Neural Perspectives on Emotion: Impact on Perception, Attention, and Memory

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In behavioral science, investigations of the structure and impact of emotion have traditionally occurred within the domains of social, personality, or clinical psychology. Studies of cognition, inspired by the computer metaphor and the information processing approach (Miller, 2003), have generally focused on characterizing functions such as perception, attention, and memory assuming little role for emotion. This traditional divide between emotion and cognition has been debated in psychological science (Lazarus, 1984; Zajonc, 1984). Underlying these debates is the notion that the mechanisms of emotion and cognition can be separated and investigated independently.

This assumption has been challenged as behavioral science has started to incorporate methods from neuroscience. One of the striking characteristics of the brain is the extensive connectivity between regions thought to underlie independent processes. This is particularly apparent in studies of emotion. Investigations of neural connectivity have shown that the amygdala, a region thought to be more or less specialized for emotion, has extensive connections throughout the brain (Young, Scannell, Burns, & Blakemore, 1994). The amygdala is a small, almond-shaped structure in the medial temporal lobe that both receives input from and projects to a wide array of brain regions implicated in cognitive processes, including those underlying perception, attention, and memory. What is the role of these connections? An examination of neural circuitry suggests that emotion and cognition are intertwined at several stages of stimulus processing. From an evolutionary perspective, this makes sense. The purpose of emotion is to highlight what is relevant (Frijda, 1986) and potentially important for survival. Given this, we might expect the mechanisms of cognition to be tuned to highlight emotional events.

In this chapter, we review recent research exploring the relation between cognition and emotion that has been informed by advances in cognitive neuroscience. Although the range of processes that comprise emotion (e.g., Scherer, 2005) is represented in several regions and circuits of the brain (Dagleish, 2004), we focus on insights from studies of the amygdala. The amygdala, because of its wide connectivity, is suggested to play a primary role in the modulation of cognition in the presence of emotional events (Anderson & Phelps, 2000). Furthermore, due to its prominence in studies of emotion across species, the amygdala is one of the most thoroughly investigated brain regions in studies of emotion (e.g., Aggleton, 1992; LeDoux, 1996). In particular, we focus on how studies of the human amygdala have enhanced our understanding of emotion's impact on perception, attention, and memory.

EMOTION'S INFLUENCE ON ATTENTION AND PERCEPTION

The influence of emotional stimuli on attention and perception has been documented using a variety of techniques. Emotion is thought to influence attention and perception in two distinct ways. First, emotion has been found to enhance or facilitate attentional and perceptual processes, thereby increasing the salience of emotional stimuli. Second, emotion has been shown to capture our attention, leading to impaired processing of nonemotional stimuli present in the environment.

Emotion Enhances Attention and Perception

A number of psychological and psychophysical paradigms have demonstrated emotion's facilitation of attention and perception. Often these are paradigms used by vision and attention researchers to show that a particular stimulus or class of stimuli has preferential access to awareness as a result of its saliency. One example is visual search, in which observers search for a target in an array of distracters. When the target

and the distracters are equally salient, people take longer to find the target because they must inspect each item in the array to determine whether it is a target or a distracter. However, when a target is salient compared to surrounding distracters, it is immediately distinguishable and is said to "pop out" (Treisman & Gelade, 1980). Ohman and colleagues (Ohman, Flykt, & Esteves, 2001; Ohman, Lundqvist, & Esteves, 2001) used the visual search paradigm to show that emotional targets (e.g., threatening faces, snakes, or spiders) pop out when embedded in an array of neutral distracters (e.g., friendly faces, flowers, or mushrooms) but the reverse is not true for neutral targets. It is proposed that an enhanced ability to detect a snake in a field of flowers may have been advantageous to survival and subject to evolutionary pressures. A similar ability to detect a flower in a pit of snakes would confer little evolutionary advantage on the possessor.

Other studies demonstrating emotion's facilitation of attention have adopted paradigms used by vision researchers to suppress awareness of visual stimuli in order to determine whether affective stimuli are less susceptible to such suppression. The attentional blink (AB; Raymond, Shapiro, & Arnell, 1992) is one such paradigm. In the AB, observers view a continuous stream of rapidly changing stimuli (e.g., 6 to 20 items per second) and indicate when one of two target stimuli appears. Typically, observers experience an attentional blink for a short period (180 to 450 ms) during which the presentation of a second target goes unnoticed. Researchers interested in the influence of emotion on attention have manipulated the affective value of the targets in the AB paradigm. Anderson and Phelps (2001) found that when the target presented during the AB period is an emotionally significant word, it is often detected, suggesting that emotional stimuli have preferential access to awareness at times when attention is limited (Anderson, 2005; Anderson & Phelps, 2001). Interestingly, Anderson and Phelps (2001) also found that patients with lesions of the amygdala do not show enhanced detection of emotional stimuli, indicating a role for the amygdala in our enhanced sensitivity to affectively salient events.

Another visual suppression paradigm used to demonstrate that emotional stimuli receive preferential access to awareness (Yang, Zald, & Blake, 2007) is continuous flash suppression (CFS; Tsuchiya & Koch, 2005), a variant of binocular rivalry. In binocular rivalry, two different images are presented to each of the eyes at the same time in overlapping regions of visual space. The brain, unable to merge the dissimilar images, compromises by switching between the two so that only one is perceived at a time. If the images are equally salient, the dominant percept will switch back and forth between the two images. If the images are not equally salient, then one will tend to dominate over the other. In CFS, the visual properties of the stimulus presented to one eye are manipulated so that it is constantly dominant—preventing the input to the other eye from reaching awareness. Yang et al. (2007) used this paradigm to show that fearful faces (both upright and inverted) were less susceptible to CFS than neutral or happy ones. Other studies involving binocular rivalry and emotional faces or aversively conditioned stimuli have found similar effects in that the emotional stimuli dominate perception compared to their neutral counterparts (Alpers & Gerdes, 2007; Alpers, Ruhleder, Walz, Mühlberger, & Pauli, 2005).

These studies demonstrate that when attentional resources are limited, emotional stimuli have preferential access to awareness. Emotion's facilitation of awareness also extends to the perception of nonemotional stimuli in the vicinity of emotional stimuli. This was demonstrated using an attentional cuing paradigm (Posner, 1980) in which fearful or neutral faces were used to cue the location of a subsequent target (Phelps, Ling, & Carrasco, 2006). The target was a simple gabor patch that varied in its visibility from trial to trial by altering its contrast. Observers had to indicate the orientation of the target. Cuing with a fearful face enhanced the perceived contrast of the subsequent target relative to cuing with a neutral face. That is, observers were able to identify the orientation of lower contrast targets when they were preceded by a fearful cue. There was an overall effect of the fear face cues on perception as well as a positive interaction between emotion and attention, providing support for separate but interacting mechanisms through which emotion and attention enhance perception. Orientation discrimination is a basic perceptual function known to rely on early visual cortex for processing. This suggests that the mechanism whereby emotion enhances perception and interacts with attention may be through the modulation of early visual areas by attentional and emotional systems.

An examination of the connectivity of the brain also suggests the amygdala may play a role in modulating the visual cortex at multiple levels. As displayed in Figure 42.1, tract-tracing studies in macaque monkeys found that the majority of the ventral visual sensory cortex (from area V1 to area TE) receives direct, topographically organized projections from the amygdala (Amaral, Behniea, & Kelly, 2003). This topographic organization indicates that the amygdala's input to the visual cortex does not serve as a diffuse, general modulator, but rather it has the spatial specificity to selectively activate different (presumably stimulus-relevant) visual regions. Further study of the termination pattern of the amygdala projections to visual cortices has revealed that they are most likely excitatory and modulatory in nature (Freese & Amaral, 2005, 2006), resembling other feedback projections into the visual
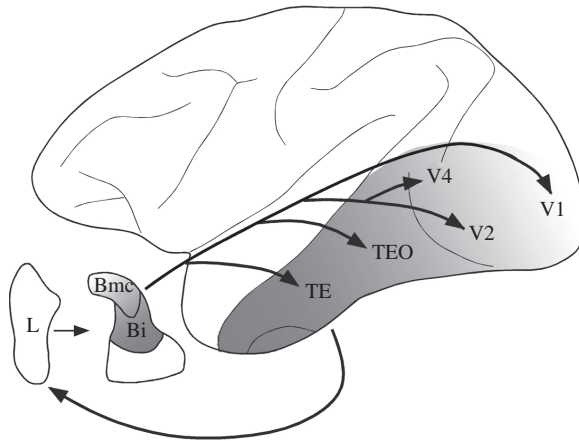
Figure 42.1 The connectivity of subregions of the amygdala (L, Bi, Bmc), and ventral visual cortical regions (V1, V2, V4, TEO, TE) in the macaque monkey.

Note: From "The Organization of Projections from the Amygdala to Visual Cortical Areas TE and V1 in the Macaque Monkey," by J. L. Freese and D. G. Amaral, 2005, *Journal of Comparative Neurology, 486,* p. 314. Reprinted with permission.

cortex that are known to facilitate neuronal responses to visual stimuli (Hupé et al., 1998, 2001). This pattern of connectivity between the amygdala and the sensory cortex is not unique to vision. Other neuroanatomical studies have found a similar topographic pattern of amygdala input to the sensory auditory cortex (Yukie, 2002) and evidence of projections to the early somatosensory cortex (Amaral & Price, 1984).

These anatomical studies suggest a pathway by which the amygdala may facilitate attention and perception in the presence of emotional stimuli by modulating processing in sensory cortices. Consistent with this, functional brain imaging studies have shown amygdala involvement in the enhancement of responses to emotional stimuli in the visual cortex. Morris and colleagues (Morris, Buchel, & Dolan, 2001; Morris, Friston, et al., 1998) reported a correlation between the magnitude of amygdala activation in response to fearful faces and fear-conditioned stimuli, relative to neutral stimuli, and the magnitude of the enhanced response to these emotional stimuli in the visual cortex. Vuilleumier, Armony, Driver, and Dolan (2001) found that activation in the fusiform face area (FFA), a region in the ventral visual stream involved in face processing (Kanwisher, McDermott, & Chun, 1997), was modulated both by attention and emotion. They also looked for regions in which there was an interaction between emotion and attention and found that this was the case in the primary visual cortex. These functional imaging studies show a correlation between amygdala activation and enhanced responses in the visual cortex to emotional stimuli, but do not indicate that the amygdala is mediating this enhanced

cortical response. By combining lesion and brain imaging techniques, Vuilleumier, Richardson, Armony, Driver, and Dolan (2004) were able to demonstrate that the enhanced response in the visual cortex to emotional stimuli may be the result of feedback from the amygdala. They showed a lack of visual cortex activation to fearful versus neutral faces in patients with focal damage to the amygdala. This finding supports the proposed role of the amygdala suggested by the anatomical connectivity studies and strongly implicates the amygdala in the enhancement of sensory cortical responses to emotionally salient stimuli.

One possible means by which the amygdala may modulate sensory cortical regions is through reciprocal connections. The amygdala receives input from the sensory cortex that allows the detection of an emotionally salient event and then, in turn, it modulates further perceptual processing. However, findings that emotionally salient stimuli both induce and, *almost simultaneously,* are the target of their *own* modulatory influences on perception and attention imply that the amygdala might also receive information about these stimuli rapidly so that it can act on early sensory representations. Researchers investigating auditory fear conditioning in rats have identified a critical, rapid, subcortical route to the amygdala from the auditory thalamus (see Phelps & LeDoux, 2005, for a review). The existence of a similar visual subcortical route from the retina to the amygdala via the superior colliculus and pulvinar nucleus of the thalamus has been suggested (see Ohman, Carlsson, Lundqvist, & Ingvar, 2007, for a review). In support of this subcortical visual pathway for the rapid detection of emotional events, studies in monkeys have shown that the earliest neural responses in the amygdala to visual stimuli occur 60 ms after the presentation of the stimulus, which suggests little to no cortical processing (Nakamura, Mikami, & Kubota, 1992).

In humans, strong evidence for a subcortical route for conveying the emotional nature of visual stimuli to the amygdala has been difficult to obtain because of the correlational nature of functional imaging techniques and the difficulty in interpreting null results. However, some studies have reported responses to fear faces in the proposed subcortical route (i.e., pulvinar and superior colliculus) and not in cortical regions to subliminal, unseen stimuli, as well as increased functional connectivity between the amygdala and these subcortical nuclei for unseen versus seen stimuli (Lidell et al., 2005; Morris, Friston, & Dolan, 1997; Morris, Ohman, & Dolan, 1998, 1999). Another imaging study by Vuilleumier, Armony, Driver, and Dolan (2003) took advantage of the hypothesis that a subcortical route would be more sensitive to crude, low spatial frequency visual information, whereas visual cortical processing is necessary to detect detailed, high-spatial frequency information. They showed

that the superior colliculus, the pulvinar nucleus, and the amygdala are all preferentially sensitive to differences in low-spatial frequency information between emotional and neutral faces. In contrast, visual areas involved in face processing were more sensitive to the high-spatial frequency content of emotional faces. These imaging studies provide some support for the existence of a visual subcortical route and indicate that it may be an important component of the amygdala's sensitivity to emotional stimuli. However, they are correlative in nature and therefore cannot be used to establish causality.

The strongest evidence for the existence of a visual subcortical route involved in the processing of emotional stimuli comes from patient studies involving blindsight. Patients with blindsight have lesions in their primary visual cortex and as a result are unaware of stimuli that are presented to the corresponding visual field. However, they maintain a residual ability to discriminate certain stimuli in the absence of conscious perception (Weiskrantz, 1990). This residual visual ability is thought to rely on the retino-colliculo-pulvinar pathway. De Gelder, Vroomen, Pourtois, and Weiskrantz (1999) showed that a patient with blindsight was able to distinguish between faces with different emotional facial expressions presented in the blind visual field. Morris, DeGelder, Weiskrantz, and Dolan (2001) used functional imaging in the same patient to demonstrate that amygdala sensitivity to fearful faces presented in the blind field remained intact while sensitivity in cortical regions involved in face processing did not. Moreover, the authors found that this amygdala sensitivity to subliminal, unseen fearful faces was correlated with activity in the superior colliculus and pulvinar, further supporting a role for these subcortical regions in the processing of emotional stimuli.

Emotion Captures Attention, Impairing Perception

The majority of work examining the effects of emotion on attention and perception has focused on the enhanced processing of emotional stimuli. However, this enhancement does not come without a price. Much like talking on a mobile phone while driving impairs one's driving ability (Strayer, Drews, & Johnston, 2003), focusing attention on one stimulus often comes at the perceptual cost of others (e.g., Carrasco, 2006; Pestilli & Carrasco, 2005). Is the attentional facilitation observed for emotional stimuli accompanied by an attentional cost for other, nonemotional, stimuli in the environment? A few studies have examined this question and found that perception of neutral stimuli is indeed impaired in the presence of emotional

stimuli, a phenomenon referred to as the *emotional capture of attention*.

As discussed, previous research has shown that emotional stimuli are more resistant to the attentional blink than neutral stimuli (Anderson & Phelps, 2001). Using modified versions of this task, other research groups have found that emotional stimuli can also exacerbate the AB. The important difference between these two types of findings lies in the placement of the emotional stimulus. In contrast to the AB paradigm used by Andersen and Phelps (2001), Most, Chun, Widders, and Zald (2005) placed emotional stimuli in a stream of distracters and investigated what would happen when an emotional distracter preceded a neutral target. They found that observers detected the target less often when it followed an emotional distracter at a delay of 200 ms, but not at a delay of 800 ms. A second study by the same group (Smith, Most, Newsome, & Zald, 2006) found a similar impairment for targets following an aversively conditioned stimulus. These findings not only provide support for the emotional capture of attention, but they also show that this capture is transient, lasting less than 800 ms. The effects of this emotional capture may be reduced using cognitive strategies, though the rate of success depends on observers' propensity to avoid harm (Most et al., 2005).

The emotional capture of attention, as demonstrated by the impaired processing of neutral stimuli, has been observed in a range of paradigms (e.g., Mathews & MacLeod, 1985), but these studies do not isolate the component of attention that is mediating this effect. In an effort to determine if emotion results in faster shifts of attention, or perhaps a difficulty in disengaging from a detected emotional stimulus to process other stimuli, spatial attention was examined with the Posner cuing paradigm (Posner, 1980). Observers fixate on a central point while a stimulus is briefly flashed (100 ms) on either the left or right side of the screen. This stimulus automatically shifts covert attention to that side of the screen. Immediately after, a target dot appears on either the left or right side, and the observer's task is to indicate on which side the target appeared. The dependent measure is reaction time, which is expected to be longer for invalid trials (when the location of the stimulus and target are not the same). Fox, Russo, Bowles, and Dutton (2001) used this paradigm to present neutral, positive, or negative words and examine whether the affective value of the words altered observers' ability to detect the subsequent target dot. They found that on valid trials, where the target appeared in the same location as the words, there was no difference in reaction time for the three types of words. This suggests that emotion does not result in faster shifts of attention to the target location. However, on invalid trials, reaction times were significantly longer for trials with negative words compared

to those with neutral or positive words. This finding indicates once attention has shifted to the location of a negative stimulus, it is harder to disengage attention from this location to respond to nonemotional targets elsewhere. They also found that this disengagement cost for threat-related stimuli was greater in subjects who scored highly on scales of state-anxiety.

There have been very few studies of neurobiological mechanisms mediating the capture of attention, and it is not yet known precisely what role the amygdala may play in this effect (Pessoa, 2008). However, a study by Pourtois and Vuilleumier (2006) identified one component of the neural circuitry underlying the emotional capture of attention. They used electroencephalography (EEG), which provides high-resolution temporal information about neural events, and functional magnetic resonance imaging (fMRI) in two experiments using a Posner-style cuing paradigm. They found that enhanced EEG responses to targets following valid fearful faces in early visual cortex were preceded by heightened responses in regions of contralateral parietal lobe that are known to be involved in attentional control to that region of visual space. This suggests that emotional stimuli can modulate attentional control mechanisms. In addition, in the fMRI study, they found evidence of an "invalidity" effect. When a face was flashed to one side of the screen, the region of the parietal attentional control network that would be engaged in shifting attention to the other side of the screen showed less activation when this face had a fearful expression (relative to neutral). In other words, fearful faces on invalid trials captured attention, producing disengagement costs reflected in fMRI activity in the parietal cortex and resulting in impaired processing of the target. These data provide convincing evidence that emotional stimuli can modulate the neural systems involved in attentional control, effectively capturing attention and impairing processing for other, nonemotional, stimuli in the environment.

EMOTION'S INFLUENCE ON MEMORY

In the *Principles of Psychology,* William James (1890) suggested, "An impression may be so exciting emotionally as almost to leave a scar upon the cerebral tissues" (p. 670). James was reflecting on the common insight that emotion creates memories that have unique qualities and are often perceived to be more vivid and accurate than memories for mundane events. Both psychological and neuroscience studies of emotion have specified a number of ways emotion can change memory. It has been proposed that emotion can alter all three stages of memory: encoding, storage,

and retrieval. Episodic memory depends on the orchestration of a number of brain regions, most critically the hippocampal complex (Eichenbaum, 2002; Squire & Zola-Morgan, 1991), which lies adjacent to the amygdala in the medial temporal lobe (see Figure 42.2). In the presence of emotional events, the amygdala may modulate the neural circuitry of memory by influencing a range of mnemonic functions.

Emotion's Impact on Encoding

The first stage of memory, encoding, refers to the processes that occur when a stimulus is first encountered. At encoding, factors that influence attention and perception will also influence later memory (Craik, Govoni, Naveh-Benjamin, & Anderson, 1996). As outlined, emotion can influence attention in two ways. Emotion facilitates attention and perception for emotional events, or those cued by emotion, and also captures attention resulting is less processing of some other, nonemotional aspects of the environment. In memory research, it has been proposed that this resulting "narrowing-of-attention" around the emotional aspects of an event results in enhanced memory for details within this narrow focus of attention and worse memory for other details (Easterbrook, 1959). This pattern of memory performance has been observed in a number of psychological studies (Heuer & Reisberg, 1992). For instance, studies of weapon focus have demonstrated how the presence of a threatening stimulus in a scene, such as a gun, can result in enhanced memory for details of the gun and stimuli in close proximity, and impaired memory for
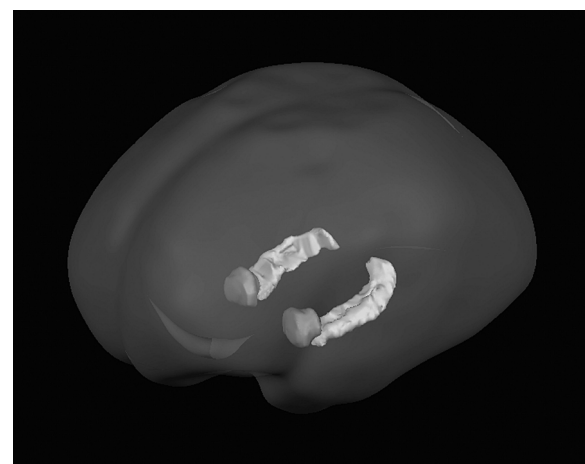

Figure 42.2 The amygdala (left, darker grey) and hippocampus (right, lighter grey).

Note: Adapted from "The Human Amygdala and Awareness: Interaction of the Amygdala and Hippocampal Complex," by E. A. Phelps, 2004, *Current Opinion in Neurobiology, 14,* p. 199. Reprinted with permission.

other scene details, such as the face of the person holding the gun (Kramer, Buckhout, & Eugenio, 1990). A study by Adolphs, Tranel, and Buchanan (2005) found that the amygdala may mediate this trade-off in memory for details. They observed that patients with amygdala damage fail to show the normal memory enhancement for details of the gist of the central aspects of an emotional scene, with no difference in memory for peripheral details.

Emotion Modulates Consolidation

By influencing encoding, emotion is altering the nature of the stimuli that are available for the second stage of memory: retention or storage. Although the storage stage is essentially passive in that it is simply the interval between encoding and retrieval and requires no action or thought, the existing evidence suggests that it is actually a neurobiologically active process. For a period of time after encoding, the neural representation that leads to a lasting memory trace can either be strengthened, in which case the event is available for later retrieval, or weakened, in which case the event may be forgotten. This time-dependent process that helps strengthen or solidify memories is consolidation. One of the primary means by which emotion can influence memory is by enhancing the consolidation or storage of emotional events (McGaugh, 2000).

Kleinsmith and Kaplan (1963) demonstrated the impact of emotion on memory storage in a classic study in which subjects were presented with word-digit pairs. The words varied in how arousing they were. At later testing, subjects were presented each word and asked to recall the digit. Some subjects were given the memory test immediately after encoding and others were given the memory test after a variety of delays ranging from 20 minutes to 1 week. When comparing recall for the digits paired with the high- versus low-arousal words, arousal impaired the immediate cued recall of the digits, but by 45 minutes after encoding, memory for digits paired with high-arousal words was significantly enhanced. This effect emerged because recall for digits paired with high-arousal words did not decline, and even improved slightly, whereas recall for the digits paired with the low-arousal words showed the standard delay dependent decay in memory (Ebbinghaus, 1885/2003). This enhanced retention with arousal is consistent with an active storage process that is modulated by emotion (see also Berlyne, 1969; Heuer & Reisberg, 1992).

In an elegant series of studies in nonhuman animals, McGaugh (2000) outlined the neural mechanism mediating this enhanced retention for arousing events. Physiological arousal is linked to the release of stress hormones from the adrenal gland, including epinephrine and cortisol, a glucocorticoid. Epinephrine indirectly activates β-adrenergic receptors in the amygdala, which in turn play an important role in mediating the impact of arousal on glucocorticoid receptors in the hippocampus. This critical role for the amygdala in modulating hippocampal consolidation has been demonstrated with a range of neuroscience techniques that impact the different components of this proposed neural mechanism. The evidence that the amygdala's modulatory role impacts the consolidation or storage of hippocampal-dependent memories comes from studies showing that influencing β-adrenergic receptors or lesioning the amygdala immediately *after* memory encoding alters arousal's impact on memory consolidation. McGaugh suggested that a possible role for a slow consolidation process is to allow the emotional impact of an event, which may unfold after the event occurs, to modulate subsequent memory. In this way, emotional events, which may provide important lessons for future survival, are more likely to be retained.

Evidence from studies with humans suggesting a role for the amygdala in the modulation of hippocampal consolidation has been observed with a number of cognitive neuroscience techniques. Brain imaging studies have reported that activation of the amygdala at encoding can predict later memory for emotional stimuli (Cahill et al., 1996; Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000). The amygdala has direct projections to the anterior portion of the hippocampus (Stefanacci, Suzuki, & Amaral, 1996). The activation of the amygdala and anterior hippocampus is correlated during the encoding of emotional scenes that were later remembered (Dolcos, LaBar, & Cabeza, 2004). Although these studies do not indicate if the enhanced amygdala activation observed at encoding is related to altered encoding or consolidation processes, it has been demonstrated that this activation is more strongly correlated with delayed compared to immediate recall (Hamann, Ely, Grafton, & Kilts, 1999). It has also been reported that patients with amygdala damage fail to show the normal enhancement of memory with arousal (Cahill, Babinsky, Markowitsch, & McGaugh, 1995). Amygdala damage results in similar forgetting curves for arousing and neutral stimuli, in contrast to normal control subjects who show enhanced retention for arousing stimuli. This lack of a retention difference for arousing and neutral stimuli is consistent with a role for the amygdala in modulating storage or consolidation (LaBar & Phelps, 1998). Finally, in a direct test of the neurochemical mechanisms thought to mediate the amygdala's influence on hippocampal consolidation, Cahill, Prins, Weber, and McGaugh (1994) administered a drug that blocked β-adrenergic receptors. The administration of this drug also blocked the normal enhanced memory observed for arousing stimuli, consistent with animal models.

One of the difficulties in isolating an effect of altered storage or consolidation for arousal on memory performance is

separating encoding from consolidation because memory retrieval reflects their combined effects. In a clever series of studies, Cahill, Gorski, and Le (2003) were able to isolate an effect of arousal on memory consolidation in humans by manipulating arousal immediately *after* stimulus encoding. In these studies, subjects were presented with scenes that had an emotional meaning (valence), but did not elicit a strong arousal response. Immediately after these scenes were encoded, half of the subjects were given an arousal manipulation and the other half a control manipulation. In one study, this arousal manipulation required subjects to place their arms in freezing water (cold pressor stress), while control subjects were required to place their arms in warm water. In a second study, subjects were given a drug that elicits physiological arousal (epinephrine), while control subjects were given a placebo (Cahill & Alkire, 2003). Both arousal manipulations resulted in enhanced memory for the low-arousal scenes immediately followed by arousal relative to the control manipulation. This effect of postencoding arousal on later memory only emerged for scenes that have an emotional meaning or valence. Memory for neutral scenes did not improve as a result of postencoding arousal. These results are consistent with the proposal that arousal modulates the consolidation or storage of events independent of emotion's impact on encoding, but suggests some limits on the types of stimuli that can elicit this effect.

Emotion Enhances the Subjective Sense of Remembering at Retrieval

Through its impact on attention, emotion facilitates encoding of salient aspects of the environment, sometimes at the decrement of nonemotional details. Those details that are encoded are then more likely to be retained via arousal's influence on memory consolidation. The results of these combined processes are observed at the final stage of memory, retrieval. However, studies of the retrieval of emotional events have also reported an effect of emotion on memory that is not readily apparent from its influence on encoding and consolidation. Independent of its effect on memory accuracy, emotion also enhances the subjective sense of remembering. Remembering is not only accompanied by the retrieval of past events, but also by the subjective judgment that the memory is or is not vivid, detailed, and held with confidence in its accuracy. These qualities make up the subjective sense of remembering.

Brown and Kulik (1977) coined the term "flashbulb memory" to describe the impact of emotion on recollection. By examining memories for highly emotional, public events, such as the assassination of John F. Kennedy, they determined that emotion results in highly vivid, detailed,

and confident memories, almost as if one is looking at a picture taken with a flashbulb. Brown and Kulik assumed these vivid recollections were also highly accurate because memory confidence is generally linked to memory accuracy (Lindsay, Read, & Sharma, 1998). However, when researchers examined memories for emotional public events over time, they found that these memories were often highly inaccurate in their details and were distinguished primarily by their sense of vividness and confidence in their accuracy (Neisser & Harsch, 1992; Talarico & Rubin, 2003). In other words, the subjective sense of remembering was enhanced for emotion, even when accuracy for details of the memory was not. Laboratory studies have reported a similar effect. When subjects are asked to indicate if they "remember" previously presented emotional or neutral scenes along with details of the encoding context, or simply "know" that the scene is familiar, they are more likely to indicate they "remember" emotional scenes, even when there is no difference in overall accuracy for emotional and neutral scenes (Ochsner, 2000; Sharot, Delgado, & Phelps, 2004).

The neural systems mediating the impact of emotion on the subjective sense of remembering have been explored using this remember/know paradigm. Studies examining both memory encoding (Dolcos, LaBar, & Cabeza, 2004) and retrieval (Sharot et al., 2004) have reported that different neural mechanisms may mediate the subjective judgment of remembering for emotional and neutral scenes. For neutral scenes judged as "remembered," stronger activation is observed in the posterior parahippocampal cortex, relative to those judged as "known." This region of the parahippocampal cortex is also known as the parahippocampal place area (PPA; Epstein & Kanwisher, 1998) and has been shown to be involved in the processing of scenes and the encoding of scene details (Kohler, Crane, & Milner, 2002). Because subjects in this task are asked to judge if their recollection of the scene is accompanied by encoding details, it is not surprising that activation of this region would be linked to this judgment. What is surprising is that emotional scenes judged as "remembered" versus "known" do not show differential activation in this region. Instead, activation of the amygdala differentiates this mnemonic judgment for emotional scenes. In other words, there is a double dissociation. Even though subjects are making the same subjective assessment of their memory, different medial temporal lobe structures seem to be mediating this judgment for emotional and neutral stimuli.

A similar pattern was observed when examining memories for September 11, 2001 (Sharot, Martorella, Delgado, & Phelps, 2007). Subjects who were in Manhattan on 9/11 were asked to retrieve personal autobiographical events from that day or the summer of 2001. They then rated these memories for arousal, vividness, confidence, sense

of reliving, and "remembering." About half of the partici-pants showed enhanced ratings for the 9/11 versus sum-mer memories. What differentiated those subjects whose 9/11 memories yielded these "flashbulb" qualities is prox-imity to the World Trade Center (WTC) during the terrorist attack. Those closest to the WTC not only rated their mem-ories as more vivid, but also were more likely to report experiencing threat and direct sensory experience of the attack (e.g., seeing, hearing, smelling). An examination of the neural systems underlying the retrieval of 9/11 versus summer memories revealed that proximity was correlated with greater amygdala activation and decreased posterior parahippocampal activation, mirroring the pattern observed in laboratory studies using the remember/know paradigm.

The enhanced subjective sense of memory for emo-tional events suggests a possible functional role for this mnemonic judgment. Our judgments about our memories can influence how we use them to guide our future actions. If we are confident in the accuracy of a memory for an event in the past, we may act decisively when encountering a similar situation in the future. However, if a memory is held with less confidence, we might seek to gather more information before acting. It has been proposed that emo-tion's impact on the subjective sense of remembering, in the absence of absolute veridicality, may serve to promote faster and less ambiguous action in the face of familiar, emotional situations (Phelps & Sharot, 2008). Even if a memory is inaccurate in its details, the strong memory for the gist of an emotional event may be sufficient to enhance the vividness and confidence of memory and allow for fast action in a similar circumstance in the future.

SUMMARY

By incorporating neuroscience methods in our efforts to understand human behavior a different perspective on behavioral science is beginning to emerge. Psychologists and other behavioral scientists have divided the study of human behavior into distinct domains, which have yielded unique subsets of academic departments, conferences, and journals. These boundaries, however, are not recog-nized by the brain. As the range of behavioral disciplines incorporating neuroscience methods expands, so does the necessity to adopt a broader and more integrative approach to the study of human behavior.

In this chapter, we highlighted how neuroscience research has informed our understanding of the relation between emo-tion and cognition. In light of our knowledge of the brain and its connectivity, it no longer appears feasible to clearly differentiate emotion processes from cognitive functions.

Emotion and cognition interact at all stages of information processing, from early perception to higher reasoning. By highlighting what is important, emotion provides a frame-work by which cognition can be tuned to respond adap-tively to environmental demands.

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