Emotion
Definition of Emotion
Emotion Perception and Attention
Memory and Learning
Interoception and Subjective Feeling States
Social Interaction
Emotion Regulation
Emotion Dysregulation

Glossary

Amygdala
- An almond-shaped cluster of interrelated nuclei and associated cortex in the anterior medial temporal lobe.

Arousal
- A dimension of emotion that varies from calm to excitement and predicts behavioral activity level.

Blood–oxygen level-dependent (BOLD) signal
- T2*-weighted signal in functional magnetic resonance imaging (fMRI) that reflects hemodynamic changes in regional perfusion evoked by neural activity.

Functional magnetic resonance imaging (fMRI)
- A non-invasive technique with good spatial resolution that detects changes in regional blood flow associated with neural activity.

Interoception
- A representation of visceral activity; the afferent limb of homoeostatic neural control of bodily organs.

Magnetoencephalography (MEG)
- A non-invasive technique with high temporal resolution that detects the changing magnetic fields associated with neural activity.

Valence
- A dimension of emotion that varies from unpleasant (negative) to pleasant (positive) to reflect motivational value.

Emotion
- Emotion is central to our everyday human experience. Emotional events or objects within our environment are assigned value, bias our attention, and enhance our subsequent memory. Neuroimaging techniques, perhaps more than other approaches, have led to a growing awareness that emotion, unlike many other psychological functions, is relatively unencapsulated and interacts with and influences multiple other areas of functioning. In addition to effects on attention, perception, memory, and learning, emotion also forms the backbone of our social relationships and is an important component of empathetic understanding of others. Emotional cues also act as powerful reinforcers, have a marked influence on our thoughts and reasoning, and serve to bias our ongoing behavior. Although emotions come in many flavors that may equally serve to bias multiple psychological functions, much of the contemporary research on emotional neuroscience has focused on the processing of fear. For the purposes of this article, we follow this focus, which also accords with an emphasis on stress responses.

- Consistent with a broad role in human functioning are the wide-ranging manifestations associated with disorders of emotion regulation. Emotion disequilibrium underlies not just anxiety and stress-related illness but the entire range of mental disorders and acts as the common denominator in much of human unhappiness. This article reviews the contributions of neuroimaging studies to our developing understanding of the neurobiology of human emotion. One particular aim is to highlight how emotion interacts with and influences other areas of cognition and to illustrate how an understanding of the mechanisms underlying these interactions can enable a greater understanding of stress-related disorders.

Definition of Emotion

- Differences in definition can lead to markedly different conceptualizations of emotion and underlie seemingly contradictory theories of emotion in the literature. A prevalent view conceptualizes emotion as a transient perturbation in an organism’s functioning evoked by a triggering (i.e., emotive) stimulus (either external or internal). Most accounts of emotion also subscribe to a multicomponential description with physiological arousal, motor expression, and subjective feelings forming the reaction triad of emotion. However, the extent to which changes in these various components are necessary and sufficient to define an episode as emotional is more controversial. For the purposes of this article, we use the following definition: emotions are transient events, produced in response to external or internal events of significance to the individual; they are typically characterized by attention to the evoking stimulus and changes in neurophysiological arousal, motor behavior, and subjective feeling state that engender a subsequent biasing of behavior.
**Emotion Perception and Attention**

Implicit within this definition is that events of significance to the individual (emotive stimuli) are susceptible to preferential perceptual processing. One mechanism through which this is achieved is through the emotional biasing of attentional processes. This is illustrated in behavioral studies using visual search paradigms, in which target items are discriminated from an array containing a variable number of distracter items. Emotionally valenced items or objects are indeed identified more rapidly than nonemotional items. Furthermore, in spatial tasks, the presentation of an emotional cue on one side of the visual space increases the speed of identification of nonemotional stimuli subsequently presented on the same side (i.e., attention is drawn to the location of the preceding emotive stimulus). Neuroimaging studies investigating the neural basis of this emotional capture of attention in spatial orientation tasks show that it is correlated with activity in regions of the frontal and parietal cortices as well as the lateral orbitofrontal cortex.

Evidence from patient studies, neuroimaging, and electroencephalography suggests that even unattended emotional stimuli are more likely to enter awareness, suggesting further mechanisms through which emotional stimuli influence perception. Neuroimaging studies continue to delineate the brain mechanisms through which unattended emotional stimuli gain enhanced access to awareness. One influential hypothesis suggests that the emotional salience of a stimulus is rapidly detected by the amygdala after cursory representational processing. The amygdala subsequently facilitates attention and perception via projections to the sensory cortices to enable more detailed sensory processing. Convergent anatomical studies suggest that this is mediated by both direct and indirect amygdala influences on sensory cortices; reciprocal direct connections exist between the amygdala and sensory cortices, and a projection from the central nucleus of the amygdala to the cholinergic nucleus basalis of Maynert enables indirect ascending cholinergic neuromodulatory influences to be exerted on the same cortical regions.

Functional neuroimaging studies have tested this hypothesis using visual backward-masking paradigms in which briefly presented visual targets are rendered invisible by subsequently presented stimuli. Unseen emotional stimuli, presented in this subliminal manner, can nevertheless still evoke neural responses in the amygdala, compared to nonemotional (neutral) stimuli. Moreover, masked presentations of face stimuli portraying fearful (vs. neutral) facial expressions enhances activation within the fusiform cortex (an extra-striate visual area containing a region implicated as being specialized for processing faces). This activation of the fusiform face area (FFA) is predicted by the magnitude of amygdala activation. Further evidence that emotional processing in the amygdala may enhance activity within sensory cortex comes from the observation that patients with amygdala damage fail to show this enhancement of activity within the face-processing visual cortex when tested on the same paradigm. The presentation of fearful face cues has also been shown to enhance even early perceptual functions such as contrast sensitivity, which is consistent with the suggestion that the amygdala may modulate even activity within the primary visual cortex.

Preattentive processing of emotional stimuli indicates early representational discrimination between emotional and nonemotional events. Studies in humans using magnetoencephalography (MEG), a neuroimaging technique with high temporal resolution, showed discriminatory responses to emotional faces as early as 100–120 ms. This compares to characteristic face-related responses that occurs much later, at 170 ms. Electrophysiological studies in humans using intracranial electrodes also showed an early, 120- to 160-ms response to aversive stimuli. The early recognition of emotionally valenced stimuli accords with animal data suggesting that the amygdala may be activated by a rapid subcortical pathway. Neuroimaging studies in both normal and brain injury subjects highlight subcortical amygdala activation in humans. One study exploited two separate findings: (1) that low- and high-spatial frequency information is processed by separate visual neural pathways and (2) that coarse emotional cues are carried in low-frequency components. When subjects were presented low-frequency (blurred) face stimuli fearful (vs. neutral face stimuli), enhanced activity was seen in the amygdala, pulvinar nucleus of the thalamus, and superior colliculus, components of a proposed subcortical circuit (Figure 1). In contrast, the presentation of the same faces at high spatial frequency activated the cortical regions, including the fusiform (face-identity-specific) cortex. Implicit processing of emotional valence can be demonstrated in patients with damage to the primary visual cortex, who are not consciously aware of stimuli presented in their blind hemifield (i.e., blindsight). These patients show amygdala activation to fearful faces presented in their blind hemifield, illustrating the presence of the subcortical visual processing of emotion to the level of the amygdala.

Together these lesion and functional imaging studies provide mechanistic insight into the role of amygdala, through interactions with the sensory cortices, in facilitating enhanced attention and perception of...
The preferential early processing of emotionally valenced material, illustrated most powerfully with fearful stimuli, sets up a primary bias in subsequent information processing that underpins the regulation of ongoing and prospective behavior.

Neuroscientific studies of human emotion have tended to focus on the visual processing of emotional facial expressions. Nevertheless, this visual communication of emotional state through changes in the facial musculature is only one part of a richer multimodal vocabulary of affect. Information signaling emotional state is also conveyed by autonomic changes in the skin (leading to color change and sweating) and pupils, by posture and bodily movements, and by content and prosody of speech. Low-level auditory processing of emotional signals are the primary source of emotional information in speech. The prioritized processing of emotional sounds, particularly non-speech intonations of emotional state (gasps, screams, etc.), is illustrated within the primary and accessory auditory cortices. As with the visual system, amygdalo-cortical interactions are implicated in enhanced auditory attention to emotive sounds. Moreover, specificity in emotional processing may cross sensory modalities, such that ventral insular regions implicated in disgust-processing may be activated by auditory and visual expressions of disgust as well as by disgusting stimuli.

A degree of regional specialization in human emotional processing is suggested from the convergence of lesion and neuroimaging studies. Acquired damage to the amygdala impairs the recognition and

**Figure 1** Neural activity in response to viewing facial expressions. a, High-spatial frequency information; b, low-spatial frequency information. High-spatial frequency images activated the fusiform cortex, specialized for the processing of facial identity. Fearful (vs. neutral) facial expressions activated the amygdala bilaterally (vertical arrows) with greater response to low-spatial frequency images. Low-spatial frequency fearful images also activated the posterior inferior thalamus bilaterally (diagonal arrows) and the superior colliculus on the right suggesting that low-spatial frequency images containing emotion information activate a subcortical pathway to the amygdala. Reprinted by permission from Macmillan Publishers Ltd: Nature Neuroscience; Vuilleumier, P., Armony, J. L., Driver, J., et al., Distinct spatial frequency sensitivities for processing faces and emotional expressions, 6, 624–631, copyright (2003).
behavioral experience of fear. Similarly, the neuroimaging literature emphasizes a predominant sensitivity of amygdala responses to threat and fear signals. As previously indicated, other studies implicate regions of insula and striatum in the selective processing of disgust. The impaired recognition of facial expressions of disgust was reported in a patient with damage to these regions, whereas the stimulation of the insula may evoke feelings of nausea or a perception of unpleasant tastes. These lines of evidence for specialized emotion-specific processing within different brain regions are generally circumscribed to fear/threat (amygdala), disgust (insula and striatum), and, to a lesser extent, sadness (subgenual cingulate activity). Many neuroimaging studies highlight a general sensitivity of amygdala responses to the emotional intensity of external emotional stimuli, for which threat is perhaps most arousing.

The insula cortex also appears to play a more complex role in emotion perception, apparently through relating perceptual information with interoceptive representations of bodily states. Thus, insula activity is engaged during the recognition and experience of disgust, sadness, happiness, and fear; during the learning and expression of threat; during the perception of noxious stimuli; and during the experience of phobic symptoms, hunger, and satiety; and even during explicit facial emotion categorization.

Memory and Learning

Emotion has a striking and well described impact on memory processes. Animal studies, particularly the work of LeDoux, highlight the central role of the amygdala in fear conditioning, a form of implicit memory. The same is true in humans, illustrated in many neuroimaging and lesion studies. Fear conditioning is a rapid form of learning that a stimulus is potentially harmful. If an adverse event (unconditioned stimulus, US; e.g., a painful shock) occurs after a relatively innocuous stimulus, the latter (the conditioned stimulus, CS) comes to predict the adverse event and will engender arousal responses associated with the presence of threat. Patients with bilateral amygdala damage do not acquire conditioned fear responses (autonomic or motor), despite having an intact explicit knowledge of the association between the CS and US. Functional neuroimaging studies also confirm the importance of the amygdala in fear conditioning (i.e., the learning of CS–US associations). However the role of the amygdala in the expression of threat responses is more time-limited and shows habituation. Consistent with animal data, neuroimaging studies also describe amygdala engagement in more general associative reinforcement learning, including operant stimulus–reward learning and appetitive behavior.

In addition to simple associative responses, human memory is characterized by declarative richness in episodic and semantic memory. These domains of memory, typically supported both at encoding and recollection by activity within the hippocampus, are strongly modulated by emotional experience. Typically, emotional events and stimuli are remembered better than nonemotional occurrences. Animal studies highlight noradrenergic mechanisms enhancing amygdalo-hippocampal connectivity in preferential encoding of emotional objects. Brain-imaging studies in humans have gone much further, highlighting amygdala activation during encoding actually predicts the accuracy of subsequent declarative memory of positively or negatively valenced stimuli (Figure 2) and in delineating the functional architecture for mood-congruency effects (in which negative information is encoded and recalled to a greater extent when the subject is in a negative mood and, likewise, positive material is encoded and recalled to a greater extent in positive mood states). However, the role of the amygdala extends beyond encoding processes; it is also engaged during the retrieval of emotional items and contexts.

Interoception and Subjective Feeling States

Changes in bodily state, reflected in both physiological arousal and motor behavior, are obligatory defining characteristics of emotion. James and Lange, and more recently Damasio, argued that emotional feeling states must have their origin in the brain’s representation of the bodily (arousal) state. Without changes in bodily arousal, there is no emotion. This peripheral account of emotion predicts that afferent feedback signals from muscles and viscera associated with physiological arousal are integral to emotional experience. These mechanisms have been illuminated in a number of neuroimaging experiments examining central representation and re-representation of autonomic arousal states and homoeostatic sensations, such as temperature.

The role of the insula cortex in this context is particularly interesting. In a positron emission tomography (PET) study, activation within the viscero-sensory mid-insula cortex correlated closely with the actual stimulus temperature, yet the subjective ratings of the perceived intensity or pleasantness of hot and cold stimuli correlated with activity in the right anterior insula and orbitofrontal cortex. This finding suggests a dissociation between a primary central representation of viscero-sensory information, within
mid-insula, and subjective feelings of warmth or cold, represented in the right anterior insula and orbitofrontal cortex. A general role for these regions in the representation of emotional feelings is also supported by their activation observed during generated states of sadness and anger, anticipatory anxiety and pain, panic, disgust, sexual arousal, trustworthiness, and even subjective responses to music.

Behavioral and neuroimaging studies in patients with selective peripheral autonomic denervation (pure autonomic failure, PAF) lend further support to the importance of viscerosensory feedback to emotional feelings. These patients, who do not have autonomic (e.g., heart-rate or skin-conductance) changes in response to emotional stimuli or physiological stressors, show a subtle blunting of subjective emotional experience. In a fear conditioning study of PAF subjects and controls, both groups showed amygdala activity during the learning of threat (face stimuli, CS, were paired with an aversive blast of white noise, US). However, compared to controls, the right insula cortex showed attenuated responses to threat stimuli in the PAF patients, suggesting this region is sensitive to the presence and absence of autonomic responses generated during emotional processing. Moreover, when the threat stimuli were presented unconsciously (using backward masking), the same insula regions (including the right anterior insula) were sensitive to both the conscious awareness of emotion events and induced bodily arousal reactions. This study, particularly, suggests that the right insula is a neural substrate for the contextual integration of external emotional events with feeling states arising from bodily reactions.

The notion that subjective emotional feelings arise from central representations of bodily arousal states predicts that people who are more aware of their bodily responses may experience more intense emotions and feelings. Investigations examining individual differences in interoceptive awareness suggest that patients with anxiety disorders are more attuned to bodily reactions such as their own heartbeat or stomach motility. One such interoceptive task was translated into a neuroimaging study. Subjects were played a series of notes, presented in groups of 10, either synchronously or out of phase with their own heartbeats (see Figure 3a). In half the trials, subjects had to judge the timing of their heartbeat in relation to the notes (the control condition was a detection of a rogue note in the sequence). When subjects focused interoceptively to the timing of their own heartbeat, there was enhanced activity in the somatomotor, insula, and cingulate cortices. However, only one region, the right anterior insula cortex, reflected a conscious awareness of internal bodily responses (i.e., how accurately subjects performed the interoceptive task). Significantly, activity in this region, and even the relative amount of right anterior gray matter here (Figure 3b), predicted day-to-day awareness of bodily reaction and the subjective experience of negative emotions, particularly anxiety symptoms across individuals. Together these studies suggest that the right anterior insula is a principal neural substrate supporting conscious emotional feelings arising from interoceptive information concerning bodily arousal state (Figure 4).

Social Interaction

A characteristic of our social interactions is an intuitive ability to understand other people’s mental and
emotional states. Humans show a marked tendency to mimic one another’s gesticulations, emotional facial expressions, and body postures, suggesting that this mirroring of activity mediates and facilitates emotional understanding among individuals. At a neural level, cells in monkey premotor cortex have been described that respond to observing or performing the same motor actions. Corresponding human imaging studies of action observation also illustrate premotor cortical activity when observing the actions of others, and magnetoencephalography (MEG) studies report resynchronization in the primary motor cortex. Significantly,
these mirror activations are somatotopic with respect to
the body part performing the action.

Accumulating evidence supports the extension of
these action-perception mechanisms to emotions and
feeling states. A common neural representation is
proposed for the perception of actions and feelings
in others and their experience in self. Thus, viewing
emotional facial expressions in others activates auto-
matically mirrored expressions on one’s own face
(surprisingly, even when the observed facial expres-
sions are masked, hence unavailable to conscious
awareness). Significantly, this automatic mimicking
of emotional expressions also extends to autonomic
expressions of emotional states such as pupil size in
expressions of sadness. Neuroimaging studies show
shared neural activation in the somatosensory cortex
when a subject experienced or observed another
being touched, right insula activity when a subject
experienced disgusting odors or observed expressions
of disgust, and the activation of a common matrix
of regions when a subject experienced or observed
pain. The imitation or observation of emotional facial
expressions also activates a largely similar network of
brain regions including the premotor areas that are
critical for action representation. There is also selectiv-
ity; compared to nonemotional facial movements, emo-
tional expressions activate the right frontal operculum
and anterior insula, and regions such as the amygdala,
striatum, and subgenual cingulate are differentially
responsive when imitating happy or sad emotions.

**Emotion Regulation**

Understanding the adaptive mechanisms through
which we can control the expression of our emotions
is clinically and socially important. Unlearning estab-
lished emotional reactions is difficult. Many studies
have examined the modulation of previously learned
emotional responses with experimental extinction;
the repeated presentation of a previously CS with-
out its associated US rapidly leads to a diminished
emotional response. Nevertheless, the relationship
between the two stimuli is not forgotten but inhib-
ited and can be rapidly reinstated. Neuroimaging
of extinction learning (or the inhibition of emotional
responses) shows increased amygdala activity in
early extinction; however, retention after a day was
associated with activity in the subgenual anterior cin-
gulate and ventromedial prefrontal cortices, which
suggests a role for this region in the longer-term recall
of extinction learning (Figure 5).

Emotional responses may also be regulated voli-
tionally, using cognitive control or reappraisal. For
example, an image of a woman crying may be inter-
preted as one of sadness, but, if the subject is then
told that the picture was taken after her daughter’s
wedding, it may be reappraised as one of great
joy. Neuroimaging studies of emotional reappraisal
demonstrate an attenuation of activity in the amygdala
associated with enhanced activity in the left middle
frontal gyrus, suggesting that activity within the lateral

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**Figure 4** A functional neuroanatomical modification of William James’s (1884) model of emotional responses. Emotional stimuli (S) elicit automatic emotional responses (R) via thalamus–amygdala pathways (solid line arrows). This low-level processing occurs independently of conscious cognitive processing. Peripheral autonomic responses are fed back to the mid-insula and then are remapped to the right anterior insula where they interact with higher-level cognitive processing. Emotional feeling states therefore result from peripheral-central interaction in the right anterior insula. Reprinted from *Trends in Cognitive Sciences*, 6(8), J. S. Morris, How do you feel?, pp. 317–319, Copyright (2002), with permission from Elsevier.
prefrontal cortex modulates emotional reactivity of the amygdala, possibly via connections to medial prefrontal cortex. Similar cognitive emotion-regulation techniques can powerfully diminish responses acquired through fear conditioning, and neuroimaging studies using this paradigm again show increased activity in the left middle frontal gyrus with cognitive control. Taken together, these studies suggest that cognitive emotion regulation and lower-level extinction learning recruit similar overlapping neural mechanisms for the regulation of the amygdala to control primary emotional responses.

**Emotion Dysregulation**

The wide-ranging influences of emotion on other psychological functions may also be seen in the variety of symptoms and presentations associated with emotional disorders. Posttraumatic stress disorder (PTSD), resulting from exposure to a highly traumatic emotional event and usually associated with injury or risk of injury to self or others, is frequently associated with symptoms in multiple psychological domains. Enhanced arousal and startle responses to previously innocuous stimuli are common, as are intrusive traumatic memories (flashbacks) of the triggering event, the numbing of emotional feelings, and impairments to social relationships. The identification of brain regions that show increased activation associated with the enhanced perception and memory for emotional events and associated feeling states enables the linkage of psychological mechanisms in conditions such as PTSD and phobias with their underlying neural substrates.

Abnormal cortisol regulation and adrenergic stress responses are also seen in PTSD, as is a reduction in hippocampal volume. Imaging studies showing a similar reduction in hippocampal volume in endocrine disorders associated with chronically elevated cortisol levels, such as Cushing’s disease, suggest an etiological role for stress hormones such as cortisol in this reduction in hippocampal volume. These conclusions are further supported by a recent study of healthy postmenopausal women, which showed a strong correlation between hippocampal volume and lifetime levels of perceived stress, suggesting an influence of stress on regional brain volumes even in the normal population.

Maladaptive cognitive interpretations of situations or events are central components of many emotional disorders such as depression and the anxiety disorders and are a feature focused on by many of the psychological therapies used in their treatment. Understanding the neural mechanisms mediating the modulation of emotional responses will be essential to developing a comprehensive neurobiological understanding of these disorders. Furthermore, a better understanding of these mechanisms offers the opportunity to develop more targeted approaches specifically focused on changing these maladaptive emotional reactions.

**See Also the Following Articles**

Amygdala; Brain and Brain Regions; Emotions: Structure and Adaptive Functions; Hippocampus, Overview.

**Further Reading**


