

Memory and Emotion

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Although the concept of memory has existed for thousands of years, its systematic study was launched in the 1880s by the seminal experiments of the German philosopher Hermann Ebbinghaus. Through careful assessments of his own memory, Ebbinghaus forged the way for the field of memory research by demonstrating that humans' ability to retain information over time could be studied scientifically. It is telling that Ebbinghaus' studies involved the intentional memorization of nonsense syllables: He believed that to understand memory processes, one should study retention of information void of meaning or personal importance. Although memory researchers seemed to embrace Ebbinghaus' views on this issue for nearly a century, over the past couple of decades there has been increased emphasis on examining memory for personally important experiences and for events that evoke emotional reactions.

Throughout this chapter, we will use terms like "emotional stimuli" as a shorthand to denote information in the environment that elicits a change in the internal, affective state of the organism. The focus of this chapter is on how these internal changes affect memory. Behavioral examinations of explicit (conscious) memory for emotional experiences have revealed three broad influences of emotion on memory: on the number (quantity) of events remembered, the subjective vividness (quality) of the remembered events, and the amount of accurate detail remembered about prior experiences. This chapter will explore these three lines of investigation, highlighting both the general conclusions that have emerged from the research and the open questions that remain. We will conclude with a brief discussion of recent research suggesting an effect of emotion on implicit (unconscious) memory. In addition to presenting the behavioral data and cognitive theories of emotional memory, this chapter also will include discussion of relevant neuroimaging and

neuropsychological research that has been influential in examining the extent to which memory for emotional experiences is supported by processes distinct from those that support memory for nonemotional events.

Emotion's Influence on the Quantity of Remembered Information

Individuals often remember more emotional events than nonemotional ones. Within the laboratory, recall rates are higher for positive and negative stimuli than for neutral stimuli (reviewed by Buchanan & Adolphs, 2002; Hamann, 2001). This finding has been documented with a variety of stimuli, including words, sentences, pictures, and narrated slide shows (e.g., Bradley et al., 1992; Cahill & McGaugh, 1995; Kensinger et al., 2002). Similar effects have been noted within the autobiographical memory literature. For example, when individuals are asked to generate memories in response to cue words, the retrieved memories often will be rated as personally significant and emotional (e.g., Conway, 1990; Rubin & Kozin, 1984). There also are many instances in which positive and negative events are more likely to be recognized than neutral ones, although the recognition memory advantage is seen less consistently than the recall advantage (reviewed by Christianson, 1992), a finding that we will return to later in this chapter.

A topic of ongoing investigation is the extent to which the valence of an event (whether it elicits positive or negative affect) influences the likelihood that the event is remembered, and virtually every conceivable outcome has been observed. Often, the boost in recall or recognition is comparable for positive and negative stimuli (e.g., Bradley et al., 1992; Kensinger et al., 2002). However, in some studies, particularly those assessing memory for verbal or pictorial stimuli presented within a laboratory setting, negative items are more likely to be recalled than positive ones (e.g., Charles et al., 2003; Ortony et al., 1983). Yet other studies, generally those assessing memory for autobiographical experiences or information encoded in reference to the self, have

revealed the opposite pattern: a greater tendency to recall positive events than negative ones (e.g., D'Argembeau et al., 2005; Linton, 1975; Matt et al., 1992; White, 2002).

Some of these conflicting findings with regard to the effect of valence on the likelihood of remembering information may be explained by the proposal that memory mechanisms have evolved to facilitate the encoding and retrieval of the affective information that is most relevant to one's goals (Lazarus, 1991; LeDoux, 1996). Remembering a negative experience often may be relevant to survival or well-being, because re-experiencing the event will help a person plan for (or avoid) its future re-occurrence (LeDoux, 1996). In these instances, more attention may be paid to the negative item, thereby enhancing memory for this negative information. However, there likely are instances in which positive events are just as relevant, or more relevant, to one's goals as negative events. Indeed, when positive and negative stimuli are equally related to one's current concerns they show similar capture of attention (Riemann & McNally, 1995). Furthermore, there is some evidence that individuals (e.g., older adults) who seek positive goal states show enhanced memory for positive as compared to negative events (reviewed by Mather & Carstensen, 2005).

Researchers have focused intensively on whether this mnemonic benefit for personally relevant and emotional information results from the engagement of processes that are related specifically to the processing of emotional information, or whether the memory boost stems from engagement of the same processes that allow accurate remembering of neutral information. Although parsimony favors the hypothesis that the same processes are recruited to remember emotional and neutral information, lesion and neuroimaging studies suggest that the amygdala, an almond-shaped region of the medial temporal-lobe, is specifically related to memory for emotional, but not for neutral, information. Patients with damage to the amygdala do not show a memory boost for emotional information: They are no more likely to remember positive or negative events than they are to remember neutral ones. The absence of the emotional memory

enhancement has been reported in patients with focal amygdala damage (e.g., Adolphs et al., 1997; Brierley et al., 2004; Cahill et al., 1995; Markowitsch et al., 1994) and in individuals with amygdala atrophy caused by Alzheimer's disease (e.g., Abrisqueta-Gomez et al., 2002; Kensinger et al., 2002; Kensinger et al., 2004). In these individuals, the amount of the amygdala damage corresponds with the degree of blunted emotional memory enhancement (Mori et al., 1999).

While these neuropsychological studies have demonstrated the necessary contribution of the amygdala to emotion-mediated memory enhancements, they do not allow investigation of the memory stage(s) during which the amygdala exerts its influence. Neuroimaging methods provide a way to address this issue: Researchers can examine the neural processes associated with the successful encoding of emotional information (by comparing brain activity while encoding items that will later be remembered versus items that will later be forgotten) or with the successful retrieval of emotional information (by comparing brain activity associated with correct endorsements versus misses). These neuroimaging studies have demonstrated that the amygdala plays a fundamental role during the encoding of emotional information. Individuals who show the greatest amygdala activity during the viewing of emotional items are those who show the greatest emotional memory enhancement (Cahill et al., 1996). Moreover, for a particular individual, those emotional items that elicit the greatest amygdala activity during encoding are those that will be most likely to be remembered (reviewed by Hamann, 2001; Phelps, 2004; Kensinger, in press). Although the vast majority of neuroimaging studies have examined the amygdala's role in encoding *negative* information, a recent neuroimaging study indicated that the amygdala was equally active during the successful encoding of positive and negative high-arousal items (Kensinger & Schacter, 2006a). This finding is consistent with research demonstrating that the amygdala is important for processing reward-related information as well as threat-related information (see Davidson & Irwin, 1999; Baas et al., 2004) and may primarily respond based on

the arousal, and not the valence, of information (Anders et al., 2004; Anderson et al., 2003; Garavan et al., 2001; Hamann et al., 2002; Kensinger & Schacter, 2006c; Royet et al., 2000; Small et al., 2003; but see Buchanan et al., 2006 for evidence that the right amygdala may be more involved in memory for negatively valenced than positively valenced information).

The amygdala, of course, does not act in isolation. It has been proposed that, once activated during the processing of emotional information, the amygdala is able to modulate the functioning of sensory cortices to assure that the information is attended (reviewed by Dolan & Vuilleumier, 2003) and to enhance mnemonic consolidation processes in the hippocampal formation to increase the likelihood that emotional information is retained in a stable memory trace (reviewed by McGaugh, 2004; Phelps, 2004). The amygdala is well suited for these modulatory functions, as it is one of the most extensively connected subcortical regions of the brain, with links to numerous cortical and subcortical regions (Amaral et al., 1992; Amaral, 2003).

Recent neuroimaging studies have provided strong evidence for these modulatory effects of the amygdala. In one study investigating the links between amygdala activity and visual attention, patients with varying amounts of amygdala damage were scanned while they performed a task in which they had to attend to fearful or neutral faces (Vuilleumier et al., 2004). Individuals with intact amygdala showed enhanced activity in the fusiform gyrus (a visual processing region) when they attended to fearful faces as compared to neutral faces. Patients with extensive amygdala damage did not show this pattern: They showed equivalent fusiform activity for neutral and fearful faces. Moreover, the amount of amygdala preservation corresponded with the amount of fusiform modulation based on the emotional content of the attended faces. These results suggest that the amygdala can modulate visual processing in humans, increasing the likelihood that an emotional item in the environment is detected and attended.

In addition to these influences on sensory processes, a number of neuroimaging studies have provided evidence for amygdalar modulation of mnemonic processes, suggesting that interactions between the amygdala and the hippocampus serve a critical role in modulating the memory enhancement for emotional information in humans (reviewed by McGaugh, 2004). In healthy individuals, there are strong correlations between the amount of activity in the amygdala and in the hippocampus during the encoding of emotional information (e.g., Dolcos et al., 2004; Hamann et al., 1999; Kensinger & Corkin, 2004; Kensinger & Schacter, 2005a). Although these correlations cannot speak to the direction of modulation, a neuroimaging study, examining encoding-related neural activity in patients with varying amounts of amygdala and hippocampal damage, provided evidence for the importance of reciprocal connections. While in the scanner, patients were asked to encode a series of emotionally aversive and neutral words. Outside of the scanner, they performed a recognition task, and the encoding trials were sorted on a post-hoc basis into those words that were later remembered and those that were later forgotten. The critical finding from the study was that the extent of amygdala atrophy correlated negatively with the magnitude of activity in the hippocampus during the encoding of emotional information, and the amount of hippocampal atrophy also was inversely related to amygdala activity (Richardson et al., 2004). Thus, bi-directional connections between the amygdala and the hippocampus may be important for modulating the encoding of emotional information (see also Kilpatrick et al., 2003).

In contrast to the extensive literature examining the amygdala's role during encoding, relatively few studies have considered its role during episodic retrieval. It is clear that the amygdala is engaged during retrieval of emotional items (e.g., Dolan et al., 2000; Taylor et al., 1998) and is more active during retrieval of information learned in emotional contexts compared to nonemotional ones (e.g., Maratos et al., 2001; Smith et al., 2004; Sterpenich et al., 2006). The strongest test for the role of the amygdala in retrieval, however, is a demonstration of an

interaction between emotional content and successful retrieval: that is, a stronger relation to successful retrieval (as compared to retrieval failures) for emotional items than for neutral items. A couple of recent studies have provided evidence for such an interaction, underscoring the potential importance of amygdala engagement during the retrieval process (Dolcos et al., 2005; Kensinger & Schacter, 2005b; Sergerie et al., 2006).

As this section has highlighted, a tremendous amount has been learned about the effects of emotion on memory by focusing on emotion-induced enhancements in the likelihood of remembering information. These studies have demonstrated that positive and negative events often are more likely to be remembered than nonemotional ones, and that the amygdala appears to be critical for this quantitative memory boost. Through its interactions with other cortical and subcortical regions, the amygdala can modulate sensory and mnemonic functions, increasing the likelihood that emotional information is perceived and retained in a stable memory trace.

Emotion and Memory: Quality-Based Influences

Although quantitative assessments of memory have been instrumental in laying the groundwork for investigations of emotion-memory interactions, they may underestimate the influence of emotion. Not all remembrances are created equal. Sometimes, we feel transported in time as we re-experience a prior event, and our memory seems to include a tremendous amount of detail about where and when the event occurred. Other times, we recognize that we've seen something before, but our memory does not include information about the context of the prior encounter: We recognize a woman in the airport but do not know where we met her, or we recognize a stretch of road without knowing when we have driven it before (reviewed by Gardiner & Java, 1993; Yonelinas, 2002).

Many of emotion's effects on memory become apparent only when the quality of a memory is considered. As noted in the section above, there are many instances in which

individuals are no more likely to correctly recognize an emotional item than a nonemotional one. One potential reason for this null effect of emotion is that successful recognition performance does not require a vivid memory: Although you can recognize an item because you vividly remember its prior presentation, simply knowing that you've seen something before is sufficient. Indeed, effects of emotion are more likely to occur when the vividness of a memory is considered. For example, when individuals are asked not only whether they recognize an item but also whether they vividly "remember" the item's prior presentation, rates of "remembering" tend to be much higher for emotional pictures or words as compared to nonemotional ones (Dewhurst & Parry, 2000; Kensinger & Corkin, 2003; Ochsner, 2000; Sharot et al., 2004). This boost in the ability to vividly remember emotional information often occurs even when overall recognition rates are equivalent for emotional and neutral information (e.g., Ochsner, 2000; Sharot et al., 2004).

In many instances, enhanced vividness defines an emotional memory. An extreme example is a "flashbulb memory": As the term implies, individuals sometimes believe they have maintained an almost photographic-quality memory of a highly emotional and consequential event (Brown & Kulik, 1977). For example, people claim to remember where they were and what they were doing when they learned of the assassination of President Kennedy (Brown & Kulik, 1977; Christianson, 1989; Winograd & Killinger, 1983), the September 11th terrorist attacks (Budson et al., 2004; Paradis et al., 2004; Pezdek, 2003; Smith et al., 2003), or the explosion of the space shuttle Challenger or Columbia (Bohannon, 1988; Kensinger, Krendl, & Corkin, 2006; Neisser & Harsch, 1986). Although these extremely vivid memories form only rarely, studies of autobiographical memory have confirmed that individuals often remember emotional experiences in a particularly vivid manner (e.g., Conway, 1990; Rubin & Kozin, 1984; Schaefer & Philippot, 2005). In all of these examples, what is noteworthy about the memories is not that the individual remembers the experience, but rather that they re-experience it with tremendous vividness.

In this section, we will examine whether the emotional qualities of events can affect how vividly they are remembered. In particular, we will discuss whether the arousal (the degree of excitation or pacification) or valence (the degree of displeasure or contentment; e.g., Russell, 1980; Lang et al., 1993) elicited by an event influences the vividness with which a person remembers those experiences.

Effects of Arousal on Memory's Vividness

The vast majority of studies examining the effects of emotion on memory's vividness have focused on stimuli that elicit high arousal. For these stimuli, mnemonic influences appear to occur via interactions between the amygdala and the hippocampus. For example, Kensinger & Corkin, (2004) compared encoding-related activity for words that participants later vividly remembered and for words that participants later forgot. For the arousing words, interactions between the amygdala and the hippocampus were found to be critical: Activity in both of these regions corresponded with the likelihood that a participant later vividly remembered a negative arousing word, and the amount of activity in the two regions was correlated strongly. For nonarousing words, hippocampal activity predicted the vividness of a memory, but amygdala activity did not. Thus, amygdala activity during encoding relates not only to an increased likelihood of remembering an emotional item (as discussed in the prior section) but also with the likelihood that an emotional item is remembered vividly (see also Dolcos et al., 2004 for evidence that amygdala activity during encoding leads to vivid memories of emotionally arousing information).

These mnemonic influences appear to occur relatively automatically. Kensinger & Corkin (2004) asked participants to study words either with full attention devoted toward the encoding task or with attention divided between the encoding task and a secondary, sound discrimination task. The addition of the secondary task impaired the vividness with which the nonarousing words were remembered, whereas it did not have a large effect on the vividness of memories for the

arousing words (see also Bush & Geer, 2001). This finding is consistent with proposals that emotional information is privy to prioritized or relatively automatic processing (reviewed by Dolan & Vuilleumier, 2003; Pessoa et al., 2003).

Although these studies demonstrate that emotional arousal can be a critical factor contributing to the emotional memory enhancement effect (see also Cahill & McGaugh, 1995; McGaugh, 2004), an arousal response is not required for emotional modulation of memory's vividness. Items that evoke changes in valence (e.g., that lead to a feeling of pleasure or displeasure), but not changes in arousal, also can be remembered with enhanced vividness (Kensinger & Corkin, 2003; Ochsner, 2000). The processes that lead to the mnemonic enhancements for nonarousing items, however, seem to be distinct from those mechanisms engaged for arousing information. In particular, the mnemonic boost for nonarousing stimuli appears to stem from controlled and elaborative processing of the stimuli (see Kensinger, 2004 for further discussion). Thus, in contrast to the minimal effect of divided attention on participants' memories for arousing items (Bush & Geer, 2001; Kensinger & Corkin, 2004), divided attention has a large detrimental effect on the likelihood that participants will vividly remember negative nonarousing items. In fact, when participants' attention is divided during encoding, the mnemonic enhancement for negative nonarousing words disappears (Kensinger & Corkin, 2004).

There also are distinct neural signatures associated with the successful encoding of arousing and nonarousing words (Kensinger & Corkin, 2004). In contrast to arousing items, which appear to be vividly remembered due to amygdala engagement, successful encoding of nonarousing items is associated with increased activity in the prefrontal cortex and hippocampus (and see LaBar & Phelps, 1998 for evidence that memory for negative nonarousing stimuli is not impaired in a patient with amygdala damage). The prefrontal cortex and hippocampus support later memory for neutral items as well, but the strength of their correspondence with later memory

is greater for the negative nonarousing items (Kensinger & Corkin, 2004). This overlap in the neural processes engaged to remember neutral and negative nonarousing words is consistent with the conclusion that participants are remembering the negative nonarousing words because of increased engagement of the same types of cognitive and neural processes that lead to a vivid memory for nonemotional information. This finding emphasizes that simply showing a memory benefit for emotional stimuli does not necessitate that a distinct mnemonic mechanism be postulated (and see Talmi & Moscovitch, 2004).

Thus, although many researchers have focused on amygdala-mediated effects of emotion on memory (thought to arise due to the action of stress hormones; McGaugh, 2000; McGaugh & Roozendaal, 2002), emotional information that does not elicit amygdalar modulation of memory also can be more vividly remembered than neutral information. These effects may arise because individuals are more likely to elaborate on the material during encoding or because to rehearse the information (see Bohannon, 1988; Brown & Kulik, 1977; Christianson & Engelberg, 1999; Isen, 1999 for discussion of effects of elaboration and rehearsal on memory for emotional information).

Effects of Valence on the Quality of a Memory

To assess the effects of valence on memory, researchers have contrasted memory for positive arousing and negative arousing stimuli. If highly arousing positive and negative experiences have different memory characteristics, then it cannot be only the arousal of the events that influences memory quality. A number of studies have suggested that the valence elicited by the event does influence the subjective vividness of the memory. Within the laboratory, negative events often are remembered with a greater sense of vividness than positive events (e.g., Ochsner, 2000; Dewhurst & Parry, 2000). Positive stimuli, in contrast, often are remembered with only a feeling of familiarity, or with general (nonspecific) information (e.g., Ochsner, 2000; Bless & Schwarz, 1999). This effect of valence on memory for detail can hold even in individuals (e.g.,

older adults) who tend to focus more on positive information than on negative, and it can exist even when overall recognition rates are equated for negative and positive information (Kensinger et al., submitted; Kensinger, Garoff-Eaton, & Schacter, submitted). Positive mood also has been associated with more memory reconstruction errors than negative mood, likely because individuals in a happy mood rely on gist-based information or on heuristics, while individuals in a negative mood are more likely to focus on the specific details of information (e.g., Bless et al., 1996; Storbeck & Clore, 2005).

It has been unclear to what extent these laboratory findings extend to real-life events infused with emotional importance. Research on autobiographical memory often has supported the opposite conclusion from laboratory research: that positive memories are more vivid than negative ones (e.g., D'Argembeau et al., 2003; Schaefer & Philippot, 2005). For example, Schaefer & Philippot (2005) asked participants to recall positive, negative, and neutral events, and for each, to rate the number of sensory, semantic, temporal, and contextual associations retrieved about the memory (using the Memory Characteristics Questionnaire; Johnson et al., 1988). They found that participants' ratings were higher for positive than for negative memories, indicating greater retrieval of contextual detail for positive events. However, some studies suggest little effect of valence on memory vividness, and instead have found intensity to be the primary predictor of autobiographical memory characteristics (e.g., Talarico et al., 2004).

A difficulty in these studies is finding positive and negative events that are comparable across a range of dimensions (e.g., duration of event, public or private nature of event, amount of media coverage or rehearsal). Two prior studies have attempted to circumvent many of these difficulties by examining whether a person's response to an event outcome (finding it positive or negative) affects what they remember about the event (Levine & Bluck, 2004; Kensinger & Schacter, in press). Levine and Bluck (2004) asked participants to indicate whether particular

events had occurred during the verdict decision in the O.J. Simpson trial. Kensinger & Schacter (in press) examined what Red Sox fans and Yankees fans remembered about the final game of the 2004 playoff series, in which the Red Sox overcame a surprising 0-3 setback in the series to win the championship. Consistent with Talarico et al (2004), both studies found that the overall amount of detail remembered about the event was not influenced by the event's valence. Valence did, however affect some memory characteristics: Levine & Bluck (2004) found that individuals who were happy about the verdict remembered the event more vividly and were more liberal in accepting that something had occurred. Similarly, Kensinger & Schacter (in press) found that Red Sox fans, who found the outcome positive, showed more memory inconsistencies and were more likely to be overconfident in their memories than were Yankees fans. In both studies, valence did not affect the quantity of remembered information, but it did influence the qualitative nature of the retrieved memories. These results emphasize the need to examine the effects of emotion not only on the likelihood of remembering information but also on the quality of remembered information.

Effects of Emotion on Memory for Detail

The prior section emphasizes that emotion can affect not only the likelihood of remembering an event but also the subjective vividness with which it is remembered. Individuals can say that they vividly remember an item for a variety of reasons, however: They may remember specific perceptual details of the event; they may recollect specific contextual details, such as something they thought of during the event; or they may be biased to say that they remember the prior experience vividly. In this section, we first examine whether emotion primarily inflates a person's confidence in their memories, or whether it also has beneficial effects on memory for detail. We then discuss the neural processes that mediate the effects of emotion on memory for detail and the types of details that are most likely to be remembered about an emotional event.

Inflated Confidence or Enhanced Detail?

When Brown & Kulik (1977) coined the term “flashbulb memory,” to refer to the vivid recollection of a surprising and consequential event, they believed that it reflected a separate memory mechanism, immune to memory distortion or disruption. Numerous studies now have demonstrated that these memories are prone to significant distortions over time. Individuals often report high confidence in so-called flashbulb memories despite low consistency in their reports over time, and there often is little or no correlation between how confident individuals are about their memories and how accurate or consistent their memories are (Neisser & Harsch, 1992; Schmidt, 2004; Schmolck et al., 2000; Talarico & Rubin, 2003). Clearly, emotional events do not leave indelible traces. Nevertheless, the question remains of whether enhanced confidence in memories of emotional experiences is justified: Are individuals just biased to believe that they have retained a detailed memory of an emotional experience, or are these events retrieved with more accurate detail than nonemotional events?

On the one hand, there is some evidence that emotion may primarily bias a person to believe that they remember a prior experience: Across a number of recognition paradigms, emotional items (and particularly negative ones) have been more likely to be falsely recognized than nonemotional ones (Budson et al., 2006; Ehlers et al., 1988; Windmann & Kruger, 1998; Windmann & Kutas, 2001). Because the increased false alarms occur not only for related lures but also for unrelated emotional words, these results suggest that individuals may be biased to believe that they have encountered an emotional item previously. One likely contributor to this bias is the fact that emotional items (and negative ones in particular) tend to be processed more fluently than neutral items (Bargh et al., 1992; Kityama, 1990; Ohman, 1988). Because items that have been studied recently tend to be processed more fluently than items that have not been encountered recently (Whittlesea, 1993; Whittlesea & Williams, 2000), participants may misinterpret the fluid processing of an emotional item on a recognition task as evidence that they have recently studied

the item. Thus, enhanced fluency could lead individuals to falsely endorse more nonpresented negative items than nonpresented neutral items. Another possible contributor relates to the semantic relatedness of most emotional items (see Talmi & Moscovitch, 2004). Because thematically-associated lures tend to be falsely endorsed more often than unrelated lures (Roediger et al., 2001; Stradler et al., 1999), emotional items may be falsely recognized more frequently because of their semantic cohesion.

Sharot et al (2004) have suggested that amygdala activity at retrieval may primarily serve to inflate a person's estimate of a memory's vividness and level of detail. They found that amygdala activity at retrieval corresponded with an individual's belief that an emotional item was vividly remembered (see also Dolcos et al., 2005), while activity in the parahippocampal gyrus (associated with visual memory) corresponded with vivid remembering of neutral information. Because the enhancement in subjective vividness for the emotional items occurred in the absence of an emotion-related boost in the ability to discriminate "old" from "new" items, they interpreted their findings as indicating that amygdala engagement at retrieval leads individuals to feel that they have a vivid memory not because they remember perceptual detail (as is the case with neutral items) but rather because of the feeling of arousal and perceptual fluency that accompanies the remembrance of emotional items.

On the other hand, however, there are instances in which emotion can increase the likelihood that details are remembered about an item. In a couple of studies (Kensinger, Garoff-Eaton, & Schacter, 2006; Kensinger et al., in press), participants were shown a series of negative and neutral objects (e.g., a spider, a blender) and later were asked to distinguish "same" objects (those identical to a studied item) from "similar" objects (those that shared the same verbal label as a studied item but that differed in any number of visual details). Individuals were more accurate at discriminating "same" and "similar" negative items than they were at distinguishing "same" and

“similar” neutral items. Importantly, this enhancement in memory specificity occurred even when the ability to recognize that a particular item type had been presented (e.g., to remember that a snake or a blender had been studied) was not influenced by emotion. These results parallel the self-report data (Ochsner, 2000; Sharot et al 2004), with negative emotional content enhancing not the ability to recognize an item from a study episode but rather the ability to vividly remember its presentation. The results of Kensinger, Garoff-Eaton, & Schacter (2006) indicate that the pattern of self-report data does not necessitate that individuals are biased to believe that they vividly remember an emotional item. Rather, emotion can affect the amount of detail remembered about a studied item while not affecting the overall proportion of items remembered.

Although these studies focused on memory for perceptual detail, emotion may have a broader effect on the ability to remember contextual (or “source”) information. Source memory is frequently defined as any contextual aspect (e.g., perceptual, spatio-temporal, affective) present when an encoding event occurred (Johnson et al., 1993). Source memory can be contrasted with item memory: the ability to recall or recognize that an item was previously encountered, without the ability to retrieve details about its encoding context. In a number of paradigms, emotion has been found to enhance memory for details such as the color in which a word was presented (Doerksen & Shimamura, 2001; Kensinger & Corkin, 2003; D’Argembeau & Van der Linden, 2004; MacKay et al., 2004), the spatial location of a word (D’Argembeau & Van der Linden, 2004; MacKay & Ahmetzanov, 2005), or whether words or objects were imagined or visually presented (Kensinger & Schacter, 2006d). Contextual information presented in a sentence also can be more likely to be remembered if the sentence is emotionally negative versus neutral (Kensinger et al., 2004; Kensinger et al., 2002). These results indicate that events with emotional meaning often are more likely to be remembered with detail than are events void of emotional importance.

Moreover, amygdala activity at retrieval can correspond with retrieval of accurate detail. Kensinger and Schacter (2005b) asked participants to view photographs of some objects but only to mentally imagine others. At retrieval, participants were required to indicate which items they had mentally imagined and which ones they had seen (i.e., to make a reality-monitoring decision). The critical finding was that activity in the orbitofrontal cortex, amygdala, and hippocampus, was greater for emotional items accurately attributed to presentation or to imagination than for emotional items misattributed. Convergent findings were revealed in an elegant study by Smith et al (2006). Participants studied neutral objects in either neutral or emotional scenes. Some of the neutral and emotional scenes contained people, while others did not. Participants were then asked to report the context in which objects had been studied. In one condition, the options were “emotional context” or “neutral context”; in another condition, the options were “context with people” or “context without people.” The data revealed enhanced hippocampal-amygdala connectivity whenever individuals retrieved information studied in an emotional context, regardless of whether the task required reporting of the emotional context (i.e., in both the “emotional/neutral” and “people/no people” conditions). When the retrieval of the emotional information was critical to successful memory performance (i.e., in the “emotional/neutral” condition), hippocampal-amygdala connectivity increased bi-directionally, modulated by the orbitofrontal cortex. Taken together, these two studies provide strong evidence that limbic engagement during memory retrieval does not relate only to an inflated confidence in the subjective richness of a memory; rather, increased limbic activity can correspond with the retrieval of details regarding an item’s presentation.

How Emotion Influences Memory for Detail

While these studies indicate that at least some details are more likely to be remembered for items with negative emotional content than for items with neutral content, they do not clarify

whether this increased memory accuracy for the negative arousing information is specifically related to the processing of the emotional information, or whether it stems from engagement of the same processes that lead to accurate memory for neutral information. The increased memory accuracy for negative arousing information could result from domain-general factors, such as the greater semantic relatedness (Talmi & Moscovitch, 2004) or the greater distinctiveness of emotional items (Schmidt, 2002), or the enhanced accuracy could stem from processes specific to emotional processing.

To adjudicate between these alternatives, we conducted a series of studies to examine the effect of emotion on reality-monitoring ability (the ability to distinguish what has been perceived from what has been imagined; Johnson & Raye, 1981). Accurate reality-monitoring attributions are thought to rely on an individual's ability to encode, and later to retrieve, details of the encoding episode. Memories for perceived events typically include more sensory and contextual information, whereas memories for imagined events often include more information about the cognitive operations that supported the internal generation of information (Johnson & Raye, 1981). Thus, retrieval of perceptual information will tend to correspond with attribution of a memory to a presented source, while retrieval of information linked to self-referential processing is related to an attribution of a memory to an internal source (Gonsalves & Paller, 2000; Kensinger & Schacter, 2006b).

We demonstrated that negative arousing items were more often accurately attributed than were neutral items (Kensinger & Schacter, 2006d). This enhanced discrimination occurred both when encoding was incidental and when it was intentional, and the effect was present both for verbal stimuli and for single objects. Using functional magnetic resonance imaging, we investigated the neural processes that led to accurate memory attributions (Kensinger & Schacter, 2005a). Most notably, while enhanced encoding-related activity in the posterior hippocampus was

related to accurate memory attributions for all items (negative arousing and nonemotional), enhanced encoding-related activity in the amygdala and the orbitofrontal cortex corresponded with a reduction in the likelihood of memory misattributions specifically for the negative arousing items. Activity in these limbic regions, often engaged during the processing of emotional information (e.g., Bechara et al., 2000; Phan et al., 2002; Zald, 2003), showed no correspondence to memory accuracy for the neutral items. Thus, the enhanced accuracy for negative arousing items did not stem solely from the additional engagement of domain-general processes that enhance accuracy for all items. Rather, domain-specific processes (processing of emotional information in the amygdala and orbitofrontal cortex) increased the likelihood of accurate memory attributions for the emotional items.

It is important to note, however, that part of the effect of these emotion-specific processes appeared to have been exerted via their interactions with regions that promote accurate encoding of both emotional and nonemotional items. In particular, activity in the amygdala was highly correlated with activity in the hippocampus during the encoding of negative arousing items later accurately attributed. A plethora of studies have demonstrated the hippocampus' critical role in binding together a nonemotional item and its context: Patients with hippocampal lesions have difficulties remembering the context in which an item was studied (Giovanello et al., 2003; Shoqeirat & Mayes, 1991); older adults who exhibit medial temporal-lobe dysfunction have deficits on these types of binding tasks as well (Chalfonte & Johnson, 1996; Collie et al., 2002); and neuroimaging studies have implicated the hippocampus specifically in the ability to learn associative information, as compared to non-associative information (e.g., Davachi & Wagner, 2002; Giovanello et al., 2004; Jackson & Schacter, 2004; but see Stark & Squire, 2001). Thus, it appears that memory for the details of an emotional event can be enhanced not because individuals bring on-line an entirely distinct set of processes to help them remember the information, but

rather because of limbic modulation of the same processes (e.g., hippocampal-binding mechanisms) that typically are recruited to remember the details of nonemotional information.

In this reality-monitoring paradigm, memory accuracy was higher for items with negative content. However, not all types of contextual details seem to be enhanced by emotional content. For example, emotion conferred no advantage when individuals were asked to remember whether they rated an item as animate-inanimate or as common-uncommon (Kensinger & Schacter, 2006a). Importantly, in this paradigm, amygdala activity corresponded only with memory for the item (i.e., knowing whether something was “old” or “new”) but not with memory for the task performed with the item (i.e., the “source”). A related finding has been reported by Adolphs and colleagues (reviewed by Buchanan & Adolphs, 2002): They have found that although emotion enhances the ability to remember the “gist” (general semantic theme) of scenes or stories, it can reduce memory for specific details. They also have provided evidence that this emotion-related effect on memory may be mediated by the amygdala: Patients with damage to the amygdala do not show the enhanced memory for gist or the impaired memory for detail (Adolphs et al., 2005).

These results highlight the fact that the role of the amygdala during encoding of event details may depend on the particular type of detail that is assessed. Emotion does not enhance memory for all aspects of an encoding episode, and amygdala engagement at encoding does not ensure that all details will be accurately remembered. Although additional research will be needed to better understand the circumstances in which amygdala activity does, and does not, relate to the encoding of event details, one possible explanation is that amygdala activity guides encoding of details that are intrinsic to an item (e.g., its physical appearance or its gist), but does not enhance encoding of attributes that are extrinsic to an item (e.g., the task performed with the item; and see Mather et al., 2006 for evidence that the neural processes supporting working memory for spatial location are disrupted for items that elicit an arousal response). Thus, details such as a word’s font

may have been enhanced by emotion (Doerksen & Shimamura, 2001; Kensinger & Corkin, 2003; MacKay et al., 2004) because those details are processed as intrinsic item attributes: A vivid memory of a word's presentation likely would include the color or location of the word. Similarly, individuals may have been more likely to remember neutral words occurring in an emotional sentence (Kensinger et al 2002, 2004) because individuals processed the entire sentence as a single stimulus rather than as a series of individual words. In contrast, focusing on the emotional item actually may preclude the processing of details extrinsic to that item. This hypothesis would be consistent with the proposal that the effects of emotion on memory may best be characterized as trade-offs: Some aspects of an event are better remembered because of its emotional salience, whereas other aspects are more likely to be forgotten (see reviews by Buchanan & Adolphs, 2002; Reisberg & Heuer, 2004). Of course, this proposal leaves open a number of questions, including how the amygdala can exert these selective effects on memory. One possibility is that, just as amygdala-hippocampal interactions at retrieval are guided by the orbitofrontal cortex (Smith et al., 2006), so does orbitofrontal activity during encoding guide the stimulus attributes that are attended and remembered.

Emotion's Effects on Implicit Memory

Although we have focused exclusively on emotion's influence on conscious retrieval of previously-learned information, emotion also modulates implicit memory, altering how recent experiences for which we do not have conscious memory impact our behavior (but see Steidl et al., 2006 for evidence that emotion can have dissociable effects on some forms of implicit memory compared to explicit memory). Implicit memory can take many forms, but here we focus on emotion's effects on priming: changes in a person's perception or response to a stimulus due to its prior exposure (for a recent review on priming, see Schacter, Dobbins, & Schnyer, 2004; for reviews on emotion's effects on other forms of implicit memory, such as fear conditioning, see

Maren, 2001; Lavond et al., 1993; LeDoux, 1995). A tremendous amount of research has indicated that prior exposure to a stimulus can influence our affective response toward it: Even when individuals are not aware that they have encountered a stimulus previously, they often will have a preference for the previously-seen item as compared to a novel one (the “mere exposure effect”; see Bornstein, 1989; Harrison, 1977; Zajonc, 2001 for reviews).

Although this research has focused on how unconscious processing of information can influence a person’s affective response to a stimulus, more recent research has begun to address whether emotional content of information influences responses within non-affective domains (see Butler & Berry, 2004 for discussion of similarities and differences between the mere exposure effect and repetition priming). For example, are individuals faster to perceptually identify or to make decisions about previously-encountered information with emotional content as compared to previously-encountered information lacking emotional meaning? The literature in this area is relatively sparse, but the studies to date suggest that emotional content of information confers an advantage on priming tasks just as it does on tasks of explicit memory: Thus, emotional stimuli show larger enhancements on perceptual and conceptual priming tasks than do nonemotional stimuli (Burton et al., 2004; Collins & Cooke, 2005; LaBar et al., 2005; Michael et al., 2005). Future studies will be required to elucidate the range of tasks for which emotion confers these priming benefits, the extent to which emotional stimuli are sensitive to manipulations that alter the magnitude of priming for nonemotional information (e.g., changes in modality of presentation, or stimulus appearance, or of task instructions), and the degree to which the affective quality of the stimuli (e.g., the valence or arousal elicited, or the discrete emotion evoked; see Burton et al., 2005) influences the strength of the priming. Future studies would also do well to investigate the neural correlates of emotional influences on priming. Neuroimaging studies of non-emotional information have consistently revealed that priming is accompanied by decreased activity in a

number of cortical regions (for reviews, see Grill-Spector et al., 2006; Schacter & Buckner, 1998; Wiggs & Martin, 1998). Initial neuroimaging evidence suggests that emotion can modulate the magnitude of such decreases (Ishai et al., 2004), but further studies of the issue are required.

Conclusions

In this chapter we have reviewed three approaches to examining the effects of emotion on memory: those focused on understanding what makes individuals more likely to remember emotional experiences than nonemotional ones, those examining why emotional memories often are re-experienced with tremendous vividness, and those investigating the types of details that are more likely to be remembered about emotional experiences than about nonemotional ones. Each of these lines of research has provided behavioral evidence of emotion-memory interactions, and neuroimaging and neuropsychological studies have demonstrated that the effects of emotion are not due to domain-general processes that boost memory for all information but rather stem from engagement of emotion-specific processing, particularly in the amygdala and the orbitofrontal cortex. The modulatory influence of these regions is apparent during memory encoding, consolidation, and retrieval; during each of these memory phases, limbic activity serves to modulate perceptual and mnemonic function to increase the likelihood that information is attended and that at least some details are retained. Thus, at least in part, emotional information is remembered better than nonemotional information not because of the engagement of processes unique to memory for emotional information, but rather because of limbic modulation of the same processes that typically are recruited to remember nonemotional information. Although there is increasing behavioral evidence indicating that this limbic modulation does not boost memory for all details of an encoding episode, future studies will be required to delineate the types of details that are better remembered for emotional than for neutral information and the neural mechanisms that allow emotion to exert selective effects on memory for some item attributes but not for others.

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