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The slow forgetting of emotional episodic memories: an emotional binding account

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Emotional events are remembered better than neutral events, and this emotion advantage becomes particularly pronounced over time. The time-dependent effects of emotion impact upon recollection rather than on familiarity-based recognition, and they influence the recollection of item-specific details rather than contextual details. Moreover, the amygdala, but not the hippocampus, is crucial for producing these effects. Time-dependent effects of emotion have been attributed to an emotional consolidation process whereby the amygdala gradually facilitates the storage of emotional memories by other medial temporal lobe regions. However, we propose that these effects can be better understood by an emotional binding account whereby the amygdala mediates the recollection of item-emotion bindings that are forgotten more slowly than item-context bindings supported by the hippocampus.

The effects of emotion on episodic memory

The most memorable events of our lives are often those that are emotionally arousing (e.g., an encounter with a vicious dog, viewing a photograph of a gruesome murder). It is well documented that emotional materials can attract more attention or garner more elaborative encoding than neutral materials, and that this enhanced encoding can lead emotional materials to be better remembered than neutral materials (see [1-4] for review). However, the beneficial effects of emotion cannot be explained solely on the basis of enhanced encoding because, as will be described below, emotional and neutral materials can often be remembered equally well shortly after they have occurred, and it is only after a delay period that the emotion advantage begins to emerge (e.g., [5-9]).

The reason why emotional memories are so resistant to forgetting is not yet fully understood. Although important advances have been made in developing models of episodic memory (see Glossary) that incorporate findings from behavioral, lesion, and neuroimaging studies, most of these models have focused on accounting for studies of memory

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for neutral materials. In the current paper we review the behavioral and neural studies examining emotion effects on episodic memory in human subjects, and we identify several well-established empirical regularities. Based on

Glossary

Consolidation: a process of stabilizing a memory trace after it has been encoded. Synaptic consolidation is used to refer to a set of cellular/molecular processes that are engaged to support the strengthening of the synapses in a local circuit, and it is thought to occur within the first few hours after encoding. Systems consolidation is used to refer to a process whereby hippocampus-dependent memories are transferred to the cortex over a period of weeks, months, or decades. Emotional consolidation refers to the idea that after encoding, the amygdala signals the hippocampus to preferentially stabilize or protect hippocampus-dependent memories of emotional compared to neutral events. **Episodic memory:** memory of a specific event that was personally experienced

at a particular time or place in the past. It is typically measured using tests of recognition or recall.

Familiarity: a memory process whereby subjects discriminate between old and new items on the basis of perceived memory strength (sometimes referred to as processing fluency or a sense of recency). It is thought to be particularly useful in tests of item recognition where old items are familiar and the new items are novel, but to be somewhat less useful in relational recognition tests or recall tests [17,100].

Recall: memory tests in which subjects are required to generate items from a previous encoding event, such as the words or images from a previous encoding list.

Receiver operating characteristic (ROC) procedure: a procedure that can be used to measure the contribution of recollection and familiarity to recognition performance [101]. The function describes the relationship between the proportion of correctly recognized studied items against the proportion of incorrectly recognized nonstudied items across variations in response criterion or confidence. A nonlinear model is fit to the observed function to estimate the probability of recollection and familiarity.

Recognition: memory tests in which subjects must discriminate between stimuli that were earlier studied from those that are new to the experimental setting. In item recognition tests, stimuli typically include words, scenes, faces, or objects. In relational recognition tests, subjects must discriminate between pairings of items or stimuli that were earlier studied from re-pairings. For example, the task may require recognizing that a particular word was studied with a particular face previously, which is sometimes referred to as associative recognition, or it may require recognizing that a particular word was encountered in a specific location, sometimes referred to as source recognition.

Recollection: a memory process whereby subjects retrieve qualitative information about a specific study event. For example, remembering that a particular object was encountered at a specific time or location, or was associated with a particular semantic and emotional state. It is expected to play a role in free recall and in tests of recognition memory, particularly relational recognition tests.

Remember/know procedure: a procedure that can be used to measure recollection and familiarity on the basis of introspective reports [102]. For each recognition response, subjects report whether they recognize items on the basis of remembering (i.e., recollection of qualitative information about the study event) or knowing (i.e., the item is familiar in the absence of recollection). Because subjects are instructed to respond 'remember' whenever they recollect a test item, the probability of a 'remember' response is used as an index of recollection, whereas the probability that an item is familiar is equal to the conditional probability that it received a 'know' response given it was not recollected [103].

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these results, we argue that emotional memories exhibit a time-dependent memory advantage because they rely on item-emotion bindings supported by the amygdala that are forgotten more slowly than item-context bindings supported by the hippocampus.

Five empirical regularities

The majority of the existing studies examining delayed emotion effects have contrasted memory for arousing negative emotional materials, such as gruesome pictures and taboo words, to memory for neutral materials, and our review will therefore focus on the effects of negative emotion as measured with these types of materials. Although this reflects a somewhat restrictive definition of emotion, later we will return to consider further whether these findings generalize to other emotional materials such as positive arousing materials, traumatic autobiographical events, as well as fear-conditioning paradigms.

The memory advantage for emotional materials increases over time

Numerous laboratory experiments have indicated that negative emotional materials are recalled and recognized better than neutral materials [1-3]. Although these effects may be due in part to enhanced encoding of emotion compared to neutral items, several studies have shown that the emotion effects are either absent or much smaller when memory is tested immediately, and they tend to increase in magnitude after a few hours [5-13].

To illustrate the delayed emotion effects we describe a study [8] in which subjects were presented with a mixture of negative and neutral images. Images were divided into two lists that were studied one day apart. Immediately after exposure to the second list, participants completed a recognition memory test for all the studied images mixed with negative and neutral nonstudied images (Figure 1). Overall recognition performance was then assessed for the emotional and neutral items that had just been studied as well as those that had been studied 24 h earlier. For the items studied and tested on the same day (i.e., the 5 minute delay condition) emotional and neutral items were recognized equally well. However, for the items studied 24 h earlier there was a recognition memory advantage for emotional materials over neutral materials. Thus, the emotional and neutral materials were equally well encoded, but after a delay an emotion advantage emerged.

Similar effects have been seen in other studies of recognition for words [6] and visual images [10,13], as well as in tests of free recall [11], and these delayed emotion effects have been shown to appear even after 2 h [10,13]. The results show that emotion effects can emerge during retention, and thus cannot be attributed to enhanced encoding. This does not preclude the possibility that emotion advantages can be seen in immediate tests. For example, encoding factors such as enhanced attention or distinctiveness can contribute to emotional memory advantages even when tested immediately (e.g., [14,15]). However, the results indicate that a simple enhanced encoding account of emotion is not sufficient to explain the long-term effects of emotion (see also [4]).

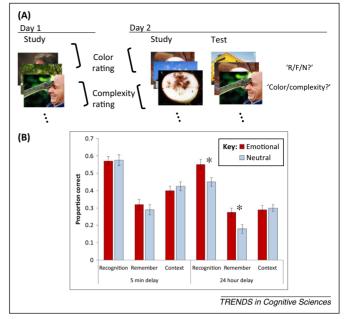


Figure 1. Procedures and results from [8]. (A) On day 1, subjects studied a mixture of negative and neutral images, half while rating visual complexity and half while rating the range of colors used in each image. On day 2, subjects studied a second list of images under similar encoding conditions, then after a 5 minute delay they received a recognition memory test containing a mixture of old items from both days and new items. For each test item subjects indicated if they could remember the occurrence of the item ('B'), if they knew it was studied on the basis of familiarity in the absence of recollection ('F'), or if they thought it was new ('N'). In addition, they indicated whether the item was encoded in the context of the color or complexity rating task. (B) The proportions of correct recognition responses are plotted for emotional and neutral materials for items tested after the 5 minute retention interval and the 24 h retention interval. Item recognition was greater for emotional than neutral materials, but only after the longer retention interval, and this effect was due to the relative increase in 'R' responses (*, statistically significant difference). By contrast, memory for the study context task was not influenced by emotion in either delay condition.

Emotion impacts recollection, rather than familiarity

Recognition memory judgments can be based either on the recollection of qualitative information about a study event or on assessments of familiarity [16–18]. Studies that have directly contrasted the contributions of recollection and familiarity to memory have indicated that emotion impacts recollection but has little or no effect on familiarity [7– 10,19–26]. Many of these studies have examined memory under conditions in which the relative increase in recollection may reflect better encoding of emotional compared to neutral items, but others have found that the recollection advantage for emotional materials is time-dependent [7-9,11,13]. For example, as seen in Figure 1, the recognition memory advantage that arose in the delay condition [8] was due to the items that were recollected. That is, in that study, a remember/know procedure was used in which subjects were required to indicate if recognition was accompanied by recollection – in the sense that they could remember some qualitative aspect of the study event, or if it was based on familiarity in the absence of recollection. The memory advantage for emotional materials that appeared in the delayed condition was entirely due to an increase in measures of recollection accuracy, and did not impact the items recognized on the basis of familiarity in the absence of recollection.

The results in this particular study were based on subjective reports of recollection and familiarity, but Download English Version:

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