

the emotion of fear with potentially threatening circumstances and generating appropriate fight-or-flight responses through the activation of downstream subcortical structures.

Vertical integration models: Fear modification

Just as fear mandates changes in emotional response, it is also important to revise fear responses when experience indicates that potentially threatening circumstances are no longer present. Indeed, the persistence of fear responses to stimuli that are no longer real threats is a hallmark of some anxiety disorders, including phobias and posttraumatic stress disorder (see Introductory Box). This unwarranted persistence of fear has been termed **emotional perseveration** and is analogous to the continued deployment of cognitive strategies when they are no longer appropriate in problem-solving tasks (see Chapter 13). In fear-conditioning protocols, the fear value of a CS can be changed simply by removing the negative reinforcer during the ongoing training. Through repeated presentation of the CS without the US (e.g., foot shock), the animal learns that the meaning of the CS has changed. The conditioned fear responses then subside in a process called **fear extinction**.

Extinction depends on the integrity of the ventromedial prefrontal cortex (vmPFC). Rats with damage to this region, while able to acquire fear normally, take much longer to extinguish a conditioned fear response than do controls. This area influences the activity of neurons in the amygdala, and stimulation of this pathway in conjunction with presentation of a CS is sufficient to suppress amygdala responses and reduce conditioned fear behavior. In humans, vmPFC damage leads to difficulty reversing stimulus-reinforcer relationships, and fMRI activity in this region correlates with the retention of extinction behavior. Because of the important implications of these prefrontal-amygdala interactions for the suppression of irrelevant fears, clinicians have had a keen interest in targeting pharmacological agents to mimic or augment these effects in patients with anxiety disorders.

Given its role in spatial processing and declarative memory (see Chapter 9), the hippocampus is a likely site for the mediation of some aspects of **contextual fear conditioning**, in which fears are associated with specific places or circumstances. Rats with dorsal hippocampal lesions can be conditioned normally to discrete cues but fail to generate and retain fear responses to the context in which the training took place. Similarly, amnesia patients with hippocampal damage exhibit conditioned SCRs to a discrete CS that predicts shock delivery, but they do not retain information about the contextual details of the conditioning episode (see Figure 10.13). The hippocampus makes similar contributions to both emotional and nonemotional forms of learning and memory that depend on associating pertinent information with the contexts in which the learning occurs. This similarity makes it inappropriate to consider the hippocampus a structure specifically dedicated to emotional processing, as was hypothesized within the limbic system theory of emotion.

Interoception and the somatic marker hypothesis

As the tumor grew bigger, it compressed both frontal lobes upward, from below ... The surgery was a success ... What was to prove less felicitous was the turn in Elliot's personality ... He needed prompting to get started in the morning and prepare to go to work. Once at work he was unable to manage his time properly ... Or he might interrupt the activity he had engaged [in], to turn to something he found more captivating at that particular moment ... One might say that Elliot had become irrational concerning the larger frame of behavior ... Elliot's job was terminated ... Elliot charged ahead with new pastimes and business

ventures. In one enterprise, he teamed up with a disreputable character. Several warnings from friends were of no avail, and the scheme ended in bankruptcy ... There was a first divorce. Then a brief marriage ... Then another divorce. Then more drifting, without a source of income ... Elliot emerged as a man with a normal intellect who was unable to decide properly, especially when the decision involved personal or social matters.

A. R. DAMASIO 1994

Observations of patients like these with damage to the orbital and ventromedial prefrontal cortex led neurologist Antonio Damasio to propose a theory about the role of emotion in decision making. This somatic marker hypothesis attempts to explain how the brain and body signal affective information that is used to guide everyday decision making. Damasio argues that the vmPFC contains indexes that link factual knowledge and bioregulatory states associated with a particular event. When a similar situation is subsequently encountered, prior knowledge calls up the relevant somatic markers, which include autonomic, endocrine, and musculoskeletal changes that constitute a particular emotional state. The vmPFC triggers reactivation of the somatosensory pattern that describes the appropriate emotion through connections to emotion-eliciting structures, such as the amygdala. Such reactivation can occur directly through a body loop that includes expression of the appropriate visceral response, or indirectly by simulating the somatosensory pattern in the insula and somatosensory cortex but without necessarily evoking physical changes in the body (called an “as if” loop).

By evoking these somatosensory patterns, reasoning and decision-making processes are constrained to options that are marked as qualitatively good or bad. In this way, somatic markers serve as a heuristic rule of thumb that permits the organism to make optimal decisions efficiently, without elaborate logical weighing of the utility of various response options. This hypothesis makes the important claim that the reactivation of emotional states facilitates logical reasoning, and without guidance from these states, as in the case of Elliot, everyday decisions are costly. Note that this theory, like James’s, emphasizes the important role of feedback from the body (or, at least, body representations) in the generation of emotional states.

Experimental evidence to support aspects of this hypothesis came from studies using the Iowa Gambling Task. In this task, participants are provided an endowment and are told to try to maximize their profit by choosing from one of four decks of cards that have different monetary gains or losses associated with them (Figure 10.14). Unbeknownst to the subjects, card decks A and B are disadvantageous in that selecting from them yields larger short-term rewards but also very large occasional punishers that lead to long-term losses. Decks C and D, by contrast, are advantageous in that they yield smaller short-term rewards but also smaller punishers, leading to higher long-term gains. Over 100 training trials, healthy subjects tend to stop choosing the high-risk decks and reap a monetary reward, whereas patients with vmPFC damage continue to select cards from the risky decks and lose their endowment. When selecting from the risky decks, healthy subjects exhibit an SCR, which Damasio argues is a somatic marker for risky actions in the context of this task, whereas vmPFC patients do not. According to the theory, patients with vmPFC damage have a compromised ability to learn from somatic marker links to risky actions, leading to nonoptimal choices and poor decision-making abilities.

In this scheme, the insula is a key brain region for monitoring the physiological state of the organism (called interoception), and for storing visceral and skeletomotor representations of emotional states that are reinstated

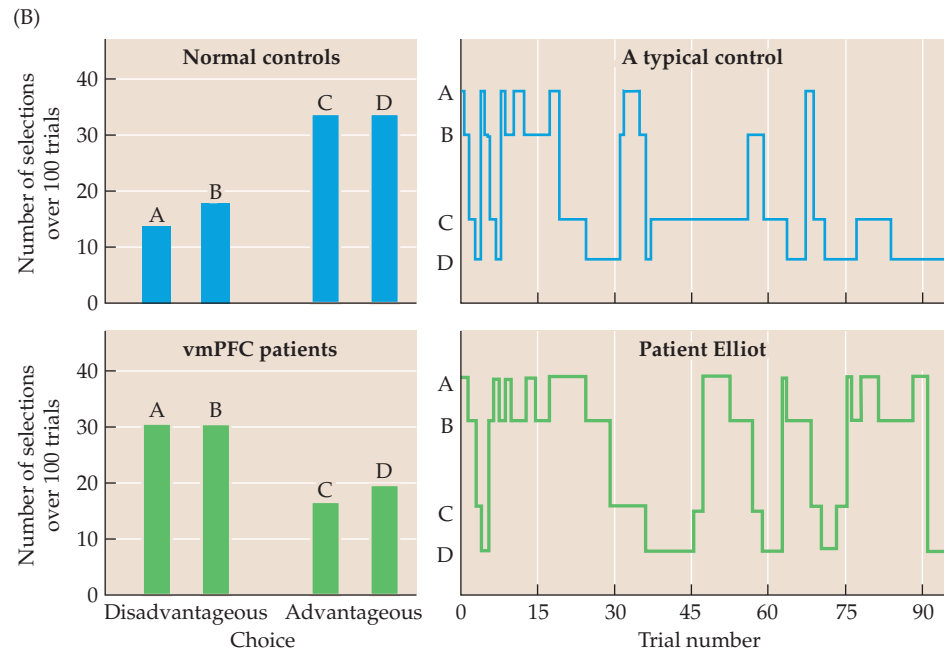
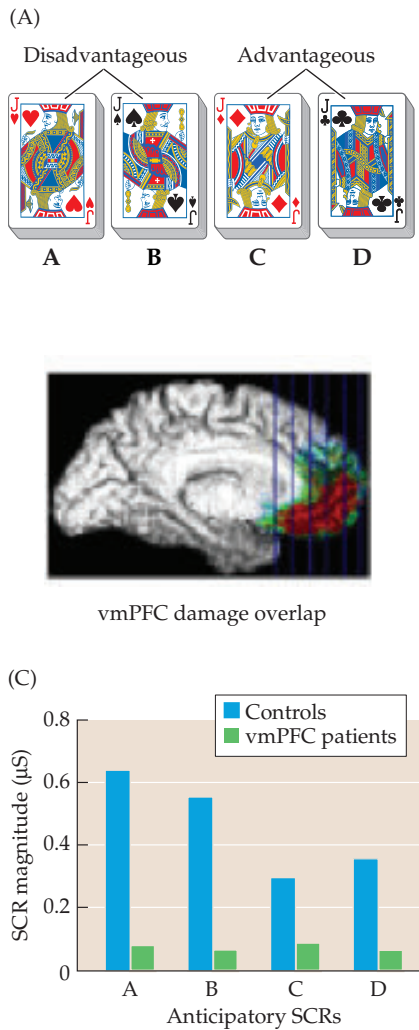


Figure 10.14 The Iowa Gambling Task (A) Across 100 trials, participants turn over cards from four decks that are associated with monetary losses or gains. Selecting cards from decks A and B is disadvantageous, resulting in long-term monetary losses; choosing from decks C and D is advantageous, resulting in long-term monetary gains. (B) Healthy control subjects learn to adapt their choices over time, choosing mostly from the advantageous decks. In contrast, patients with vmPFC damage (inset) continue to choose from the disadvantageous decks throughout the task. (C) Choosing from the risky decks (A and B) elicits anticipatory skin conductance responses (see Box 10A for an explanation of the methodology) from control subjects but not patients. The somatic marker hypothesis argues that such visceral input to decision-making systems is important in order for the organism to learn the motivational value of response options. μ S, microsiemens. (A brain image from Anderson et. al 1999; B,C after Bechara et al. 1994.)

during decision making. The insula is an evolutionarily older cortical region that lies hidden beneath the confluence of the frontal and temporal lobes on the brain's lateral surface. A posterior-to-anterior gradient in the insula provides a pathway for homeostatic regulation (Figure 10.15A). The posterior insula receives ascending information from pain and temperature pathways via the ventromedial thalamus, and parallel input from the cranial parasympathetic nerves, including the vagus and glossopharyngeal nerves, through brainstem projection sites. Information from the posterior insula is fed forward to the mid-insula, where it is integrated with exteroceptive input from somatosensory cortices and limbic regions, such as the amygdala. In primates, the anterior insula contains an additional level of integration, particularly in the right hemisphere, which is interconnected with the anterior cingulate cortex, orbitofrontal cortex, and dorsolateral prefrontal cortex. At each station along the way there is an increasingly complex rerepresentation of the body state that ultimately informs decision making and, in humans, conscious awareness of one's motivational and affective state.

Evidence supporting a role for the insula in body state monitoring and awareness includes studies that correlate anterior insula activation with the ability to detect one's own heartbeat (Figure 10.15B). Moreover, anterior insula activation during fMRI correlates with the subjective experience of temperature changes induced by a thermal probe applied to the hand. Insula damage in some patients who are smokers can even dampen internal cravings for cigarette

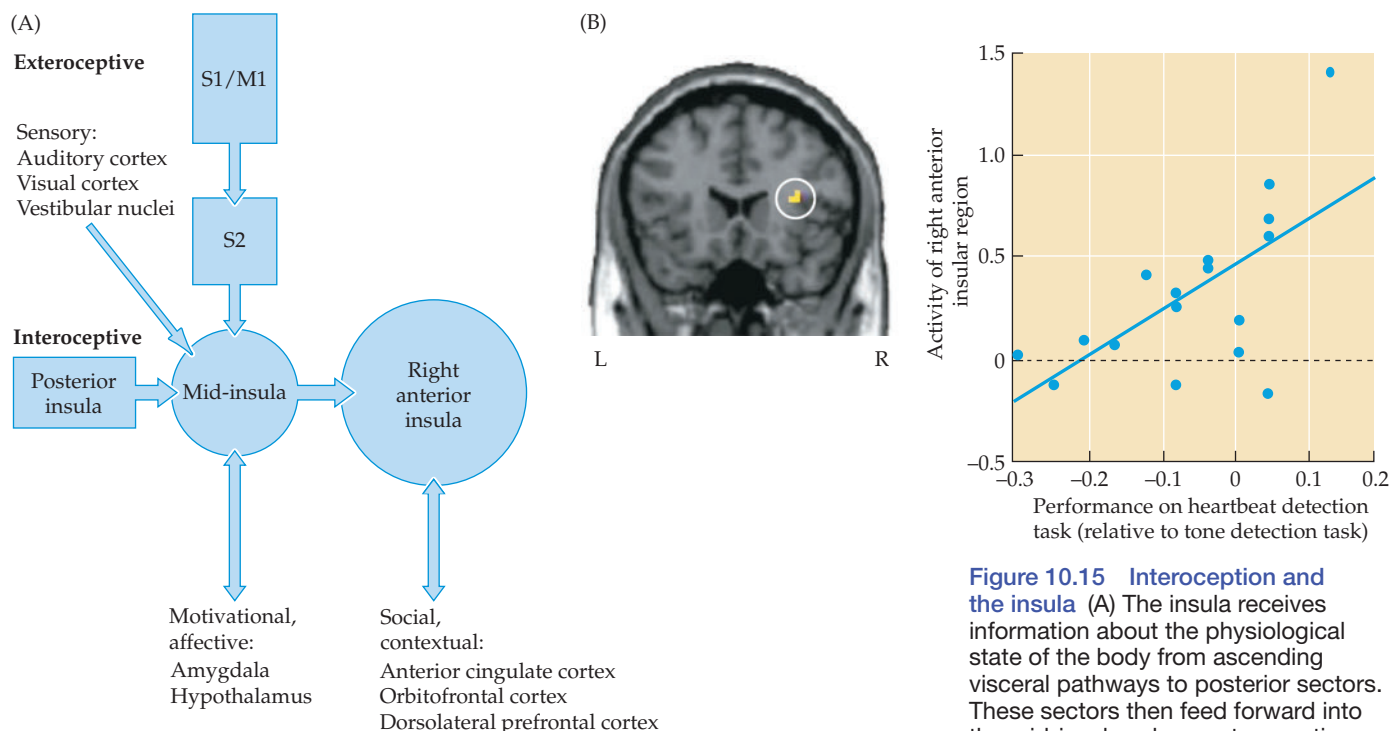


Figure 10.15 Interoception and the insula (A) The insula receives information about the physiological state of the body from ascending visceral pathways to posterior sectors. These sectors then feed forward into the mid-insula, where exteroceptive inputs from somatosensory (S1, S2) and motor (M1) cortices are integrated with motivational and affective inputs. In primates, there is an additional body representation in the anterior insula, particularly the right hemisphere, which integrates visceral-state information with anterior cingulate and prefrontal cortex regions to guide goal-directed behaviors. Each level of body state representation is thought to be more complex and ultimately leads to the conscious experience of motivational and affective state in humans. (B) Across subjects, the magnitude of right anterior insula activity correlates with accuracy in detecting one's own heartbeat relative to a control task. During the heartbeat detection task, participants determined whether or not a series of tones was timed to be in synchrony with their heartbeat (which was achieved by a computer trigger from a pulse meter). The control task required participants to detect a tone that was deviant in pitch from its predecessors in a series. (A after Craig 2007; B after Critchley et al. 2004.)

smoking and promote abstinence; other patients lose their ability to appreciate music, presumably because of difficulties in evaluating the affective meaning of visceral responses to musical passages.

Although some researchers have argued for alternative interpretations of the Iowa Gambling Task and have criticized the “as if” loop clause, which makes the hypothesis hard to falsify, the somatic marker hypothesis is important in bringing the James-Lange idea of bodily feedback into contemporary neuroscience and in emphasizing the potentially beneficial effects of emotion, including negative emotion, in complex cognitive functions. Other contributions of the prefrontal cortex and insula to affective and risky decision making are covered in Chapter 14.

In search of categories of emotional experience

When humans consciously describe their affective state in response to the common question “How do you feel?” they often use verbal labels for specific emotional categories, such as those depicted in Figure 10.2. What information conveyed by the nervous system leads to this subjective experience of an emotion? While the interoceptive pathways just described suggest a general means of intuiting one’s emotional state, whether specific emotions have unique autonomic or neural signatures remains unanswered.

The psychological theories reviewed at the beginning of the chapter predict different ways in which neuroscientists could proceed to answer this question. Recall that dimensional theories suggest that emotional categories emerge from points in a two-dimensional space formed by crossing axes of arousal and valence (or related motivational constructs of approach and avoidance; see Figure 10.3). According to these models, insights would be gained by characterizing brain regions that selectively code for these dimensions. The hemispheric-asymmetry models described earlier use this approach and have found some evidence, derived largely from alpha-band EEG recordings or observations of patients with larger cortical lesions, for the signaling of different valences across the hemispheres of the frontal lobe (with a preference for positive emotions in the left hemisphere and negative ones in the right). However, recall that most individuals

do not show strong EEG asymmetries; indeed, neuroimaging studies of healthy individuals have failed to find a clear dichotomy between positive and negative affect signaling using more spatially refined hemodynamic measures.

In line with categorical theories of emotion, other studies support the idea of neural specialization for discrete emotions in limbic and paralimbic brain regions. For instance, the insula appears to be particularly important for the emotion disgust, which is related to its role in gustatory processing (see Chapter 4). As Figure 10.2 shows, facial reactions of disgust, which curl the upper lip, wrinkle the nose, and protrude the tongue, have evolved in part to facilitate the physical ejection of toxic substances from the oral cavity. Consistent with this idea, disgust is associated with the parasympathetic circuitry that mediates nausea and the vomiting reflex. Some patients with damage to the insula are specifically impaired in their ability to recognize facial and vocal expressions of disgust compared to other emotions (**Figure 10.16A**). Functional neuroimaging studies have confirmed involvement of the insula (and other brain areas) in disgust, including the recognition of someone else reacting to a disgusting situation. Investigators conducting other studies have argued that, given its role in interoception more generally, the insula contributes to the experience of many emotions, for which disgust is a particularly good example because of its evolutionary association with the rejection of toxic substances (see also the discussion of empathy in Chapter 11).

In a similar vein, the amygdala has been specifically linked to fear in numerous studies, including the fear-conditioning research described earlier. Further evidence comes from studies of facial-expression processing in amygdala-lesioned patients, such as S.M., a patient described by Antonio Damasio and his colleagues. In addition to her fear-conditioning deficits (see Figure 10.13A), S.M. has a specific deficit in recognizing fear in facial expressions. Patient S.M. has congenital damage to the amygdala caused by a rare disease (**Urbach-Wiethe syndrome**) that can sometimes produce calcification of structures in the medial temporal lobe. The recognition of facial affect in other amygdala-lesioned patients, while pronounced for fear, can extend to other negative emotions, such as anger and surprise (**Figure 10.16B**). S.M. has particular difficulty extracting information from the eye region of the face, which is critical for identifying the “wide-eyed” feature in expressions of fear. When directed to attend to the eyes alone, S.M.’s ability to identify fear in faces improves. Thus, her deficit in recognizing fear may be secondary to an underlying problem in attending to a facial feature relevant to the evaluation of some emotions. This insight makes strong claims about fear specificity difficult to defend, despite the clear relationship between the amygdala and defensive systems in the brain.

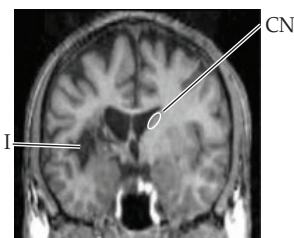
Neuroimaging studies that compare brain activity in response to discrete emotions have yielded mixed results regarding the signaling specificity in regions like the insula and amygdala. Recent meta-analytic studies that have pooled data from hundreds of research articles have failed to find obvious markers of specific emotions. Indeed, involvement of particular structures like the amygdala or insula seems to depend on the nature of the task (e.g., whether it emphasizes emotional evaluation versus experience), the intensity of the emotions elicited, and a host of other factors. Such context-dependent findings challenge efforts to identify neural correlates of emotion categories. Indeed, a lack of clear evidence has compelled some researchers to abandon the notion of emotion categories as having unique neural signatures.

Neuroscientists interested in emotion are now considering novel approaches to identifying the representation of specific emotional states. One strategy is to use multivariate statistics to reveal more complex patterns of neural and autonomic activity that carry information to differentiate emotions. Recall from Chapter 2 that statistical tools such as pattern classifiers can yield additional

(A)

Recognition of Emotion in Facial Expression		
FACIAL EXPRESSION	FACIAL SET 1	FACIAL SET 2
Anger	9/10	5/8
Contempt	—	3/8
Disgust	5/10*	4/8**
Fear	7/10	8/10
Happiness	10/10	8/8
Sadness	8/10	8/8
Surprise	8/10	8/8

Recognition of Emotion in Vocal Expression		
VOCAL EXPRESSION	NONVERBAL SOUNDS	EMOTIONAL PROSODY
Anger	10/20	7/10
Disgust	3/20***	4/10
Fear	14/20	8/10
Happiness	14/20	9/10
Sadness	18/20	7/10
Surprise	15/20	—



(B)

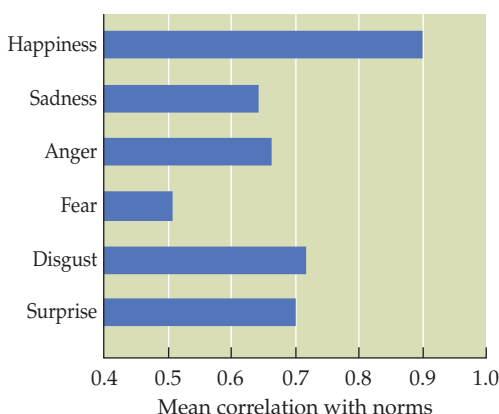


Figure 10.16 Consequences of amygdala and insula damage to emotional evaluation (A) Recognition (by a patient known as N.K.) of emotions in facial and vocal expressions. The extent of the lesion in the left insula (I), caudate nucleus (CN), and putamen is indicated. N.K. correctly chooses the label “disgust” on only a small number of trials. Asterisks indicate accuracy levels significantly below those of healthy controls: *, $p < .05$; **, $p < .01$; ***, $p < .001$. (B) Amygdala damage alters ratings of the emotional intensity of facial expressions. Nine patients with damage to the medial temporal lobe, including the amygdala, were shown pictures of actors portraying each of the six basic emotions. They were asked to rate how intensely various emotions were expressed in each face. Their ratings were then correlated with ratings from healthy control participants. The correlations were high for happy faces but lower for several negative emotions, especially fear. (A after Calder et al. 2000; B after Adolphs et al. 1999.)

insights into complex data sets by analyzing the simultaneous interaction of many variables. Applying these tools involves training a pattern classifier on a set of biological data to discriminate specific states in response to emotional stimuli (such as responses to happy versus sad music). Once trained, the classifier is then tested on a new set of data (using new subjects or new music passages in the same subjects), and its discrimination accuracy is scored. How the data from different brain regions and autonomic indices are relatively weighted and grouped to correctly classify different emotions can provide important clues to their organizational structure. Emotion categories are likely to be “read out” by different combinations of activity patterns (including neural activity in cortical and limbic areas, as well as autonomic changes) that may be weighted in different ways across emotions to specify feelings. This approach could provide an analytic solution to the Cannon-Bard criticism that autonomic indices may be too undifferentiated to discriminate specific emotions.

Such approaches may help validate psychological theories of emotion that postulate different architectures underlying specific emotional experiences. This goal of affective neuroscience—explaining the basis of conscious feelings—depends on further refinement and integration of psychological theories and advanced neuroscientific methods.

Interactions with Other Cognitive Functions

Concomitant with body and brain responses to emotional elicitors, various cognitive processes are altered to help the organism understand, learn from, and cope with the situation at hand. In this section, we describe how emotional processing regions interact with other brain areas that contribute to perception and attention, learning and memory, and self-regulation.

Emotional influences on perception and attention

Processing sensory information that has emotional significance takes priority over processing inconsequential sensory information. Such prioritization is