72 The Human Amygdala and Awareness: Interactions Between Emotion and Cognition

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ABSTRACT Traditional approaches to the study of human cognition considered emotion as a distinct process that could be studied independently. Initial investigations of the neuroscience of emotion supported this distinction by identifying brain structures, such as the amygdala, that appeared to be specialized for emotion. However, recent studies indicate that the amygdala interacts extensively with brain systems linked to cognition and awareness, suggesting a means for the interaction of emotion and cognition. Cognition and awareness can influence the amygdala through the verbal communication of emotion information or the cognitive control of emotional responses. The amygdala can influence cognition and awareness by altering the retention of memory with arousal and facilitating attention and perception. Evidence from cognitive neuroscience suggests that in order to understand the neural systems of cognition, a consideration of its interaction with emotion is necessary.

The relation between emotion and cognition has been a topic of debate since the days of the early philosophers. Aristotle suggested that emotion (the sensitive soul) and cognition (the rational soul) are different grades of the human soul, with only the rational soul (cognition) being unique to humans. The influence of this early philosophical work laid the groundwork for future discussions concerning cognition and its relation to emotion. In the 1980s, the psychologists Robert Zajonc and Richard Lazarus debated the appropriate role for emotion in our understanding of cognition. Zajonc (1980, 1984) argued that emotional responses can occur independently and prior to cognition and awareness, whereas Lazarus (1981, 1984) emphasized that emotional responses are dependent on cognitive interpretations.

Investigations of the neural systems of emotion are beginning to contribute to this debate. The amygdala, a small, almond-shaped structure in the medial temporal lobe, is a brain region that seems to be specialized for emotion (e.g., LeDoux, 1996, 2002). Animal models of the role of the amygdala in emotion processing have suggested it is a critical structure in the acquisition and expression of fear learning. Using a fear conditioning paradigm, researchers such as Joseph LeDoux (1996), Michael Davis (2000), and Bruce Kapp (e.g., Kapp et al., 1992) have traced the pathways for fear learning from stimulus input to response output (see Schafe and LeDoux, this volume). When these paradigms were extended to humans, the separation between emotion and cognition became apparent. Consistent with the animal models, patients with amygdala damage failed to demonstrate normal fear conditioning as assessed by physiological measures of autonomic nervous system arousal (Bechara et al., 1995; LaBar et al., 1995). However, these same patients indicated a cognitive awareness and understanding of the parameters of fear conditioning. The acquisition of the ability to remember and explicitly report the procedures of fear conditioning depended on a neighboring temporal lobe structure, the hippocampus (Bechara et al., 1995).

For example, patient S.P., who had sustained bilateral amygdala damage, and normal control subjects were presented with a blue square paired with a shock to the wrist. After several pairings, the normal control subjects began to show a physiological arousal response to the blue square presented alone, indicating acquisition of a conditioned fear response. S.P. failed to show an arousal response to the blue square. When S.P. was shown the data indicating that she did not demonstrate a normal conditioned fear response as assessed by autonomic arousal, she commented,

> I knew that there was an anticipation that the blue square, at some particular point in time, would bring on one of the volt shocks. But even though I knew that, and I knew that from the very beginning, except for the very first one I was surprised. That was my response—I knew it was going to happen. I expected that it was going to happen. So I learned from the very beginning that it was going to happen: blue and shock. And it happened. I turned out to be right, it happened!

It is clear that S.P. was aware of the fear conditioning procedure, even though she failed to show a conditioned fear response (Phelps, 2002). Patients with hippocampal damage and an intact amygdala show the opposite pattern of results.

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That is, they are unable to explicitly report the relation between the different stimuli, but they show normal conditioned responses (Bechara et al., 1995).

This dissociation between the neural systems of conditioned fear responses and explicit memory for the procedures of fear conditioning suggests that the amygdala can operate independently of awareness and cognitive interpretation. This independence, however, is limited. More recent research suggests that the relationship between the amygdala and cognitive awareness is more complex. In this chapter, I will outline how emotion and cognition interact through the amygdala. The relation between the amygdala and cognitive processes is bidirectional, with the amygdala influencing cognition and awareness, and vice versa.

Cognition to emotion: Cognition and awareness influence the amygdala

The amygdala is often described as a brain structure that is specialized for emotional processing (LeDoux, 2002). Most of the research examining amygdala function across species has highlighted its role in fear; however, more recent research has suggested it may also be involved in the processing of arousing, positive stimuli (e.g., Hamann et al., 1999; LaBar et al., 2001; Anderson, Christoff, Stappen, et al., 2003). There are two primary ways in which cognitive processes have been shown to influence the amygdala.

FEAR LEARNING THROUGH INSTRUCTION In the classic fear conditioning paradigm, a previously neutral stimulus acquires aversive properties by being paired with an aversive event. For instance, a person could be afraid of a neighborhood dog because the dog once bit that individual. This would be analogous to learning with fear conditioning. The previously neutral dog has acquired aversive properties by virtue of the individual's direct, personal experience of a painful bite. However, a person could also acquire a fear response to a neighborhood dog, not because it bit that person but because a neighbor told him or her that it was a mean dog that might bite. This type of symbolic communication is a common means of learning in human experience. In this case, the individual was verbally instructed about the aversive nature of the dog. This is an example of an *instructed fear* paradigm.

Animal models of the role of the amygdala in fear conditioning have suggested that the amygdala is critical in both the acquisition and expression of conditioned fear (LeDoux, 1996; but see also Cahill et al., 1999). In contrast, learning through verbal communication, or instruction, does not require the amygdala. During instructed fear, the subject is told that a particular stimulus, for example a blue square, predicts the possible occurrence of an aversive event, such as a shock to the wrist. This ability to understand and remember the relationship between the blue square and shock depends on neural systems underlying language and episodic memory. Instructed fear results in the subject's acquiring an awareness of the aversive properties of the blue square without any direct, personal aversive experience. The question is, does the amygdala play any role in this cognitive means of fear learning?

In an effort to address this question, subjects participating in a functional magnetic resonance imaging (fMRI) study were instructed that they might receive a mild shock to the wrist when a blue square was presented (the threat stimulus). They were told that they would never receive a shock when a yellow square was presented (the safe stimulus). Although none of the subjects actually received a shock, all of the subjects reported that they believed a shock would be presented (Phelps et al., 2001). Consistent with this subjective report, subjects showed greater physiological arousal during presentations of the threat stimulus (blue squares) than during presentation of the safe stimulus (yellow squares). In addition, subjects showed an increase in blood-oxygen-level-dependent (BOLD) signal in the left amygdala during presentations of the threat relative to presentations of the safe stimulus, indicating amygdala involvement in the processing of instructed fear (figure 72.1).

In an effort to determine the specific role of the left amygdala in instructed fear, brain-injured patients with right, left, or bilateral amygdala damage participated in a similar study. Normal control subjects and patients with damage confined to the right amygdala demonstrated a greater or potentiated startle reflex response to the threat stimulus than to the safe stimulus, an indication of a fear response to verbal threat. Patients whose damage included the left amygdala failed to show a potentiated startle response to the threat stimulus (Funayama et al., 2001).

These results suggest that the left amygdala mediates the physiological expressions of fears that are learned through verbal communication. In such a situation, awareness of the emotional properties of the stimulus, independent of direct experience, results in amygdala involvement. In fear conditioning, awareness is not even necessary for the expression of a learned fear response. Öhman and colleagues (Öhman and Soares, 1993; Esteves, Dimberg, and Öhman, 1994) have shown that subliminal, masked presentations of a conditioned stimulus result in a conditioned response. This begs the question of whether awareness is necessary for the expression of instructed fear learning.

To investigate this question, Olsson and Phelps (in press) assessed physiological fear responses to both masked (subliminal) and unmasked (supraliminal) presentations of stimuli that had been linked to aversive, emotional consequences (i.e., a shock to the wrist). Some of the subjects learned this link through fear conditioning in which the stimulus was paired with the shock. Others learned through

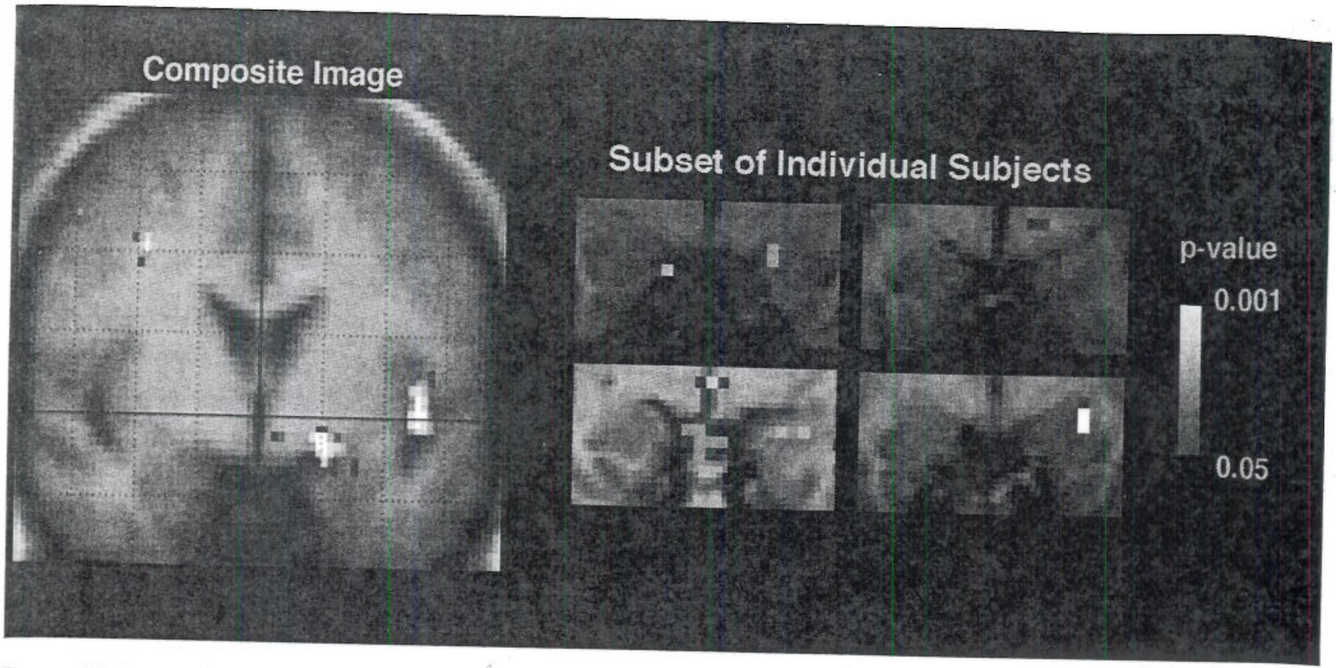

FIGURE 72.1 Activation of the left amygdala in response to instructed fear. Shown are composite activation response to threat versus safe stimuli (left) and selected individual subjects' responses (right). (Adapted with permission from E. A. Phelps et al., Activation of the left amygdala to a cognitive representation of fear. *Nat. Neurosci.* 4:437–441. © 2001 by the Nature Publishing Group.) (See color plate 59.)

instruction. They were told that a particular stimulus predicted a shock. A third group learned this link through observation. They watched a confederate who received a shock paired with a specific stimulus. None of the subjects in the instruction or observation learning conditions actually received a shock. During unmasked (supraliminal) presentations of the stimulus linked to shock, all subjects showed similar levels of physiological arousal (as measured by skin conductance), indicating that fear learning occurred in all conditions. When the stimulus linked with shock was presented briefly and masked (subliminal presentation) subjects who had undergone the fear conditioning procedure continued to show an arousal response, replicating earlier results (Öhman and Soares, 1993; Esteves, Dimberg, and Öhman, 1994). In contrast, subjects who had learned through instruction failed to show any response to the masked stimuli. This suggests that awareness is necessary for the expression of fear learning through instruction. Interestingly, the results from subjects in the observation condition were similar to those in the fear conditioning condition. Vicarious learning through observation resulted in expression of the learned fear response when the stimulus linked to shock was presented both subliminally and supraliminally. The results from the observation learning group are consistent with the idea that vicarious experience may more directly mirror the neural (Rizzolatti, Fogassi, and Gallese, 2002; Carr et al., 2003) and behavioral (e.g., Öhman and Mineka, 2001) effects of learning through personal experience.

Demonstrating the amygdala's involvement in instructed fear learning is important because in everyday human experience, symbolic and vicarious means of communication are a primary means of knowledge transfer. This indicates that animal models of neural systems of fear conditioning may be applicable to a wider range of human behavior. Unlike fear conditioning, learning through instruction requires only the left amygdala for expression, whereas damage to either the right or left amygdala leads to deficits of conditioned fear (LaBar et al., 1995). This laterality difference may be due to the fact that instructed fear depends on left-hemisphere-dominant functions, such as verbal communication and cognitive interpretation (e.g., Gazzaniga, 2000). When learning through instruction or observation, there is an awareness of the emotional properties of the stimulus that is acquired without any direct aversive experience. This suggests that the amygdala is important in the expression of cognitive fears that are imagined and anticipated but never actually experienced.

EMOTION REGULATION Another means by which cognition and interpretation have been shown to influence the amygdala is emotion regulation. Emotion regulation refers to using a cognitive strategy or attentional focus to alter emotional reactions. It is not uncommon in everyday human experience to attempt to modulate a negative emotional state by focusing on nonemotional or positive aspects of a situation. The common phrase "the glass is half-full" (as opposed to half-empty) refers to a strategy of focusing on positive rather than negative possible interpretations or consequences of a situation. This is an example of the emotion regulation strategy of reappraisal.

Typical studies of reappraisal ask subjects to view scenes or film clips of emotional events (see Gross, 2002, for a review). Subjects are instructed either to simply attend to the stimuli or to reinterpret the events depicted in a way that makes them less negative. For example, if a scene shows a group of people crying outside of a church, a common interpretation is that the scene depicts a funeral. Another possible interpretation is that the scene depicts a wedding in which there are tears of joy. Subjects who are instructed to reappraise the scene are encouraged to focus on possible nonemotional or positive interpretations of the scenes. Subjects who successfully reappraise the emotional significance of an event report less distress and show decreases in physiological arousal responses to the negative emotional stimuli.

In an effort to assess whether cognitive reappraisal can alter amygdala function, Ochsner and colleagues (2002) presented subjects with pictures of emotional scenes and asked them either to attend to the pictures or to reappraise the situations depicted. Consistent with previous studies, subjects rated their subjective reaction to the emotional, negative scenes as less negative on the reappraisal trials relative to the attended trials. Using fMRI, Ochsner and colleagues found that the presentation of negative scenes on the attended trials resulted in more activation of the amygdala relative to the reappraisal trials (see Schaefer et al., 2002, for a similar finding). During the reappraisal trials there was relatively more activation of the left lateral prefrontal cortex (LPFC), a region that has also been implicated in the executive control of working memory (e.g., Smith and Jonides, 1999; Miller and Cohen, 2001). There was a negative correlation between these two brain areas. Subjects who showed greater left LPFC activation in response to viewing the negative scenes on the reappraisal (vs. attend) trials also showed less amygdala activation (figure 72.2). Our current understanding of the neuroanatomical connections between the amygdala and the prefrontal cortex suggests that the LPFC may not be altering amygdala function through direct projections (McDonald, 1991; Stefanacci and Amaral, 2002) but by a more indirect route. This research suggests that the ability to engage executive control processes during reappraisal can change the amygdala's response.

In addition, studies examining the influence of attentional demands on amygdala function have found that in limited circumstances, a distracting attentional task can also influence the amygdala response. Although most studies examining the effect of attention on the amygdala have reported that the allocation of attention has no effect on the strength of the amygdala response to an emotional stimulus (Vuillemier et al., 2001; Anderson, Christoff, and Panitz, 2003), there are exceptions. Pessoa, McKenna, and Gutierrez (2002) used a demanding attention task that required subjects to respond to stimuli presented in the peripheral region of perceptual space. This task was conducted while fearful faces and neutral faces were presented at the center of the screen. When attentional demands were minimal, there was greater amygdala activation in response to the fearful versus neutral faces. However, the amygdala response to fearful faces was diminished during the peripheral attention task (see also Anderson, Christoff, Panitz, et al., 2003). This highlights a situation where the focus of attention can influence amygdala processing. Along with the reappraisal study mentioned earlier, these studies indicate that the amygdala's reaction to an emotional situation can be altered by cognitive demands and interpretation.

Summary: Cognition to Emotion Studies of fear conditioning in humans suggest that the amygdala plays a role in the acquisition and expression of learned fear, irrespective of awareness of the emotional properties of the stimulus and more cognitive means of learning. These results highlight the independence of the neural systems of emotion and cognition. However, this evidence from fear conditioning does not rule out a role for awareness and cognitive intrepretation in amygdala processing. Both symbolic means of emotional learning (i.e., language) and cognitive strategies can alter amygdala function. It appears that cognition may influence the amygdala and emotional reactions in a range of circumstances.

Emotion to cognition: The amygdala's influence on cognition and awareness

The demonstration that the amygdala's response can depend on cognition indicates the complex relationship between emotion and cognition. There is also evidence to suggest that cognition and awareness can depend on the amygdala. In many ways, the amygdala is well situated to influence cognition. There are direct projections between the amygdala and both mnemonic and sensory processing regions (e.g., Stefanacci and Amaral, 2000; Amaral, Behniea, and Kelly, 2003). Consistent with its neuroanatomical connectivity, it has been suggested the amygdala can influence cognition and awareness in two different ways: by modulating memory and by modulating attention or perception.

The Amygdala and Episodic Memory The most important development in memory research that has emerged in the last 50 years is the recognition of many kinds of memory and corresponding memory systems. In humans, the most dominant type of memory is episodic memory (also called declarative or explicit memory), which allows us to be aware of past events. Episodic memory depends on the hippocampal complex for acquisition, and damage to this brain

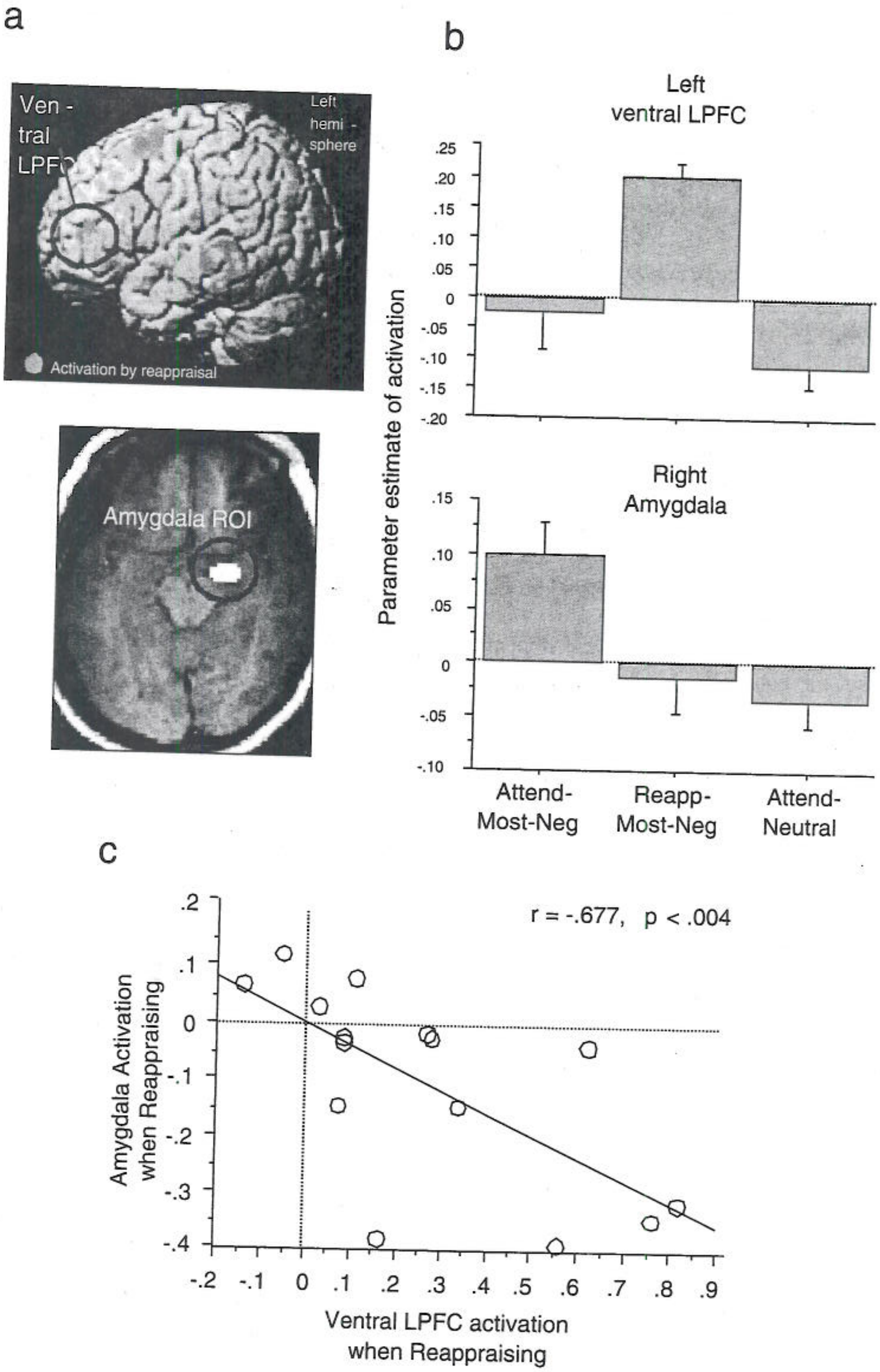

FIGURE 72.2 (*a*) Activation of the left, ventral LPFC during reappraisal versus attended trials (top) and right amygdala activation during attended versus reappraisal trials (bottom). (*b*) Parameter estimates of activation to the right amygdala and left, ventral LPFC. (*c*) Scatterplot depicting the correlation activation of the amygdala and ventral LPFC for reappraisal versus attended trials. (Adapted with permission from K. N. Ochsner et al., Rethinking feelings: An fMRI study of the cognitive regulation of emotion. *J. Cogn. Neurosci.* 14:1215–1229. © 2002 by the Society for Neuroscience.) (See color plate 60.)

region results in extreme difficulty in everyday functioning. One of the ways in which the amygdala can alter cognition and awareness is by modulating the hippocampal memory system. Research on emotion and memory has shown that discrete or mild arousal can enhance episodic memory performance (e.g., Christianson, 1992). Consistent with this behavioral data, McGaugh and colleagues (e.g., McGaugh, 2000) have identified a pathway by which the amygdala can influence hippocampal processing with arousal. In a series of studies, they have shown that the amygdala modulates the consolidation of hippocampal-dependent memories. Hippocampal consolidation is a slow process by which memories become more or less stable over time. By enhancing consolidation with arousal, the amygdala is altering the storage component of episodic memory formation (McGaugh et al., 1992).

To demonstrate that the amygdala modulates memory storage, McGaugh and colleagues disrupted or enhanced amygdala processing in rats *after* encoding, and examined the effect of arousal on memory. For example, Packard and Teather (1998) gave rats a maze-learning task that depended on the hippocampus. Immediately after learning, some of the rats received intra-amygdala injections of amphetamine and others received saline. Those rats whose amygdalas were pharmacologically excited after learning showed better retention for the maze. The mechanism by which the amygdala modulates consolidation is related to the neurohormonal changes that occur with arousal. Physiological arousal is linked to activation of the β-adrenergic system in the amygdala. Drugs that block the action of the β-adrenergic system also block the effect of arousal on episodic memory in both rats (e.g., McGaugh et al., 1992) and humans (e.g., Cahill et al., 1994). McGaugh (2002) and colleagues have suggested that one of the adaptive functions of having a long consolidation process for the storage of hippocampal-dependent memories is to allow time for the arousal response to enhance the retention of events linked to emotional consequences.

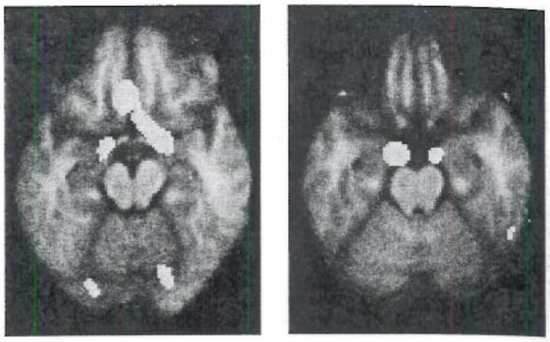

Figure 72.3 Amygdala activity during encoding correlated with subsequent memory for positive (left) and negative (right) picture stimuli. (Adapted with permission from S. B. Hamann et al., Amygdala activity related to enhanced memory for pleasant and aversive stimuli. *Nat. Neurosci.* 2:289–293. © 1999 by the Nature Publishing Group.)

A number of studies have shown that the human amygdala plays a role in the long-term recollection of arousing events. Brain imaging studies have observed a correlation between the strength of the amygdala response to an emotional stimulus at encoding and the likelihood of successful recollection at a later time (e.g., Cahill et al., 1996; Hamann et al., 1999; Canli et al., 2000). Patients with damage to the amygdala fail to show arousal-enhanced memory (e.g., Cahill et al., 1995). If arousal, via the amygdala, is modulating the storage of episodic memory, there should be different forgetting curves for arousing and nonarousing stimuli. This has been demonstrated in a number of behavioral studies (see Christianson, 1992). In a classic study, Kleinsmith and Kaplan (1963) presented subjects with word-digit pairs. Half of the words were emotional and arousing and half were neutral. Subjects were given a cued recall task in which they were presented with the word and asked to recall the digit. Some of the subjects were given the memory task immediately after encoding and others were tested a day later. Comparing across the groups, there was forgetting over time for the neutral word-digit pairs, but memory for the arousing word-digit pairs did not diminish over time. Consistent with the idea that the amygdala enhances consolidation or storage processes, patients with amygdala damage, unlike normal controls, show similar patterns of forgetting for arousing and neutral words (LaBar and Phelps, 1998). In addition, using positron emission tomography (PET), Hamann and colleagues (1999) found that amygdala activity at encoding for positive and negative arousing scenes predicted recognition success 1 month later (figure 72.3). There was no relation between amygdala activation and memory performance on an immediate test of recollection. Thus, both research in patients and neuroimaging studies support a role for the human amygdala in the storage of episodic memories.

By influencing the retention of hippocampal-dependent memories, the amygdala alters the information that can be recollected over time. Long-term memory and awareness for events can be modulated by the amygdala. Although many other factors influence the retention of both emotional and nonemotional events (e.g, Phelps et al., 1998; Schacter, 2001), arousal, via the amygdala, is one of the mechanisms by which emotion can influence cognition and awareness.

Emotional Modulation of Attention/Perception

Research on the neural systems of memory and emotion suggest that the amygdala can modulate the storage component of episodic memory. It has also been suggested that emotion can affect the encoding stage of memory by altering attention or perceptual processing (e.g., Christianson and Loftus, 1991). Although there is no direct evidence that the

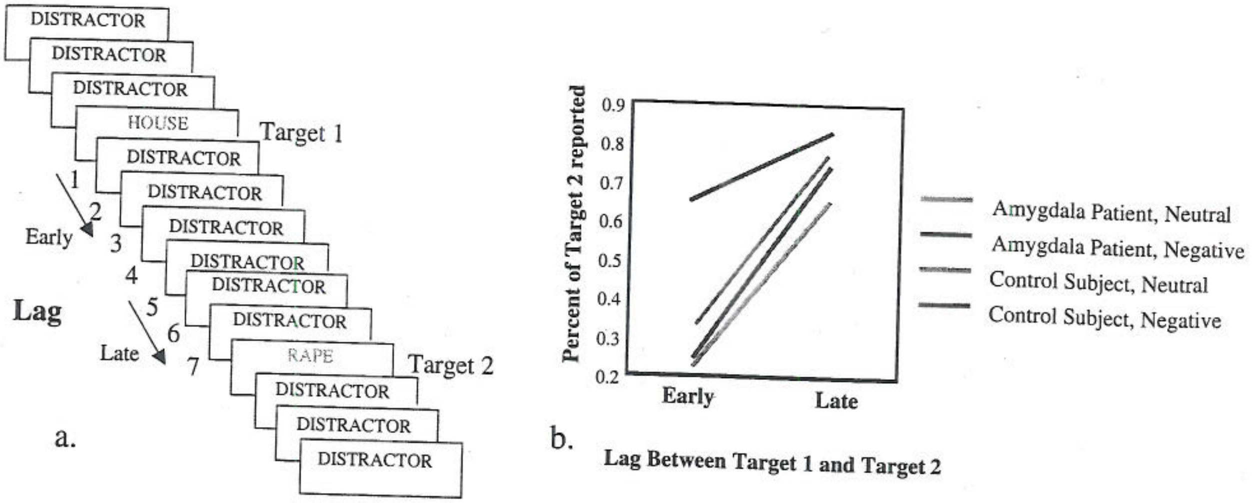

FIGURE 72.4 (*a*) Schematic illustration of the attentional blink paradigm with an emotion word in the second target position. (*b*) Percent correct identification of target 2 reported in the early and late lag periods for negative and neutral words. Results are for normal control subjects and a patient with bilateral amygdala damage. (Adapted with permission from A. K. Anderson and E. A. Phelps, The human amygdala supports affective modulatory influences on visual awareness. *Nature* 411:305–309. © 2001 by the Nature Publishing Group.) (See color plate 61.)

amygdala affects memory by enhancing encoding, there are data indicating that the amygdala may play a role in the modulation of attention or perception.

The claim that emotion can influence attention or perception has been documented in behavioral studies. Emotion has been shown both to capture attention (e.g., Fox et al., 2001) and to enhance attentional processing (e.g., Öhman, Flykt, and Esteves, 2001), depending on the task. At present, there is evidence that the human amygdala may play a role in the enhancement of attentional processing. This evidence comes from studies of the attentional blink. In this task, subjects are presented with stimuli very quickly. For instance, a series of 15 words may be presented at a rate of one every 10 ms. In this type of rapid serial visual presentation (RSVP) paradigm, the stimuli are presented too quickly for the subjects to encode each item, and subjects are unable to report the items that appeared. However, if the subjects are told that they can ignore most of the items, for instance those printed in black ink, and selectively focus on a few items, for instance those printed in green ink, then the subjects are usually able to attend selectively to the few target items and report them (figure 72.4*a*). The ability of the subjects to report more than one item in an RSVP paradigm depends on the timing of the presentation of the items. If a second target item appears soon after the first target item (i.e., during the early lag period), subjects have more difficulty reporting the item than if a second target item is presented later in the visual stream (during the late lag period). It is as if noticing and encoding the first target creates a short refractory period during which it is difficult to notice and encode the second target item. This brief refractory period is described metaphorically as an attentional blink.

Anderson and Phelps (2001) manipulated the emotional salience of the second target item. When the second target presented in the early lag period was an emotional, arousing word it was more likely to be reported than a neutral word. There was an attenuation of the attentional blink effect with emotion. In order to assess the role of the amygdala in the enhancement of attentional processing, patients with right, left, and bilateral amygdala damage performed the attentional blink paradigm with emotional and neutral items in the second target position. Unlike normal control subjects, patients with left amygdala damage showed similar decrements in reporting neutral and emotional items when those items appeared in the early lag period (figure 72.4*b*). These patients failed to exhibit the normal emotional attenuation of the attentional blink effect.

The attentional blink results indicate that in situations where attentional resources are limited, emotional stimuli are more likely to reach awareness. It has also been demonstrated that patients with attentional neglect are more likely to perceive emotional stimuli in the neglected field than neutral stimuli (Vuilleumier and Schwartz, 2001), consistent with the idea that perceiving emotional stimuli requires fewer attentional resources. The amygdala plays a role in this enhanced attentional processing. However, it is unclear exactly how the amygdala may affect performance.

One possibility is that the amygdala enhances attentional performance by altering perceptual encoding. Research with nonhuman animals has suggested two possible mechanisms by which the amygdala may influence perception. The first mechanism suggests that emotional learning, such as fear conditioning, can alter the cortical representation of stimuli linked to potential aversive consequences (Weinberger,

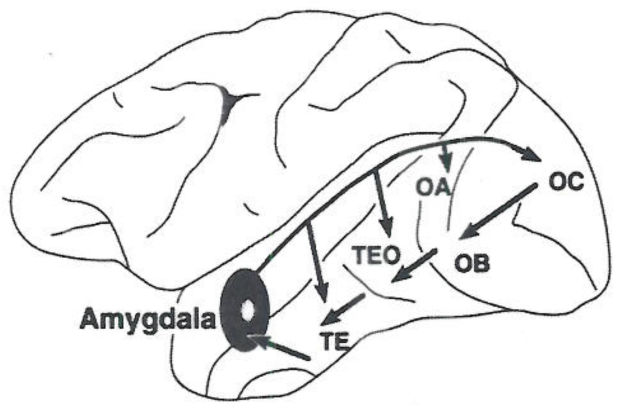

FIGURE 72.5 Schematic illustration of the relationship of the amygdala with visually related cortices in of the temporal and occipital lobes. (Adpated with permission from D. J. Amaral et al., Topographic organization of projections from the amygdala to the visual cortex in the macaque monkey. *Neuroscience* 118:1099–1120. © 1992 by the Society for Neuroscience.)

1995). For instance, if a tone of a specific frequency is repeatedly paired with a shock, eventually the cortical representation of that tone is changed in such a way that the rat is now especially sensitive to tones of that frequency. Through emotional learning, the amygdala is providing feedback allowing sensory cortical representations to be tuned for enhanced perception of emotional stimuli.

The second mechanism by which the amygdala can alter perceptual processing is more general. The amygdala has reciprocal connections with sensory cortical processing regions (figure 72.5). LeDoux and colleagues have shown that there are two pathways by which the amygdala can receive information about the emotional significance of a stimulus (see Schafe and LeDoux, this volume). The amygdala receives crude sensory input quickly via a subcortical route that bypasses cortical processing. It also receives more fully processed sensory information from cortical sensory regions. Because of the reciprocal connections with sensory cortex, the amygdala can provide feedback to perceptual systems in the presence of emotional stimuli. Through projections back to sensory cortical regions, the amygdala may enhance further perceptual processing in the presence of emotional or threatening stimuli, resulting in an overall heightened perceptual vigilance (Kapp, Supple, and Whalen, 1994; Whalen, 1998).

Although the evidence for a role of the human amygdala in the modulation in perception is not conclusive, several recent neuroimaging, patient, and behavioral studies are consistent with this idea. For instance, neuroimaging studies have demonstrated that the amygdala can respond to emotional stimuli presented subliminally, so quickly that subjects are unaware of their presentation (Morris, Öhman, and Dolan, 1998; Whalen et al., 1998). It has also been shown that there is enhanced activation of the visual cortex to visual emotional stimuli (e.g., Kosslyn et al., 1996). The magnitude of this enhanced visual cortex activation in response to emotional stimuli is correlated with the strength of amygdala activation in response to these same stimuli (Morris, Buchel, and Dolan, 2001). Together, these neuroimaging results are consistent with a mechanism by which the amygdala receives information about the emotional nature of a stimulus early in visual processing and then modulates further perceptual processing by influencing activity in the visual cortex (see figure 72.5).

Although subjects' lack of awareness does not necessarily indicate a subcortical pathway for perception, these neuroimaging results suggest that the amygdala detects emotion early in stimulus processing. Studies of patients with blindsight provide more direct support for the idea that the emotion can be perceived without complete perceptual processing. Damage to the striate cortex in the occipital lobe, an early visual region, can result in blindsight. Affected patients appear blind, but they are able to detect some simple visual stimuli through a pathway that bypasses the striate cortex. Recent studies have demonstrated that patients with blindsight can detect emotion in facial expressions (de Gelder, Vroomen, and Pourtois, 1999). They also show physiological evidence of fear conditioning to visually conditioned stimuli (Hamm et al., 2003). These results indicate that emotional information from visual stimuli that are not fully processed by the visual cortex can be perceived, consistent with the idea of a subcortical pathway for conveying emotional information to the amygdala.

Studies in patients with blindsight and neglect suggest that the amygdala may pick up on emotional information that has not been fully perceptually processed. But these studies do not specify how perception could be affected by these early signals. A few recent studies have started to explore the precise perceptual mechanisms that may be influenced by emotion or the amygdala. An fMRI study by Vuillemier and colleagues (2003) showed that the amygdala is particularly sensitive to low-spatial-frequency visual information in emotional stimuli. It is suggested that the subcortical pathway for conveying information about emotional, threatening stimuli to the amygdala may primarily code low-spatial-frequency information. In addition, Ling and colleagues (2004) recently demonstrated that emotion can enhance visual contrast sensitivity, particularly when cued by covert attention. These recent studies are starting to specify exactly how emotion and the amygdala can influence perceptual processing.

Our understanding of the role of the human amygdala in perception and attention is rapidly progressing, but the precise mechanisms are still not known. Studies on the role of the amygdala in attention provide support for the notion that the amygdala modulates enhanced awareness for emotional events in situations with limited attentional resources. Although there is not yet any evidence that the human amyg-

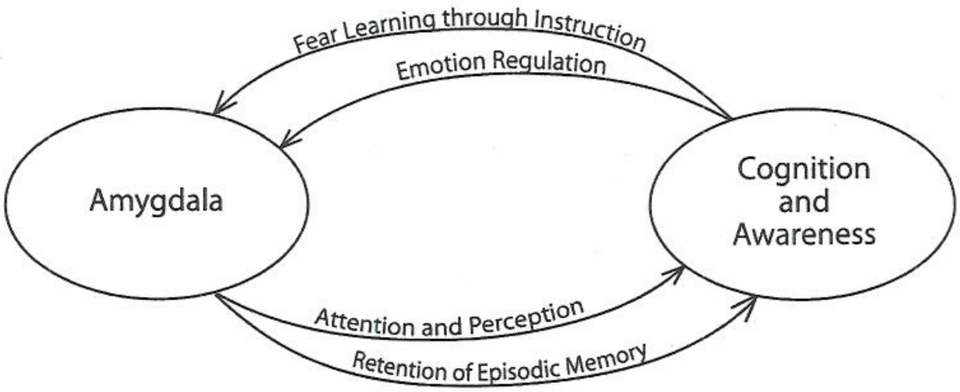

FIGURE 72.6 Schematic illustration of the current understanding of the complex interactions between the amygdala and cognition and awareness.

dala underlies any specific perceptual process, the bulk of evidence from a range of techniques strongly supports the hypothesis that the amygdala enhances perceptual processing when cued by emotional stimuli.

By modulating attention and perception with emotion, the amygdala gives priority to emotionally salient stimuli in cognitive processing. Emotion, via the amygdala, alters the ease with which stimuli are available to conscious awareness. How this enhanced awareness influences cognition broadly remains to be determined. Through its influence on attention and perception, the amygdala could potentially have a significant impact on a range of cognitive processes, including working memory, categorization, and episodic memory encoding.

SUMMARY: EMOTION TO COGNITION Evolutionary arguments support the idea that emotion should influence cognitive processes. In order to survive in a changing environment, it is especially important that an organism remember those stimuli and events that are linked to emotional consequences. It is also important to be particularly vigilant and aware of emotional stimuli in the environment in order to allow for quick assessment and reaction. Research examining the role of the human amygdala suggests it may play a critical role in enhancing memory, attention, and perception with emotion.

Conclusions

Research on the cognitive neuroscience of emotion has provided a fresh perspective on the debate concerning the role of emotion in cognition. Traditionally, emotion has not been considered an important component in efforts to understand cognition (Neisser, 1976; Anderson, 1999). Because certain brain structures seem to be specialized for processing emotion, such as the amygdala, it could be argued that the traditional approach of studying emotion independently from cognition is justified. However, as outlined in this chapter, there are complex interactions between neural systems that are more or less specialized for cognition and emotion (figure 72.6).

Learning through fear conditioning seems to depend on the amygdala, with little influence from cognition and awareness. However, cognition and awareness influence the amygdala in a number of ways. Fear learning through symbolic means (verbal communication) can alter amygdala function, and the expression of this learning depends on the amygdala. This relationship illustrates that the amygdala plays a role in the expression of fears that are generated through imagination. Cognitive and attentional strategies that regulate emotional reactions have also been shown to change the amygdala's response to a situation. This relationship demonstrates cognitive control over an amygdala response. The amygdala can also influence cognition and awareness. By modulating the retention of episodic memory with arousal, the amygdala helps determine which information in the environment will be accessible for later conscious recollection. The amygdala also influences online stimulus processing by altering the ease with which emotional information can reach awareness with limited attentional resources. The amygdala's influence on attention may be related to enhanced perceptual processing with emotion.

Researchers' efforts to understand the function of the human amygdala have led to the conclusion that understanding the neural systems of emotion requires a consideration of cognition and vice versa. A separation between emotion and cognition seems artificial when one is trying to understand everyday human function in a social environment. Although emotion may be considered a specific topic within the study of cognition, much as memory and attention are considered separate topics, research on the cognitive neuroscience of emotion highlights the fact that our efforts to understand the neural systems of cognition must include the study of emotion.

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