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Enhancing Retention Through Reconsolidation: Negative Emotional Arousal Following Retrieval Enhances Later Recall

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Abstract

When information is retrieved from memory, it enters a labile state rendering it amenable to change. This process of reconsolidation may explain, in part, the benefits that are observed in later retention following retrieval of information on an initial test. We examined whether the benefits of retrieval could be modulated by an emotional event occurring after retrieval. Participants studied Swahili-English vocabulary pairs. On a subsequent cued-recall test, each retrieval was followed by a blank screen, a neutral picture, or a picture inducing negative affect. Performance on a final cued-recall test was best for items whose initial retrieval was followed by negative pictures. This outcome occurred when a negative picture was presented immediately after (Experiment 1) or 2 s after (Experiment 2) successful retrieval, but not when it was presented after restudy of the vocabulary pair (Experiment 3). Postretrieval reconsolidation via emotional processing may enhance the usual positive effects of retrieval.

Keywords

testing effect, reconsolidation, emotion and memory

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Retrieval of an event from memory provides a powerful boost to later recall of that event. Retrieving information while taking a test, for example, improves later retention of the information to a much greater extent than does restudying the same material (i.e., the testing effect; Carrier & Pashler, 1992; for a review, see Roediger & Karpicke, 2006). In addition, retrieval attempts that are more effortful, such as those following a long retention interval, enhance retention more than retrieval attempts that are less effortful, such as those following a short retention interval (e.g., Bjork, 1994; Pyc & Rawson, 2009). Explanations of why retrieval benefits later retention have typically focused on the processing involved in the retrieval attempt itself. For example, the elaborative processing involved in retrieval may enrich existing memory traces (e.g., McDaniel & Masson, 1985) or may increase the number of retrieval routes used to access memories (Bjork, 1975). To date, however, no theories of the testing effect have considered the role of processing taking place *after* the retrieval attempt has concluded. Here, we implicate the period immediately following retrieval as playing a part in the benefits conferred by retrieval. We present three experiments that explored the possible role of reconsolidation in strengthening a memory following its reactivation during a test.

The construction of memory—an extended period of encoding and consolidation—has long been considered a dynamic and complex process (Müller & Pilzecker, 1900). One view of memory construction is that once an event has been encoded, its trace remains relatively fixed. However, many studies (including those of the testing effect) have shown that reactivation of a memory trace changes its subsequent retrievability, either positively (e.g., Roediger & Karpicke, 2006) or negatively (e.g., Bartlett, 1932; Loftus & Palmer, 1974). Research targeting the neurobiological course of such memory reconsolidation has recently generated much excitement (for a review, see Dudai, 2006), and fresh attention has been focused on the finding that when memories are retrieved, they become labile and amenable to change (e.g., Lee, 2009; Nader, Schafe, & LeDoux, 2000; Sara, 2000; see also Lewis 1979; Mactutus, Ferek, George, & Riccio, 1982; Misanin, Miller, & Lewis, 1968).

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Research testing the reconsolidation hypothesis (i.e., that memory can be modified via reactivation and reconsolidation) with animal models has demonstrated that memories can be disrupted when amnestic treatments that block reconsolidation, such as electroconvulsive shock or protein synthesis inhibitors, are administered following memory reactivation (for a review, see, e.g., Sara, 2000). Retrieved memories have also been shown to be susceptible to interference from new learning introduced at the time of their reactivation. This technique has been the principal method used to investigate the reconsolidation process in humans, and results have usually demonstrated disruption of retention of the original event (e.g., Forcato et al., 2007; Hupbach, Gomez, Hardt, & Nadel, 2007; Schiller et al., 2010; Walker, Brakefield, Hobson, & Stickgold, 2003). Demonstrations of enhanced reconsolidation (i.e., facilitation following a postretrieval treatment) are quite rare. The only cases of which we are aware involve electrical stimulation (e.g., DeVietti, Conger, & Kirkpatrick, 1977) and pharmacological treatments (Blaiss & Janak, 2006; Gordon, 1977) in animal models. Our experiments provide the first demonstration of facilitation from a postretrieval manipulation in humans.

Taking a test requires retrieval and reactivation of a memory. If the testing effect results only from the processes involved in achieving retrieval, then any event that follows successful retrieval presumably should not exert any influence on later retention. However, if the processes subsequent to retrieval play a role in the testing effect, then memories should be susceptible to the modulatory effects of experiences introduced after the memories are successfully retrieved (as predicted by a reconsolidation account). We hypothesized that an emotionally arousing event following soon after retrieval may enhance reconsolidation because emotional centers of the brain (primarily the amygdala) have close interconnections with the hippocampus, an area involved in consolidation and reconsolidation (see Cahill & McGaugh, 1998, and Kensinger, 2009).

To test this hypothesis, we asked participants to study Swahili-English translations (e.g., "mashua–boat") and then take a cued-recall test. Upon the successful retrieval of a Swahili word's English translation during the test, a blank screen, a neutral picture, or a negatively valenced arousing picture was presented. Negatively valenced arousing pictures have been shown to elicit the psychophysiological responses that accompany emotional arousal (Lang, Greenwald, Bradley, & Hamm, 1993). We examined whether an emotional event (the negative picture) could enhance the benefits of a successful retrieval, as measured on a final, delayed test. Our hypothesis was that viewing an emotional picture following retrieval would permit greater final recall than would viewing either a neutral picture or a blank screen.

Although we predicted a positive effect, prior literature could lead one to expect that viewing a negative picture would either inhibit or facilitate memory for that item. One line of research on the effects of emotional arousal during encoding suggests the possibility of inhibition. Such research has shown that presentation of an emotional stimulus diminishes retention of a neutral stimulus that immediately precedes it (for a review, see Mather, 2007). The paradigm often used to elicit this effect is the *oddball paradigm*, in which one item—the emotional oddball—is inserted into a list of neutral items (Strange, Hurlemann, & Dolan, 2003). The method is similar to that of Tulving (1969), who showed impaired recall for neutral items that preceded presentation of a single "high priority" famous name (see also Schultz, 1971). Because processing emotional content is attention demanding (Bradley, Cuthbert, & Lang, 1996; Jenkins & Postman, 1948), continued encoding or consolidation of items preceding an emotional item may be diminished. Given this prior work, we reasoned that in our paradigm, final recall for successfully retrieved items followed by an emotional picture might be diminished compared with final recall for successfully retrieved items followed by a blank screen or a neutral item.

In contrast, recent evidence from a different paradigm (Anderson, Wais, & Gabrieli, 2006) indicates that emotional arousal can sometimes create facilitation during encoding. If this finding can be generalized to the case of retrieval (i.e., if emotional pictures strengthen rather than disrupt the testing effect), our paradigm might provide the first case of facilitatory reconsolidation in humans. In an attempt to resolve the contradiction in prior experiments examining effects of emotion on encoding, Knight and Mather (2009) argued that the amount of attention paid to the neutral items before the presentation of the emotional event was critical. They noted that in the typical oddball paradigm, many neutral items are presented before the emotional oddball is shown, so that attention is diffused over a group of items. They also noted that, in contrast, in the study by Anderson et al., only one neutral item was shown before an emotional stimulus, so neutral items were afforded a high level of attention. In our paradigm, retrieval at test should engage a high level of attentional focus for each item. Accordingly, we hypothesized that the arousing postretrieval event would enhance the benefits of testing (McGaugh, 2006).

Experiment 1

Method

In our first experiment, 40 undergraduates studied 10 lists, each of which contained 10 pairs of Swahili-English vocabulary words that ranged from difficult to easy, as established by Nelson and Dunlosky (1994; e.g., *lulu-pearl* is an easy pair and *ubini-forgery* is a difficult pair). Participants were told at the start of the experiment that after studying each set of 10 pairs, they would take a cued-recall test, and that all 100 pairs would be tested at the end of the experiment. They were also told that during each initial cued-recall test, they would be learning a second list made up of pictures and that they would have a recognition test on the pictures.

During study, each vocabulary pair was presented for 2 s. After studying 10 pairs, participants solved multiplication problems for 1 min, so that effects of short-term memory would be removed. They then took a cued-recall test on the 10 studied pairs; the Swahili terms were presented one at a time, and the task was to type in the English translation for each word. Immediately following a successful retrieval, participants were presented with one of three, randomly determined postretrieval events (500-ms duration): a blank screen, a neutral picture, or a negatively valenced arousing picture. As in the oddball paradigm, an arousing picture was presented at most once per 10-item list; but as in the Anderson et al. (2006) paradigm, the neutral target item was the focus of attention (i.e., successful retrieval brought the target into the focus of attention before the postretrieval event). Blank screens and neutral pictures were presented equally often after all successful retrievals that were not followed by arousing pictures.

The negatively arousing pictures (e.g., dead cat, pointed gun) were selected from the International Affective Picture System (Lang, Bradley, & Cuthbert, 2008) and had a mean arousal rating of 5.86 and a mean valence of 2.74 (the scales ranged from 1 through 9, with higher values indicating higher arousal or more positive valence). The neutral pictures (e.g., shoelaces, fork) were taken from a set that had been developed for use in other studies; their arousal and valence ratings (on the same 9-point scales) were 3.53 and 5.74.

Following an unsuccessful retrieval, participants were presented with either a blank screen or a neutral picture, but never with an emotional picture (because we were interested in the effects of arousal on successfully retrieved items only). In the case of both successful and unsuccessful retrievals, the postretrieval event lasted for 500 ms, after which the screen cleared and the next Swahili cue was presented for testing.

Following the initial cued-recall test, participants completed 1 min of multiplication problems. This phase was followed by an old/new recognition test in which all of the pictures presented on the recall test were mixed with new pictures. This test was included simply to ensure that participants attended to each picture.

This study-test cycle was repeated with all 10 lists. Each participant studied and was tested on each picture (neutral and arousing) once, and each participant saw the pictures in a different random order. The list position of the emotional picture varied randomly from list to list. After completion of the 10 study-test cycles, participants were given a final cued-recall test of all 100 Swahili-English pairs. In this test, they were given the Swahili words and were instructed to fill in the English translations. The entire experiment was presented on iMac computers in testing rooms with groups of 1 to 4 participants.

Results and discussion

On the initial recall test, the overall average proportion correct was .37 (SE = .02). Our primary interest was in final cued-recall performance for successfully recalled items in each postretrieval condition. As illustrated in Figure 1, final recall was better when successful retrieval on the initial test was followed by a negative picture than when it was followed by a blank screen or a neutral picture. A one-way ANOVA revealed a significant effect of condition, $F(2, 78) = 5.96$, $MSE = 0.02$, $\eta_p^2 = .13$, $p < .05$. Final recall was significantly better for pairs that were followed by an emotionally arousing picture (M = .57, SE =.04) than for pairs that were followed by a blank screen (M = .48, SE =.03) or those that were followed by a neutral picture (M = .44, SE =.03), $t(39) = 2.14$, $p < .05$, and $t(39) = 3.07$, $p < .01$, respectively. Performance for items in the neutral and blank conditions did not differ significantly, $t(39) = 1.35$, $p > .05$.

These data are the first to show that arousal following successful retrieval of information enhances later recall of that information. Because this finding was novel, we conducted a second experiment with the goal of replicating the effect. In addition, we sought to extend our results with a characterization of the time course of the effect. In Experiment 2, we delayed the onset of the postretrieval event by 2 s. Does enhancement occur only when the arousing picture is presented immediately following successful retrieval, or would the enhancing effect of arousal also occur when the picture came following a short delay? If the effect persisted, this would suggest that an extended period of processing follows successful retrieval.

Experiment 2

Method

Fifty-six Washington University students participated in Experiment 2. The materials and procedure were identical to those of Experiment 1 except that the postretrieval event occurred 2 s after retrieval, rather than immediately following retrieval. When the participant entered the correct response, a 2-s blank screen appeared; in the appropriate conditions, this screen was followed by a neutral or negatively valenced picture for 500 ms. Finally, the screen cleared, and the next cue was presented.

Results and discussion

On the initial test, the overall average proportion correct was .40 (SE = .02). The data from the final test, depicted in Figure 1, replicated the pattern of emotional enhancement found in Experiment 1. There was a main effect of postretrieval condition, $F(2, 110) = 3.76$, $MSE = 0.04$, $\eta_p^2 = .06$, $p < .05$. Final recall performance was best for pairs followed by an emotionally arousing picture in the initial test (M = .58 SE = .04), next best for items followed by a blank screen (M = .50, SE = .02), and poorest for items followed by a neutral picture (M = .47, SE = .02). Performance for items followed by arousing pictures was significantly better than performance for items followed by neutral pictures, $t(55) = 2.32$, $p < .05$, and

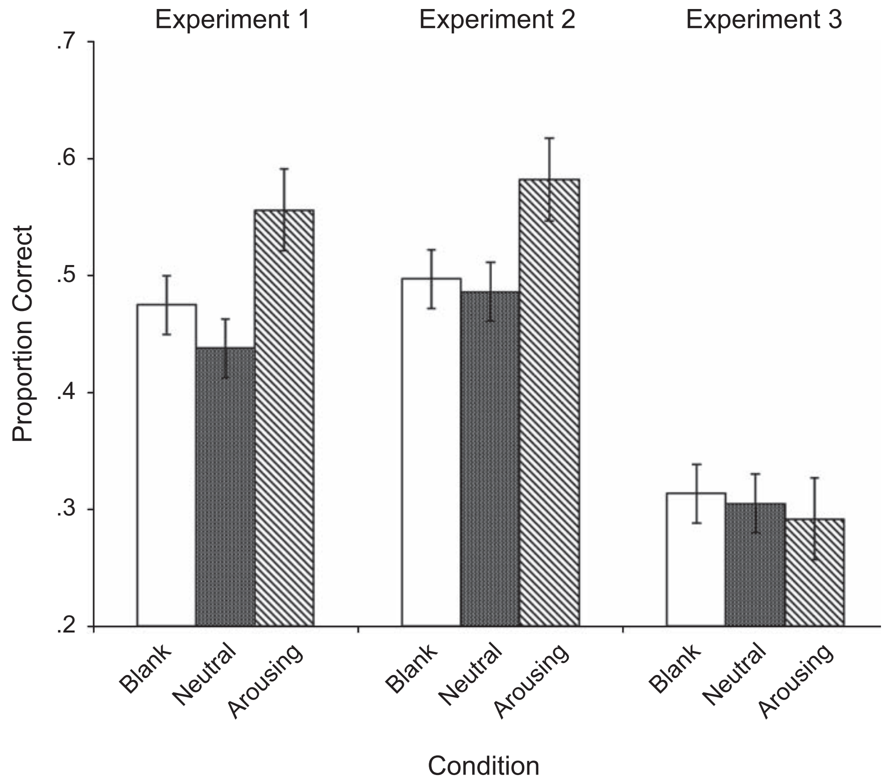

Fig. 1. Mean proportion correct on the final recall test for items answered correctly on the initial test in Experiments 1 and 2, and items restudied in Experiment 3. Results are shown for the three experimental conditions, which differed in whether the items were followed by a blank screen, a neutral picture, or a negatively arousing picture during the initial test. Error bars depict standard errors of the mean.

marginally better than performance for items followed by a blank screen, $t(55) = 1.92$, $p = .06$. Performance for items in the neutral and blank conditions did not differ significantly, $t(55) = 0.39$, $p > .05$.

By replicating the results of Experiment 1, Experiment 2 firmly established that negative emotional arousal following a successful retrieval enhances later recall. We were able to extend our results by showing that a negative picture enhanced final recall even when the picture followed retrieval by 2 s. These results suggest that postretrieval processing is not fleeting, but extends beyond the conclusion of a successful retrieval by at least 2 s.

In a final experiment, we sought to rule out a distinctiveness-based explanation of the enhancement effect found in Experiments 1 and 2. The effects of arousal in our first two experiments could represent an isolation effect, whereby the distinctiveness of an emotional event rendered the prior vocabulary pair more memorable than pairs in the control conditions (Hunt, 2006; Schmidt, 1991). If an emotional picture facilitated later recall of the preceding pair regardless of whether retrieval had occurred, then the enhancement effect should also emerge when a negatively arousing picture follows an item presented for restudy. A restudy event does not require retrieval, and therefore reconsolidation would not be involved. Accordingly, in Experiment 3, we tested whether emotional arousal would enhance recall when items were restudied.

Experiment 3

Method

Sixty-one Washington University students participated in Experiment 3. The materials and procedure of this experiment were nearly identical to those of Experiments 1 and 2. One critical difference is that vocabulary words were presented for restudy, rather than tested, before the picture manipulation occurred. During study, subjects were presented with the same word pairs as in the previous experiments. They were then given the list again for restudy; immediately following a 2-s restudy presentation of each word, a blank screen, a neutral picture, or a negatively valenced picture was presented for 500 ms. An emotional picture was presented once per block of 10 items. List position of the emotional picture and which of the emotional pictures was presented were randomly determined. The second change to the procedure in Experiment 3 was that the final criterion test occurred after every two lists. A pilot experiment in which all of the items were tested after all 100 items had been presented (as in Experiments 1 and 2) yielded floor-level performance. Thus, to avoid floor effects, we tested recall of the previous 20 items after every two lists.

Results and discussion

The data, depicted in Figure 1, did not show the pattern of emotional enhancement found in Experiments 1 and 2. There was no main effect of postretrieval condition, $F < 1$, $p > .05$. Unlike in the previous experiments, mean performance was actually lowest for pairs followed by an emotionally arousing picture, albeit not reliably so. There were no significant differences among the conditions (all *p*s > .05).

In Experiments 1 and 2, we analyzed the later recall of items that were successfully recalled on the initial test. These successfully retrieved items were likely to be the easier items. In Experiment 3, however, data for all items were analyzed. To ensure that the pattern of findings in Experiment 3 was the same for easy and difficult items, we conducted a 2 (ease: easy or difficult; determined by a median split of the items using Nelson & Dunlosky's, 1994, norms) × 3 (postretrieval event: blank screen, neutral picture, or emotional picture) ANOVA on final-test performance. There was a significant main effect of ease, $F(1, 60) = 93.26$, $MSE = 0.02$, $\eta_p^2 = .61$, $p < .001$, but there was no main effect of postretrieval event, $F(2, 120) = 1.16$, $MSE = 0.02$, $\eta_p^2 = .02$, $p > .05$, nor was there a significant interaction, $F(2, 120) = 2.43$, $MSE = 0.01$, $\eta_p^2 = .04$, $p > .05$. This analysis confirmed that neither easy nor difficult restudy items give rise to the enhancement effect observed with retrieval. Restudying the words before picture presentation did not elicit the positive effects of emotional pictures on later recall. Thus, a simple distinctiveness-based interpretation of the results from Experiment 1 and 2 is ruled out.

General Discussion

The results of Experiments 1 and 2 provide the first evidence for memory enhancement via postretrieval processing in humans and are consistent with the view that reconsolidation via reactivation enables memory updating. The results also contribute to the literature on the testing effect by showing that processes underlying this effect are not constrained to the period during retrieval, but also extend to a period of reconsolidation following successful retrieval. Performance on a final cued-recall test was enhanced for pairs that had been successfully retrieved on a prior test when those pairs had been followed by an emotionally arousing picture. If the benefit derived from testing were due solely to processes in the period leading up to and including retrieval, then no differences in recall would have emerged from our manipulations. Yet we found that successful retrieval followed by an arousing picture enhanced later recall in comparison with successful retrieval followed by a neutral picture or a blank screen.

A second experiment replicated and extended our finding of postretrieval emotional enhancement. When we delayed the postretrieval event by 2 s, the pattern of emotional enhancement of later recall persisted. In follow-up experiments, we are systematically delaying the onset of the postretrieval event to determine the time course of the reconsolidation process in more detail. We also are examining whether pictures arousing positive emotion have the same effect as negative pictures.

Critically, the enhancement effect was demonstrated only with items that had been successfully retrieved on a prior test. Experiment 3 showed that active retrieval of the pairs is necessary to obtain the effect of emotional arousal on later recall. When vocabulary pairs were simply represented for restudy, no differences in final-test performance emerged across the postrestudy conditions.

The findings presented here are consistent with the extensive evidence showing that emotion influences the accuracy of memory (e.g., Kensinger, 2007). Evidence suggests that the enhancement observed in our study may occur by means of a modulatory relationship between the amygdala and the hippocampus (e.g., Kensinger, 2009). Together, our results and those of Anderson et al. (2006) indicate that emotional pictures can enhance both consolidation and reconsolidation. In sum, our findings demonstrate that retrieval is key for the emotional enhancement of the testing effect observed in Experiments 1 and 2, and support the view that reconsolidation contributes to the memory-enhancing benefits of testing.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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References

Anderson, A., Wais, P., & Gabrieli, J. D. E. (2006). Emotion enhances remembrance of neutral events past. *Proceedings of the National Academy of Sciences, USA*, *103*, 1599–1604.

Bartlett, F. C. (1932). *Remembering: A study in experimental and social psychology*. Cambridge, England: Cambridge University Press.

Bjork, R. A. (1975). Retrieval as a memory modifier. In R. Solso (Ed.), *Information processing and cognition: The Loyola Symposium* (pp. 123–144). Hillsdale, NJ: Erlbaum.

Bjork, R. A. (1994). Memory and metamemory considerations in the training of human beings. In J. Metcalfe & A. Shimamura (Eds.), *Metacognition: Knowing about knowing* (pp. 185–205). Cambridge, MA: MIT Press.

Blaiss, C. A., & Janak, P. H. (2006). Post-training and post-reactivation administration of amphetamine enhances morphine conditioned place preference. *Behavioral Brain Research*, *171*, 329–337.

Bradley, M. M., Cuthbert, B. N., & Lang, P. J. (1996). Picture media and emotion: Effects of a sustained affective content. *Psychophysiology*, *33*, 662–670.

Cahill, L., & McGaugh, J. L. (1998). Mechanisms of emotional arousal and lasting declarative memory. *Trends in Neurosciences*, *21*, 294–299.

Carrier, M., & Pashler, H. (1992). The influence of retrieval on retention. *Memory & Cognition*, *20*, 632–642.

DeVietti, T. L., Conger, G. L., & Kirkpatrick, B. R. (1977). Comparison of the enhancement gradients of retention obtained with stimulation of the mesencephalic reticular formation after training or memory reactivation. *Physiology and Behavior*, *19*, 549–554.

Dudai, Y. (2006). Reconsolidation: The advantage of being refocused. *Current Opinion in Neurobiology*, *16*, 174–178.

Forcato, C., Burgos, V. L., Argibay, P. F., Molina, V. A., Pedreira, M. E., & Maldonado, H. (2007). Reconsolidation of declarative memory in humans. *Learning & Memory*, *14*, 295–303.

Gordon, W. C. (1977). Similarities between recently acquired and reactivated memories with production of memory interference. *American Journal of Psychology*, *90*, 231–242.

Hunt, R. R. (2006). The concept of distinctiveness in memory research. In R. R. Hunt & J. B. Worthen (Eds.), *Distinctiveness and memory* (pp. 3–25). New York, NY: Oxford University Press.

Hupbach, A., Gomez, L., Hardt, O., & Nadel, L. (2007). Reconsolidation of episodic memories: A subtle reminder triggers integration of new information. *Learning & Memory*, *14*, 47–53.

Jenkins, S.O., & Postman, L. (1948). Isolation and “spread of effect” in serial learning. *American Journal of Psychology*, *61*, 214–221.

Kensinger, E. A. (2007). Negative emotion enhances memory accuracy: Behavioral and neuroimaging evidence. *Current Directions in Psychological Science*, *16*, 213–218.

Kensinger, E. A. (2009). *Emotional memory across the adult lifespan*. New York, NY: Psychology Press.

Knight, M., & Mather, M. (2009). Reconciling findings of emotion-induced enhancement and impairment of preceding items. *Emotion*, *9*, 763–781.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2008). *International Affective Picture System (IAPS): Affective ratings of pictures and instruction manual* (Tech. Rep. No. A-8). Gainesville: University of Florida, Center for Research in Psychophysiology.

Lang, P. J., Greenwald, M. K., Bradley, M. M., & Hamm, A. O. (1993). Looking at pictures: Affective, facial, visceral, and behavioral reactions. *Psychophysiology*, *30*, 251–273.

Lee, J. L. C. (2009). Reconsolidation: Maintaining memory relevance. *Trends in Neurosciences*, *32*, 413–420.

Lewis, D. J. (1979). Psychobiology of active and inactive memory. *Psychological Bulletin*, *86*, 1054–1083.

Loftus, E. F., & Palmer, J. C. (1974). Reconstruction of automobile destruction: An example of the interaction between language and memory. *Journal of Verbal Learning and Verbal Behavior*, *13*, 585–589.

Mactutus, C. F., Ferek, J. M., George, C. A., & Riccio, D. C. (1982). Hypothermia-induced amnesia for newly acquired and old reactivated memories: Commonalities and distinctions. *Physiological Psychology*, *10*, 79–95.

Mather, M. (2007). Emotional arousal and memory binding: An object-based framework. *Perspectives on Psychological Science*, *2*, 33–52.

McDaniel, M. A., & Masson, M. E. J. (1985). Altering memory representations through retrieval. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *11*, 371–385.

McGaugh, J. L. (2006). Make mild moments memorable: Add a little arousal. *Trends in Cognitive Sciences*, *10*, 345–347.

Misanin, J. R., Miller, R. R., & Lewis, D. J. (1968). Retrograde amnesia produced by electroconvulsive shock after reactivation of a consolidated memory trace. *Science*, *160*, 554–555.

Müller, G. E., & Pilzecker, A. (1900). Experimentelle Beitrage zur Lehre von Gedächtnis [Experimental contributions on the theory of memory]. *Zeitschrift für Psychologie Ergänzungsband*, *1*, 1–300.

Nader, K., Schafe, G. E., & LeDoux, J.E. (2000). Fear memories require protein synthesis in the amygdala for reconsolidation after retrieval. *Nature*, *406*, 722–726.

Nelson, T. O., & Dunlosky, J. (1994). Norms of paired-associate recall during multitrial learning of Swahili-English translation equivalents. *Memory*, *2*, 325–335.

Pyc, M. A., & Rawson, K. A. (2009). Testing the retrieval effort hypothesis: Does greater difficulty correctly recalling information lead to higher levels of memory? *Journal of Memory and Language*, *60*, 437–447.

Roediger, H. L., III, & Karpicke, J. D. (2006). The power of testing memory: Basic research and implications for educational practice. *Perspectives on Psychological Science*, *1*, 181–210.

Sara, S. J. (2000). Retrieval and reconsolidation: Toward a neurobiology of remembering. *Learning & Memory*, *7*, 73–84.

Schiller, D., Monfils, M. H., Raio, C. M., Johnson, D. C., LeDoux, J. E., & Phelps, E. A. (2010). Preventing the return of fear in humans using reconsolidation update mechanisms. *Nature*, *463*, 49–53.

Schmidt, S. R. (1991). Can we have a distinctive theory of memory? *Memory & Cognition*, *19*, 523–542.

Shultz, L. S. (1971). Effects of high priority events on recall and recognition of other items. *Journal of Verbal Learning and Verbal Behavior*, *10*, 322–330.

Strange, B. A., Hurlemann, R., & Dolan, R. J. (2003). An emotion-induced retrograde amnesia in humans is amygdala- and beta-adrenergic-dependent. *Proceedings of the National Academy of Sciences, USA*, *100*, 13626–13631.

Tulving, E. (1969). Retrograde amnesia in free recall. *Science*, *164*, 88–90.

Walker, M. P., Brakefield, T., Hobson, J. A., & Stickgold, R. (2003). Dissociable stages of human memory consolidation and reconsolidation. *Nature*, *425*, 616–620.