, comparisons between making moral-personal (e.g., the footbridge dilemma), moral-impersonal (e.g., the trolley dilemma), and neutral (or nonmoral) decisions revealed that MPFC and posterior cingulate gyrus are significantly more active in the moral-personal condition than in the moral-impersonal and the nonmoral conditions. MPFC activation also emerges when morality is measured by eliciting disgust or indignation from the observer. For instance, participants who read a series of disgust-inducing (e.g., "A friend told you about a newspaper headline. A man had died after he ate a living rat") or indignation-causing (e.g., "As you arrived home, you saw that the nurse has put a spider on the baby's face") statements showed heightened MPFC and orbitofrontal activation to both the disgust- and indignation-inducing statements. Disgust also elicited greater amygdala and anterior cingulate response as compared to indignation, whereas the latter elicited greater insula and right inferior frontal gyrus.

Substantial evidence has also been found in the patient literature that lends support to these findings. Patients who have experienced damage to regions of the prefrontal cortex, including MPFC and orbitofrontal cortex, early in life (i.e., before 2 years) show extensive deficits in their ability to engage in moral reasoning tasks. Together, the findings from emerging neuroscience and patient research suggest that the prefrontal cortex, particularly the MPFC, has a critical role in moral reasoning.

Conclusions

Although neuroimaging research on social emotions is in its early days, it has already revealed a strong overlap with the neural networks that give rise to social cognition and processing emotions. Imaging studies have indicated a prominent role of the MPFC for social emotions (especially self-conscious emotions) that require inferences to be made about the mental states for self or others. The extant literature also implicates the amygdala in social emotions, although it remains an open question as to whether the amygdala is selectively responsive to specific social emotions or whether it plays a more general role in emotional responding (i.e., arousal or vigilance). Moreover, initial imaging studies also indicate an important role for the anterior cingulate in detecting conflicting social information, such as detecting social rejection, and perhaps in getting behavior back on track. Indeed, burgeoning research on the neural correlates of social emotions include studies on the neural networks underlying attachment, love, and perceiving stereotypes. Considered as a whole, patient and neuroimaging research are producing important insights into social emotions. In order to successfully guide social interactions, social emotions require self-awareness, the ability to understand the mental states of others, and mechanisms to detect conflicts between personal behavior and appropriate social rules. It is likely that neuroimaging research will continue to provide insights into this important aspect of emotion.

See also: Cognition: An Overview of Neuroimaging Techniques; Emotion Systems and the Brain; Emotion: Neuroimaging; Emotion: Computational Modeling; Neuroimaging.

Further Reading

Adolphs R (2003) Cognitive neuroscience of human social behaviour. *Nature Reviews Neuroscience* 4(3): 165–178.

Adolphs R, Baron-Cohen S, and Tranel D (2002) Impaired recognition of social emotions following amygdala damage. *Journal of Cognitive Neuroscience* 14(8): 1264–1274.

Amodio DM and Frith CD (2006) Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience* 7(4): 268–277.

Botvinick MM, Cohen JD, and Carter CS (2004) Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences* 8: 539–546.

Feinberg TE and Keenan JP (2005) *The Lost Self: Pathologies of the Brain and Identity.* New York: Oxford University Press.

Frith CD and Frith U (2006) How we predict what other people are going to do. *Brain Research* 1079: 36–46.

Gallagher HL and Frith CD (2003) Functional imaging of 'theory of mind' *Trends in Cognitive Sciences* 7(2): 77–83.

Gusnard DA (2005) Being a self: Considerations from functional imaging. *Consciousness and Cognition* 14: 679–697.

Heatherton TF, Macrae CN, and Kelley WM (2004) A social brain sciences approach to studying the self. *Current Directions in Psychological Science* 13: 190–193.

Kerns JG, Cohen JD, MacDonald AW, Cho RY, Stenger VA, and Carter CS (2004) Anterior cingulate conflict monitoring and adjustments in control. *Science* 303(5660): 1023–1026.

Moran JM, Macrae CN, Heatherton TF, Wyland CL, and Kelley WM (2006) Neuroanatomical evidence fordistinct cognitive and affective components of self. *Journal of Cognitive Neuroscience* 18: 1586–1594.

Raichle ME, MacLeod AM, Snyder AZ, Powers WJ, Gusnard DA, and Shulman GL (2001) A default mode of brain function. *Proceedings of the National Academy of Sciences of the United State of America* 98(2): 676–682.

Singer T, Seymour B, O'Doherty JP, Stephan KE, Dolan RJ, and Frith CD (2006) Empathic neural responses are modulated by the perceived fairness of others. *Nature* 439: 466–469.

Stuss DT and Levine B (2002) Adult clinical neuropsychology: Lessons from studies of the frontal lobes. *Annual Review of Psychology* 53(1): 401–433.

Whalen PJ (1998) Fear, vigilance, and ambiguity: Initial neuroimaging studies of the human amygdala. *Current Directions in Psychological Science* 7(6): 177–188.