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Deborah Talmi
University of Manchester

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Abstract

Memory for emotional events is typically more vivid and accurate than memory for neutral ones. The modulation model focuses on the consolidation of memory traces to provide a partial account of enhanced emotional memory. Mediation theory focuses on encoding and retrieval to explain the selective enhancement of memory for emotional aspects of a complex event and why emotional memory also can be enhanced immediately after the experience, before consolidation has occurred. Mediation theory can therefore complement the modulation model, and together they may provide a more comprehensive account of human emotional memory.

Keywords

memory, emotion, arousal, attention, semantic relatedness, organization, distinctiveness

Memory for emotional stimuli and events is typically more vivid (Todd, Talmi, Schmitz, Susskind, & Anderson, 2012) and more accurate than memory for neutral stimuli and events (Labar & Cabeza, 2006). Researchers often explain this phenomenon of enhanced emotional memory using the *modulation model* (McGaugh, 2004; Schmidt & Saari, 2007): Emotional arousal during an experience causes secretion of the stress hormones adrenaline and cortisol in the body, which initiates a chain of events culminating in the activation of the amygdala, a brain region that boosts the consolidation of memory traces stored elsewhere. The modulation model, established on the basis of findings from single-trial conditioning paradigms in animals, provides a parsimonious explanation of many memory phenomena, but as Cahill and McGaugh (1998) point out, it provides only a partial account of emotional memory.

First, according to the modulation model, because the consolidation of emotional memory traces takes hours, the effects of emotion on memory should emerge only after a delay and should not be evident when memory is tested soon after the initial exposure to the stimuli (Cahill & McGaugh, 1998). Yet most of us believe that we will remember an aggravating or frightening occurrence better than a more mundane one even when our memory is probed just minutes later. Tests that take place shortly after encoding, but after a distractor task that purges working memory, probe early long-term memory. The

next section describes empirical data that support the prevalent intuition that emotion enhances early long-term memory and describes how mediation theory accounts for this effect. The putative neural substrate of this effect is then reviewed.

Second, emotional-memory experiments typically present a mix of emotional and neutral stimuli in quick succession, so any rise in systemic stress hormones may influence the entire course of the experiment. The modulation model predicts that memory for all stimuli should be enhanced in that situation. Yet there is plenty of evidence for focal effects of emotion, where memory of emotional stimuli is enhanced and memory for neighboring neutral stimuli is unchanged or even impaired.

The modulation model focuses on the storage/consolidation phase of memory. My argument is that what happens when emotional memories are initially created, as well as when they are retrieved, is also important. I review mediation theory, which could complement the modulation model by accounting for the two issues outlined earlier, and the development of a more comprehensive account of human emotional memory.

Corresponding Author:

Deborah Talmi, School of Psychological Sciences, University of Manchester, Coupland 1, Oxford Road, Manchester, M139PL, England, UK
E-mail: deborah.talmi@manchester.ac.uk

Explaining Enhanced Memory for Emotional Material in Early Long-Term Memory Tests

This section provides empirical evidence that emotion enhances early long-term memory, an effect that is outside the scope of the modulation model. Mediation theory (Talmi, Schimmack, Paterson, & Moscovitch, 2007) complements the modulation model by accounting for this effect and suggests that emotional events recruit cognitive resources such as attention, distinctive processing, and organization more than do neutral events, resulting in a memory advantage for emotional stimuli. The influence of cognitive resources means that the magnitude of the emotional memory effect is very sensitive to the specifics of the experimental methodology (see Table 1).

For example, emotional stimuli capture attention involuntarily, to the detriment of competing neutral stimuli. Thus, especially under limited-capacity conditions, emotional information will receive more attention resources than neutral information. Second, when emotional and nonemotional stimuli are presented together, the emotional stimuli stand out. This distinctiveness may alter the way emotional stimuli are encoded and also aid retrieval. Third, participants may automatically evaluate emotional stimuli as sharing a thematic link (e.g., the words *shark*, *blood*, and *ambulance*) but may not recognize links among neutral stimuli (e.g., the words *raven*, *curiosity*, *ring*), especially when cognitive capacity is limited. Tighter organization of emotional stimuli can function as a schema to support encoding and retrieval. Although attention, distinctiveness, and organization are dissociable from emotion per se, they are often elevated in real-life emotional experiences as well as in the laboratory.

By manipulating the factors that differentiate the processing of emotional and neutral stimuli, researchers can reveal their influence on the memory advantage of emotional stimuli. This logic is most clearly illustrated by examining the factor of organization. Many studies compare emotional stimuli and randomly selected neutral stimuli. Because participants perceive emotional stimuli to be interlinked, this practice favors memory for emotional stimuli. When both emotional and neutral words are equally semantically interrelated, the memory advantage for emotional stimuli disappears (Buchanan, Etzel, Adolphs, & Tranel, 2006; Talmi & Moscovitch, 2004). Although semantic relatedness is important, it does not fully account for emotional memory enhancement. When presented with stimuli that are more arousing, such as taboo words or pictures (Buchanan et al., 2006; Talmi et al., 2007), study participants remember them better than they do neutral stimuli matched on relatedness. Further work shows that semantic relatedness interacts with attention in influencing emotional memory: In a recent study, its effect was limited when participants were distracted by

a concurrent task (Talmi & McGarry, 2012). The data reviewed throughout this section demonstrates that cognitive factors display additive and interactive influences on emotional memory.

Two studies best illustrate the interplay among the key cognitive factors of attention, distinctiveness, and organization. Schmidt and Saari (2007) asked participants to name the font color of emotional taboo and nontaboo words and neutral words matched on organization, and then they asked the participants to recall the words freely. Memory for emotional words was enhanced when they were encoded or retrieved together with neutral words and thus were processed more distinctively than their neutral neighbors at encoding and were more distinct at retrieval. But when the three types of words were presented in separate lists, thereby equalizing distinctiveness, the memory advantage of emotional nontaboo words was abolished, whereas that of taboo words remained. This result indicates that distinctiveness fully accounts for the memory advantage of emotional nontaboo words over related neutral words but not for enhanced memory for taboo words. In this study, font color-naming latency served as a measure of attention to the words. Attention to all emotional words was enhanced—both taboo and nontaboo—but only enhanced attention to taboo words was associated with enhanced memory for them. To summarize, the study revealed a key role for distinctive processing in enhanced memory for emotional stimuli as well as a contribution of attention to memory for taboo but not nontaboo emotional words, perhaps because the taboo words were more arousing.

Talmi and McGarry (2012) took the next step, examining the role of attention in memory for emotional and neutral pictures. Like Schmidt and Saari (2007), they controlled organization and distinctiveness. In their dual-task condition, which resembled Schmidt and Saari's encoding procedure, participants had to classify tones while they viewed pictures. Participants allocated more attention to emotional pictures, and this additional attention accounted for enhanced emotional memory. When the amount of attention allocated to emotional and neutral pictures was equalized, this enhancement was abolished; the same occurred when participants were directly asked to dedicate their full attention to each stimulus, both emotional and neutral. Emotional memory enhancement in Talmi and McGarry's study manifested not only when more attention was allocated to emotional stimuli but also when the control over either distinctiveness or organization was relaxed—when emotional and neutral stimuli were presented together or when the neutral stimuli were less interrelated. This study provided evidence for a necessary and sufficient role for attention, distinctiveness, and organization in emotional memory.

The claim that these three factors are necessary to account for emotional memory helps us understand

disparities between studies that focused on only a single cognitive factor. For example, although Talmi and McGarry (2012) found that attention fully mediated emotional memory enhancement when organization and distinctiveness were controlled, in studies that did not control these factors, attention did not mediate emotional memory enhancement (Christianson, Loftus, Hoffman, & Loftus, 1991; Steinmetz & Kensinger, 2013; Talmi & McGarry, 2012; Talmi et al., 2007) or did so only partially (Pottage & Schaefer, 2012; Riggs, McQuiggan, Farb, Anderson, & Ryan, 2011).

The hypothesis that cognitive factors are necessary to account for emotional memory enhancement in early long-term memory contradicts suggestions that this phenomenon is driven automatically by emotional arousal. Such suggestions are supported by findings that the memory advantage for emotional stimuli is larger under shallow encoding relative to deep encoding (Jay, Caldwell-Harris, & King, 2008; Ritchey, Bessette-Symons, Hayes, & Cabeza, 2011) and when encoding takes place under divided attention relative to full attention (Kensinger & Corkin, 2004; Kern, Libkuman, Otani, & Holmes, 2005). These findings are frequently interpreted on the basis of the assumption that participants obey instructions to allocate only minimal processing resources to emotional stimuli. Yet we know that attention to emotional stimuli is often involuntary (Schmidt and Saari, 2007; Talmi et al., 2007). Structural equation modeling (e.g., Pottage & Schaefer, 2012; Talmi & McGarry, 2012) supports the hypothesis that whenever processing capacity is constrained, emotional stimuli grab a relatively larger share of resources than neutral stimuli. The greater memory advantage of emotional stimuli under constrained conditions can be explained by their relatively greater share of processing resources under these conditions.

It is difficult to equalize the processing of emotional and neutral stimuli. This is especially true when stimuli are not randomly allocated to conditions (i.e., when stimuli that induce emotional arousal, such as a picture of a crime scene, are compared with neutral ones, such as an office scene). Instead of spending time and effort on equalizing these stimulus types to avoid a host of potential confounds, future research may benefit from modeling perceptual and cognitive differences explicitly (e.g., by computing their salience; Itti & Koch, 2000) or from inducing arousal after the encoding of an individual item is complete (e.g., by following neutral stimuli with an electric shock; Schwarze, Bingel, & Sommer, 2012).

Neural Mechanisms of Emotionally Enhanced Early Long-Term Memory

Many neuroimaging studies have reported that activation in the amygdala and the correlation between

activations in the amygdala and medial temporal lobes are associated with successful encoding of emotional relative to neutral stimuli (Dolcos, Denkova, & Dolcos, 2012). For example, although successful encoding activated the hippocampus regardless of emotion, the amygdala was activated only by successful encoding of arousing words (Kensinger & Corkin, 2004). Such findings seem to support the modulation model, providing evidence for the effect of the amygdala on consolidation of emotional memory traces in the medial temporal lobes. The trouble with this interpretation is that long-term memory consolidation is a process that takes hours, but subsequent memory effects in the amygdala are observed even when the memory test occurs mere minutes after encoding.

The amygdala is activated by emotionally arousing stimuli and projects directly to regions up and down the processing stream to optimize encoding (LeDoux, 2000). The improved perceptual and semantic encoding of emotional stimuli is reflected in the visual, parietal, and prefrontal regions, where activations are consistently associated with enhanced successful encoding of emotional stimuli (Mickley-Steinmetz, Addis, & Kensinger, 2010; Murty, Ritchey, Adcock, & Labar, 2010). The association between amygdala activation and enhanced long-term memory for emotional stimuli may therefore be due to the amygdala's role in encoding, without recourse to consolidation mechanisms. This may explain why amygdala activation at encoding is predictive of subsequent early long-term emotional memory even when memory for emotional and neutral stimuli was equally good (a consequence of tight control of the encoding phase; Sommer, Glascher, Moritz, & Buchel, 2008), and why, in a study that tested memory at two intervals, amygdala activation predicted subsequent memory equally well, regardless of delay (Ritchey, Dolcos, & Cabeza, 2008). The same logic could also explain impaired emotional memory in people with amygdalar lesions (Labar & Cabeza, 2006). Finally, the increased correlation between the amygdala and the medial temporal lobes for successful encoding of emotional stimuli, compared with neutral stimuli, may simply reflect the increased perceptual and semantic processing associated with amygdala activation by emotional stimuli, which, in turn, leads to better encoding and greater activation of the medial temporal lobes.

Mediation theory complements, rather than replaces, the modulation model. Clearly, cognitive factors at encoding and retrieval should play a smaller role in late than early long-term memory, because after a delay, arousal-dependent modulation effects should also become manifest. The increase of emotional memory advantage with time, as consolidation progresses and exerts its effects (Sharot, Delgado, & Phelps, 2004), the modulation of this increase by amygdalar lesions (Labar & Phelps, 1998),

Table 1. How to Obtain a Large Emotional Memory Enhancement Effect on an Immediate Memory Test: A Humorous Summary

1. Use the most intensely arousing stimuli your ethics committee will allow.
2. Pick emotional stimuli with negative valence. Somewhat in contradiction with Tolstoy, in the experimental laboratory the causes for unhappiness appear to be more universal than the causes for happiness. While some people will find a picture of a baby to be intensely positive, others would not be moved; but almost everyone will be startled by a picture of a severely injured child.
3. Select neutral stimuli that are not related to each other, avoiding “interesting” stimuli of any kind.
4. Present the emotional and the neutral stimuli together in one mixed study list.
5. Limit processing by dividing participants’ attention or presenting the stimuli relatively quickly.
6. Limit the depth of processing at encoding by not mentioning the upcoming memory test, so that participants will not invest special effort into memorizing the neutral stimuli.
7. Use a test that is sensitive to gist rather than detail.

and the stronger influence of amygdala–medial-temporal-lobe connectivity on late long-term memory (Ritchey et al., 2008) support this prediction.

Focal Effects of Emotion on Human Memory

Focal effects of emotion on memory present a challenge for the modulation model. In animal research on emotional memory, the ideal paradigm involves animals’ encoding a single aversive event. By contrast, human participants in laboratory studies are typically exposed to an intermixed study list of emotional and neutral stimuli, such as pictures or words, presented in quick succession. The aversive event in animal paradigms causes the release of stress hormones in the body that remain active for many minutes. This response to emotional events is conserved in humans (Joels, Fernandez, & Roozendaal, 2011) and forms the first step of the modulation mechanism that culminates in enhanced consolidation. Given this time course, the modulation model should predict enhanced memory for all stimuli in the human laboratory study list, not only the emotional ones, but also their neighbors—those neutral stimuli that occur close in time to or are presented together with emotional stimuli (McGaugh, 2006).

It is accepted that when human participants experience emotional arousal after encoding is complete (a manipulation that should trigger the modulation mechanism), their late long-term memory is enhanced (Nielson & Bryant, 2005) in accordance with the modulation

model. The issue is that the hallmark of enhanced emotional memory in humans is the focal enhancement of memory for emotional over neighboring neutral stimuli and that in the dominant study paradigm reported in this literature, emotional and neutral materials are presented in close temporal and often spatial proximity. Another issue is that emotional stimuli are not only remembered better than the neutral stimuli in the same list but can also enhance (Anderson, Wais, & Gabrieli, 2006; Knight & Mather, 2009) or, more typically, impair (Knight & Mather, 2009; Steinmetz & Kensinger, 2013; Strange, Hurlmann, & Dolan, 2003) memory for neutral stimuli that precede or follow them. The peripheral hormones at the core of the modulation model are activated too slowly to account for these item-by-item effects of emotional stimuli on memory (Bass, Partain, & Manns, 2012).

To resolve this discrepancy, some researchers have suggested that the modulation mechanism interacts with the arousal that participants experience at encoding. In support of this idea, some studies show that arousal induced after participants encode a mixed list of emotional and neutral stimuli improves memory only for the emotional stimuli (e.g., Cahill & Alkire, 2003; Cahill, Gorski, & Le, 2003). Arousal-biased competition theory (Mather & Sutherland, 2011) neatly accounts for the effects of postencoding arousal induction by suggesting that only high-priority memory traces benefit from the modulation mechanism, and that both a list containing only neutral items and emotional stimuli in a mixed emotional/neutral list are prioritized. This theory cannot, however, explain the findings of another study in which arousal improved postencoding memory for all stimuli but did not influence the memory advantage of emotional relative to neutral stimuli (Nielson & Lorber, 2009).

Mediation theory can explain focal effects of emotion on human memory because it focuses on cognitive factors that can selectively and speedily target individual items. Taking the mediation and arousal-biased competition theories together, stimulus priority may encourage deployment of cognitive factors; cognitive factors could also drive priority assignment. These selective effects are likely to be evoked by moment-by-moment fluctuations in subjective emotional reactions and served by central neurobiological responses, such as amygdala and locus ceruleus activation, and interplay with central responses to stress hormones (Hurlmann et al., 2007; Joels et al., 2011; Sara & Bouret, 2012).

Integration

There is strong evidence that the modulation model accounts for behavioral and neural changes that occur between tests of early and late long-term memory. Mediation theory emphasizes encoding and retrieval to

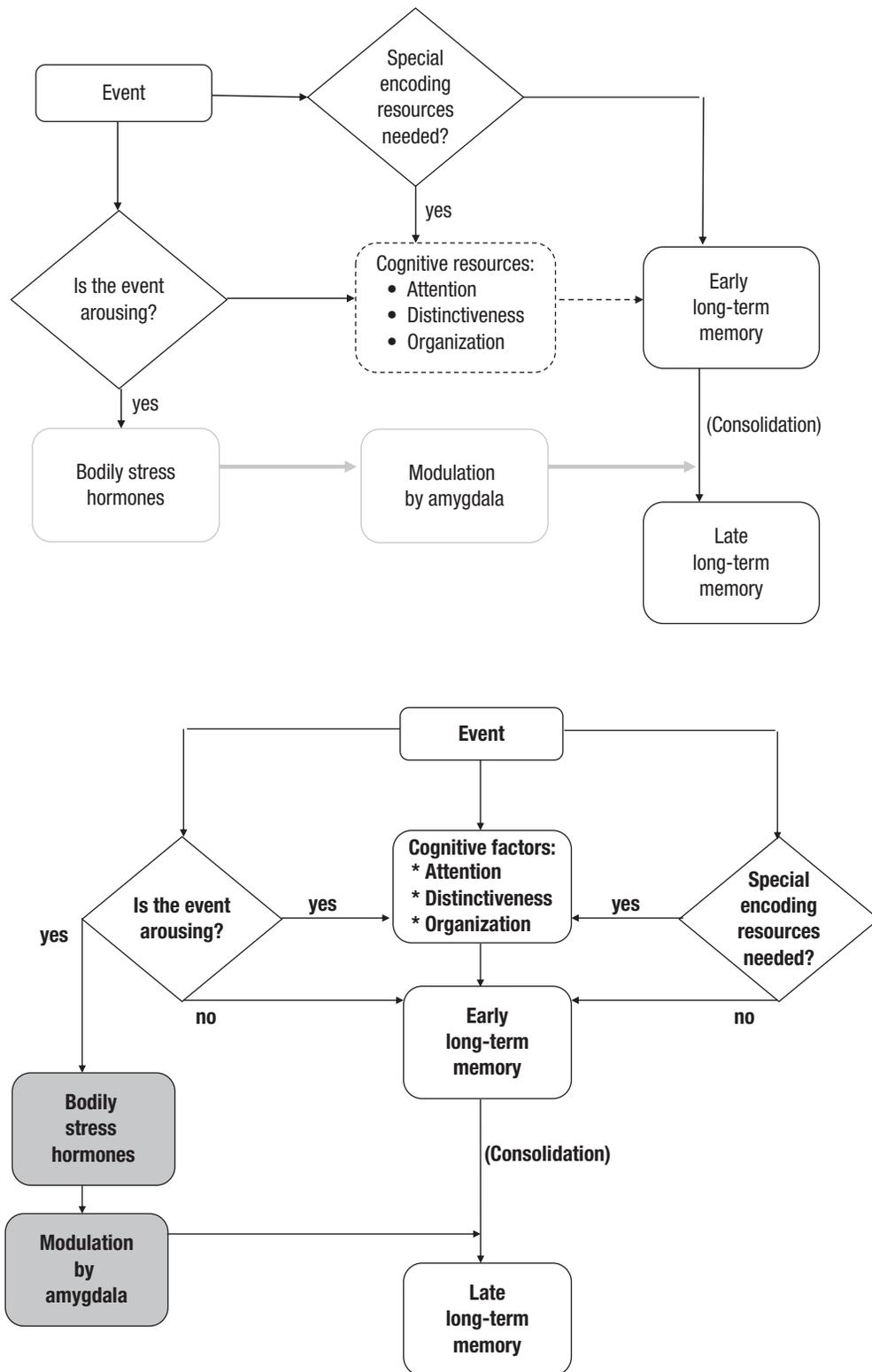


Fig. 1. Mediation theory of emotional memory enhancement. An event that is appraised as emotionally arousing will activate the modulation mechanism (gray boxes), which will strengthen the consolidation of early long-term memory traces. The automatic or effortful appraisal of the event as emotionally arousing, or other reasons to deem encoding the event to be important, may trigger the allocation of cognitive resources to the event. Three types of cognitive factors are listed. According to mediation theory, the effect of emotion on early long-term memory for the event is mediated by these cognitive factors.

account for the immediate effects of emotion on memory, on which later modulation can operate (see Fig. 1). It may thereby complement the modulation model to achieve a more comprehensive model of emotional memory. Such a model would benefit from conclusive evidence that cognitive factors influence early more than late long-term memory and that an advantage for emotional stimuli in delayed tests is observed even when tight control over cognitive factors abolishes this advantage in immediate tests.

The relationship between altered processing of emotional material at encoding and retrieval, on the one hand, and modulated consolidation, on the other hand, is currently a matter of controversy. A recent study (Bass et al., 2012) found that brief stimulation of the amygdala after rats explored certain objects selectively enhanced late, but not early, long-term memory for those objects, without affecting memory for other objects presented in close temporal proximity. These results may aid in revision of the modulation model to allow it to explain the focal effects of emotion on memory. Elucidating the neural mechanism for this effect—and teasing it apart from the neural effect of cognitive factors, which nascent work in animal models is beginning to uncover—is a goal for future research.

Recommended Reading

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- Labar, K. S., & Cabeza, R. (2006). Cognitive neuroscience of emotional memory. *Nature Reviews Neuroscience*, *7*, 54–64. A review of the human evidence for the modulation model.
- Talmi, D., & McGarry, L. M. (2012). Accounting for immediate emotional memory enhancement. *Journal of Memory and Language*, *66*, 93–108. A recent article discussing mediation theory in detail.
- Mather, M., & Sutherland, M. R. (2011). Arousal-biased competition in perception and memory. *Perspectives on Psychological Science*, *6*, 114–133. A review of ABC theory, discussing top-down and bottom-up effects of arousal.

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Declaration of Conflicting Interests

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