Behavioral Neuroscience

Reactivation, Interference, and Reconsolidation: Are Recent and Remote Memories Likewise Susceptible?

Sonja Wichert, Oliver T. Wolf, and Lars Schwabe

Online First Publication, August 29, 2011. doi: 10.1037/a0025235

CITATION

Wichert, S., Wolf, O. T., & Schwabe, L. (2011, August 29). Reactivation, Interference, and Reconsolidation: Are Recent and Remote Memories Likewise Susceptible?. *Behavioral Neuroscience*. Advance online publication. doi: 10.1037/a0025235

Behavioral Neuroscience

© 2011 American Psychological Association
0735-7044/11/$12.00 DOI: 10.1037/a0025235

Reactivation, Interference, and Reconsolidation: Are Recent and Remote Memories Likewise Susceptible?

Sonja Wichert, Oliver T. Wolf, and Lars Schwabe
Ruhr-University Bochum

The retrieval of a consolidated, apparently stable memory can return it to a labile state, necessitating another period of stabilization, termed *reconsolidation*. During reconsolidation, memories are susceptible to modifications, thus providing the opportunity to change unwanted memories. In a test of whether the possibility to alter retrieved memories depends on the age of the memories, participants learned a set of emotional and neutral pictures and recalled it 1, 7, or 28 days later. Immediately after retrieval, participants learned a second set of pictures. Memory retrieval per se enhanced 28-day-old memories but had no effect on 1-day- or 7-day-old memories. Learning new pictures interfered with 1-day-old and 28-day-old memories but not with 7-day-old memories. Evidence for reconsolidation effects was generally rather weak and at most present for 7-day-old memories. These findings show that retrieval and interference have opposite effects on memory that depend on the remoteness of the memories and raise the question under which conditions reconsolidation effects occur in human memory.

Keywords: memory, memory age, retrieval, interference, reconsolidation

New memories are initially fragile and a consolidation process is needed to stabilize them and to store them permanently. For decades, it has been commonly assumed that memories are not subject to further modification once they are consolidated (McGaugh, 2000). Recent years, however, have seen renewed interest in the more than 40-year-old idea (Misanin, Miller, & Lewis, 1968) that reactivating or retrieving a consolidated memory renders it labile again, thus requiring another period of stabilization which is referred to as reconsolidation (Dudai, 2004; Nader, 2003; Sara, 2000). In line with this view, converging evidence from human and animal studies demonstrates that during the reconsolidation process, reactivated or retrieved memories are susceptible to the same amnesic manipulations as newly acquired memories (Forcato et al., 2007; Hupbach, Gomez, Hardt, & Nadel, 2007; Nader, Schafe, & LeDoux, 2000; Przybyslawski, Roullet, & Sara, 1999; Walker, Brakefield, Hobson, & Stickgold, 2003).

These findings not only underline the dynamic nature of memory but have also stimulated a new approach to the treatment of psychiatric disorders that are characterized by overly strong memories, such as posttraumatic stress disorder (PTSD). According to the concept of memory reconsolidation, emotional or traumatic memories may be changed by psychological or pharmacological manipulations during or shortly after the retrieval of the memories. Indeed, recent studies indicate that the introduction of new information or the administration of a beta-blocker, which blocks the noradrenergic activity that is needed for memory formation, shortly after the retrieval of a conditioned fear memory reduces the fear significantly and lastingly in healthy participants (Kindt, Soeter, & Vervliet, 2009; Schiller et al., 2009). Moreover, there is first evidence that the administration of a beta-blocker after retrieval of a traumatic event reduces subsequent emotional responding to the mental imagery of that event in PTSD patients (Brunet et al., 2008). Although these findings are promising, they raise the question whether there is a critical time window for such treatments. Or, more generally: Are younger and older memories likewise sensitive to modifications during reconsolidation?

There is some evidence from rodent studies that older memories are less susceptible to postretrieval manipulations than younger ones and that the vulnerability of memories decreases as the time interval between initial learning and retrieval increases (Milekic & Alberini, 2002; Suzuki et al., 2004). However, these findings remain controversial, as other animal studies did not find an effect of memory age (Debiec, LeDoux, & Nader, 2002; Lee, Di Ciano, Thomas, & Everitt, 2005). Whether there is an effect of memory age on the reconsolidation of memories in humans has not yet been investigated.

In the present experiment, healthy participants learned new pictures immediately after they had retrieved a set of previously learned pictures (*retrieval* + *interference* conditions), a manipulation that altered memory performance in earlier studies (Hupbach et al., 2007; Schwabe & Wolf, 2009). In order to assess the impact of memory age on the reconsolidation processes, retrieval/interference took place 1, 7, or 28 days after initial learning. In addition, participants retrieved the first picture set without subsequent learning of new pictures (*retrieval* condition) or learned the second picture set without prior retrieval of the first picture set (*interference* condition) to ensure that memory was not affected by retrieval or interference per se. Further groups of

---

Sonja Wichert, Oliver T. Wolf, and Lars Schwabe, Department of Cognitive Psychology, Ruhr-University Bochum.

We gratefully acknowledge the assistance of Britta Wenske during data collection. We thank Tobias Otto for his technical assistance.

Correspondence concerning this article should be addressed to Lars Schwabe, PhD, Department of Cognitive Psychology, Ruhr-University Bochum Universitaetsstrasse 150, 44780 Bochum, Germany. E-mail: Lars.Schwabe@rub.de

participants did neither retrieve the learned picture set nor learn a new picture set (*control* condition) to control for the mere effect of time on memory. If there is a temporal gradient in human memory reconsolidation, interference after memory retrieval should reduce subsequent memory performance when there is a 1-day interval between initial learning and retrieval, but not (or to a lesser extent) when there are longer learning–retrieval intervals of 7 or 28 days.

Method

Participants and Design

One hundred forty-four students of the Ruhr-University Bochum (72 men, 72 women; mean age = 24.0 years, standard error of the mean [*SEM*] = 0.3 years) participated in this study. They received either course credits or a moderate monetary compensation for participation. Exclusion criteria comprised current or chronic psychological disorder, any medical condition, drug abuse, and current treatment with medication.

We used a fully crossed between-subjects design with the factors retrieval (yes vs. no), interference (yes vs. no), and memory age (interval between initial learning and retrieval/interference: 1 day vs. 7 days vs. 28 days), thus resulting in 12 experimental groups (see Figure 1). Six men and six women were randomly assigned to each of these groups. Participants in the retrieval + interference conditions learned a new set of pictures immediately after they had recalled a set of previously learned pictures. Additional groups of participants retrieved the first picture set without subsequent learning of new pictures (retrieval condition) or learned the second picture set without prior retrieval of the first picture set (interference condition). Moreover, some participants did neither retrieve the learned picture set nor learn a new picture set (control condition).

Stimulus Materials

The stimulus materials included two sets of 24 pictures taken from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 1997). Each set comprised eight negative, eight neutral, and eight positive pictures. The pictures of the two sets were matched with respect to emotional valence and emotional arousal, based on the IAPS standard scores for valence and arousal. To ensure that the pictures were indeed experienced as neutral and emotionally arousing, participants rated each picture with respect to valence and arousal on two 0–100 scales with the endpoints being *very negative* versus *very positive* and *not arousing* versus *very arousing*, respectively. In retrospect, these ratings confirmed the classification of the pictures as neutral, negative, and positive. Neutral pictures (mean [M] = 53.5, *SEM* = 0.9) were rated significantly lower in valence than positive pictures (M = 72.0, *SEM* = 1.0) and significantly higher in valence than negative pictures (M = 16.1, *SEM* = 0.8; all $p < .001$). Furthermore, neutral pictures (M = 18.4, *SEM* = 1.1) were associated with significantly lower emotional arousal than were positive pictures (M = 30.5, *SEM* = 1.6), which were rated as significantly less arousing than negative pictures (M = 72.4, *SEM* = 1.4; all $p <$ .001).

Procedure

Testing took place on three experimental days: Day 1, learning; Day 2, retrieval and/or interference; Day 3, memory testing (see Figure 1). After their arrival in the lab on Day 1, all participants saw a set of 24 neutral and emotional pictures (Set 1; see above) on a computer screen. They were instructed to memorize the pictures, but not explicitly told about the subsequent memory tests. While viewing each picture, participants gave valence and arousal ratings by clicking on scales shown under the picture. An immediate free recall test took place directly after the presentation of the picture set to control for possible group differences in encoding. Participants were asked to write down all pictures they could remember in as much detail as possible. In line with previous studies (Hupbach et al., 2007; Hupbach, Hardt, Gomez, & Nadel, 2008), this procedure was repeated (without valence and arousal ratings) until participants remembered at least 20 of the 24 pictures or until a maximum of three learning trials was reached. There was no time limit for the free recall test. Most participants finished the learning session within 30 min.

To examine the impact of memory age on memories' susceptibility to retrieval, interference and reconsolidation effects, experimental Day 2 took place 1 day, 7 days, or 28 days after experimental Day 1. The procedure on Day 2 depended on the experimental condition. Participants in the retrieval conditions were asked to sit down quietly, to close their eyes, and to think of the pictures that were presented on Day 1. Retrieval lasted for 2 min and took place in the same spatial context as the learning session on Day 1. In line with previous studies (Hupbach et al., 2007; Hupbach et al., 2008), we did not ask participants to list the pictures they had learned on Day 1. Immediately after memory retrieval, participants in the retrieval + interference conditions learned a second set of neutral and emotional pictures (Set 2) following the same procedure as on Day 1; participants in the retrieval conditions did not learn new pictures after reactivation. Participants in the interference conditions learned the novel pictures without prior memory retrieval; to avoid spontaneous reactivation of the initial learning experience the novel learning took place in a different testing room (in another part of the university building) than the initial learning (Hupbach et al., 2008). Participants of the control conditions omitted experimental Day 2.

On Day 3, 24 hours after Day 2, all participants completed a free recall test for the pictures they had learned on Day 1. They were asked to write down all pictures of Set 1 that they could remember in as much detail as possible.

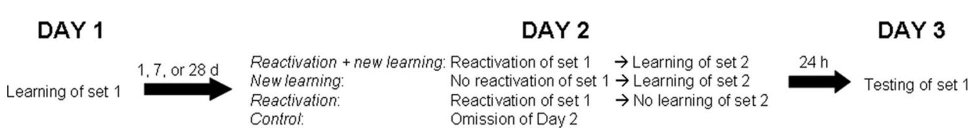

Figure 1. Illustration of the experimental design.

Memory performance was expressed as the number of pictures that were remembered. Participants' memories were analyzed by two independent raters. The agreement between the two raters was very high (interrater reliability = 0.99). Discrepancies were discussed until an agreement was reached.

Results

Learning of Picture Sets 1 and 2

Participants took on average 1.8 trials ($SEM = 0.1$) to reach the learning criterion (correct recall of ≥ 20 pictures) on Day 1. The 12 groups did not differ in their learning performance ($p = .48$). On Day 2, participants took on average 1.8 trials ($SEM = 0.1$) to reach the learning criterion for the Set 2 pictures. The retrieval + interference and interference groups did not differ in their learning performance and there was no effect of the Day1–Day2 interval ($ps > .33$).

Memory Performance on Experimental Day 3

Memory performance, expressed as number of pictures remembered, was analyzed by a Group (retrieval + interference, retrieval, interference, control) × Emotionality (negative vs. neutral vs. positive) × Day1–Day2 interval (1 day vs. 7 days vs. 28 days) analysis of variance (ANOVA). This analysis revealed that negative and positive stimuli were overall better remembered than neutral stimuli, $F(2, 264) = 16.22$, $p < .001$, $\eta^2 = 0.11$, and that memory performance was worse after the 28-day-interval than after the 7-day- or 1-day-interval, ($F(2, 132) = 20.74$, $p < .001$, $\eta^2 = 0.24$. Most important, however, the effects of memory retrieval and interference were dependent on the Day1–Day2 interval, Group × Day1–Day2 Interval interaction: $F(6, 132) = 4.08$, $p = .001$, $\eta^2 = 0.16$, without a three-way interaction with emotionality.

One-day-interval. Learning new pictures on Day 2 reduced memory for the pictures that were initially learned when there was a 1-day-interval between Day 1 and Day 2, group effect: $F(3, 44) = 6.41$, $p = .001$, $\eta^2 = 0.30$. Figure 2 shows that the retrieval + interference group remembered fewer pictures than the control group and the retrieval group ((Least significant difference (LSD) post hoc tests, both $ps < .005$). It is important that the interference group did not differ from the retrieval + interference group, suggesting that the detrimental effect of interference was independent of the prior retrieval of the previously learned material and thus not a reconsolidation, but a retroactive interference effect.

Seven-day-interval. After a 7-day-interval between initial learning and retrieval/interference, the influence of interference by new learning depended on the prior retrieval of the original material, group effect: $F(3, 44) = 3.32$, $p < .03$, $\eta^2 = 0.19$: The retrieval + interference group remembered significantly fewer pictures than the control group and the retrieval group (LSD post hoc tests, both $ps < .05$) and tended to recall fewer pictures than the interference group ($p = .08$). This finding suggests the presence of a reconsolidation effect.

There were no effects of interference or memory reactivation per se. As displayed in Figure 2, participants in the retrieval and interference groups remembered a similar number of pictures as participants in the control group.

Twenty-eight-day-interval. The impairing effect of interference after memory retrieval disappeared when the interval between Day 1 and Day 2 was 28 days. At this interval, the retrieval + interference group did not differ from the control group (see Figure 2).

However, the retrieval of the old memories and the interference per se had opposite effects on subsequent memory performance, group effects $F(3, 44) = 9.04$, $p < .001$, $\eta^2 = 0.38$, see Figure 2: The retrieval group performed significantly better and the interference group significantly worse than the respective other three groups (LSD post hoc tests, all $ps < .05$). These opposite effects

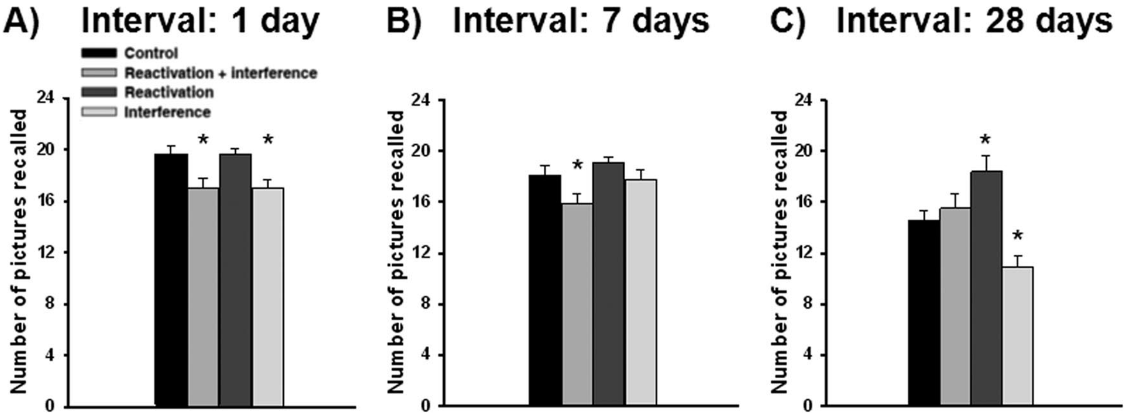

Figure 2. Memory performance (number of pictures recalled) on experimental Day 3. (A) The retrieval + interference group and the interference group remembered significantly fewer pictures than the control group and the retrieval group ($^* p < .05$) if the interval between experimental Day 1 and Day 2 was 1 day. (B) The retrieval + interference group remembered fewer pictures than the other three groups ($^* p < .05$; interference vs. retrieval + interference: $p = .08$) if the Day1–Day2 interval was 7 days. (C) Memory performance was significantly enhanced in the retrieval group and significantly reduced in the interference group ($^* p < .05$) if the Day1–Day2 interval was 28 days. Data represent means ± standard errors of the mean.

seemed to cancel each other out in the retrieval + interference group.

Influence of participants' sex. To assess whether there were any differences between men and women in memory performance, we included sex as an additional factor in our analyses. These analyses revealed that women learned the first picture set (on experimental Day 1) faster than men ($M = 1.6$, $SEM = 0.07$ vs. $M = 1.9$, $SEM = 0.07$; LSD post hoc test $p < .001$). On experimental Day 2, however, there were no differences in learning the new picture set between men and women. Moreover, there was no significant influence of participants' sex on the effects of memory reactivation and interference on experimental Day 3 of the different Day1–Day2 intervals.

Influence of learning performance on Day 1. Because previous research showed that reconsolidation effects may be modulated by the strength of initial learning (Wang, de Oliveira Alvares, & Nader, 2009), we classified our participants as fast versus slow learners (one vs. three trials needed to reach the learning criterion on Day 1) and included the factor fast versus slow learning in our analyses. These analyses, however, revealed no significant main or interaction effect of fast versus slow learning.

Discussion

This study aimed to examine whether recent and remote memories are likewise susceptible to reconsolidation effects. To this end, participants learned neutral and emotional new pictures immediately after the retrieval of pictures they had learned 1 day, 7 days, or 28 days before. Our findings indicate that memory retrieval and interference by new learning per se had opposite effects on memory performance that were dependent on the remoteness of the memories. Memory retrieval enhanced only the subsequent recall of remote memories, whereas retroactive interference (i.e., learning of new information) exerted its impairing effect on recent and remote memories but not on "middle-aged" (i.e., 7-day-old) memories. Indications for memory reconsolidation, that is, the enhanced vulnerability to interference after prior memory retrieval, however, were generally weak and at most present for middle-aged memories. Moreover, our study provides first evidence that episodic memories become sensitive to reconsolidation effects, irrespective of their emotionality: neutral and emotional memories were likewise susceptible to retrieval, interference, and their interaction in reconsolidation.

One possible explanation for the absence of a reconsolidation effect at the 1-day and 28-day intervals might be that the reactivation method did not succeed in retrieving the learned material. We consider this explanation, however, rather unlikely, because previous research showed that even the learning context per se (without any explicit instruction to retrieve) may reactivate the learned material (Hupbach et al., 2008). Moreover, the same retrieval and new learning procedure led to a reconsolidation effect at the 7-day interval and we observed an effect of retrieval per se after the 28-day interval.

The finding that a reconsolidation effect emerged for 7-day-old memories but not for 28-day-old memories is in line with animal data suggesting a temporal gradient in memory reconsolidation (Milekic & Alberini, 2002; Suzuki et al., 2004). Why should older memories be less sensitive to the disruptive effects of new learning after their retrieval than younger ones? With the passage of time, memories become completely (Dudai, 2004; Squire, 1992) or at least partially (Nadel & Moscovitch, 1997) independent of the brain structures that are involved in encoding. Retrieval of more recent, not completely consolidated memories may reengage the hippocampus with the effect that "the initial memory is partially overwritten in the interest of storing more recently acquired information" (Myers & Davis, 2002). Older memories, in contrast, are stored in neocortical brain areas that are different from the encoding circuits and are therefore less readily modifiable. Moreover, consolidated neocortical traces may be more resistant to modifications after retrieval because they are widely distributed across different cortical areas (Lee et al., 2005; McClelland, McNaughton, & O'Reilly, 1995).

If there is a temporal gradient in memory reconsolidation, then the question is why we did not find any evidence for a reconsolidation effect for recent (1-day-old) memories. One explanation could be the intensity of initial learning. In the present study, participants repeated the learning procedure until they reached the relatively strict criterion of 20 out of 24 pictures. There is recent evidence that stronger memories are less susceptible to reconsolidation effects (Suzuki et al., 2004) and that intensive training, which creates strong memories, significantly reduces effects of reconsolidation in rodents (Wang et al., 2009). Although we did not find a modulating effect of fast versus slow learning on the influence of memory retrieval and interference, effects of learning strength cannot be ruled out because we did not manipulate the strength of learning explicitly. It seems justified to assume that such training effects are particularly strong if the interval between learning and testing is short.

Alternatively, although new learning did not take place in the same spatial context as the learning session in the interference only group to avoid spontaneous memory reactivation (Hupbach et al., 2008), it cannot be completely ruled out that these participants might have reactivated their memory for the previously learned item. As such, the effect in the interference only group would not be due to interference per se, but could actually be a reconsolidation effect. Such spontaneous reactivation effects are particularly likely if the interval between original learning and new learning is short (e.g., 1 day). According to this interpretation, reconsolidation takes place for both recent and middle-aged memories, providing the expected temporal gradient. Interference per se would then only be effective for remote memories, thus removing the issue of why it is ineffective for 7-day-old memories. One way to control for spontaneous reactivation effects in future studies could be to ask participants at the end of the experiment whether they had thought about the initially learned material when they come to the lab on experimental Day 2.

Our finding that memory retrieval may have a positive effect on subsequent recall performance is in line with the results of earlier studies (Carrier & Pashler, 1992; Karpicke & Roediger, 2008). However, the present results extend these previous findings in three important ways. First, whereas earlier studies used cued-recall procedures during retrieval, we obtained a memory enhancing effect of retrieval even without the presentation of any task-related cues. Second, while previous studies examined the effect of retrieval shortly after learning, our results demonstrate that memory retrieval may strengthen subsequent memory even if it takes place considerable time after learning. Finally, by investigating three different time intervals between learning and memory retrieval, we found evidence that the beneficial effect of retrieval was time dependent. Older but not younger memories benefited from retrieval; 28-day-old memories, but not 1- or 7-day-old memories, were better recalled if they were retrieved 24 hours before the final memory test. This time-dependency may be at least partly owing to changes in memory over time. Memory performance was overall relatively high when the interval between original learning and memory testing was only 2 days, thus leaving not much room for improvement. As the time interval between learning and testing increased, recall performance decreased in the control groups but remained remarkably constant in participants that retrieved the memory (without new learning) 24 hours before testing.

In addition to the memory enhancing effects of retrieval per se, memory retrieval could also compensate for the detrimental effects of interference by new learning if the learning–retrieval interval was 28 days but not if it was only 1 day. This could indicate that memory retrieval counteracted the disruptive effects of interference. Alternatively, it may be that the act of retrieval opposes the natural loss of the memory over time. Consistent with this view, the number of pictures recalled by both the retrieval group and the retrieval + interference group and the difference between the two remain fairly consistent across all time periods, whereas the control group shows a steeper memory decay gradient.

Our finding that learning new information reduced memory performance for recent and remote memories is in line with a large body of literature on retroactive interference (e.g., Barnes & Underwood, 1959; Bäuml, 1996; Bower, Thomson-Schill, & Tulving, 1994; Wickelgren, 1965). However, the majority of these studies presented the interfering material relatively shortly after the initial learning. Here, we show that new learning may interfere with previous learning even if the interval between original learning and new learning is as long as 28 days. One possible explanation for the finding that interference per se affected only the memory of the 28-day-old memories could be the relative strengths of the original and newly learned material after the different time intervals. For instance, after 28 days, the newly learned pictures are relatively fresh in memory in comparison to pictures that were learned 1 month ago. Hence, the relative ease with which the new pictures can be recalled could interfere with recall of the remote memory, whereas for 1-day and 7-day delays, the relative strengths of the memories of the originally and the newly learned items are more comparable.

Finally, a limitation of the present study needs to be addressed. We did not quantify the reactivation of the initially learned pictures, which makes it difficult to rule out possible group differences in memory consolidation or the extent to which the original memories were reactivated. Future studies should measure memory reactivation explicitly.

In summary, we show that the act of retrieval may enhance memory, that interference may impair memory, and that both effects depend critically on the age of the memories. Evidence for memory reconsolidation was obtained only for middle-aged memories. Given the potential to change unwanted memories selectively during the reconsolidation window (Brunet et al., 2008; Kindt et al., 2009; Schiller et al., 2009), determining the exact conditions under which reconsolidation occurs in human episodic memory is a challenge for future studies.

References

Barnes, J. M., & Underwood, B. J. (1959). "Fate" of first-list associations in transfer theory. *Journal of Experimental Psychology, 58,* 97–105. doi:10.1037/h0047507

Bäuml, K.-H. (1996). Revisiting an old issue: Retroactive interference as a function of the degree of original and interpolated learning. *Psychonomic Bulletin & Review, 3,* 380–384. doi:10.3758/BF03210765

Bower, G. H., Thomson-Schill, S., & Tulving, E. (1994). Reducing retroactive interference: An interference analysis. *Journal of Experimental Psychology, 20,* 51–66.

Brunet, A., Orr, S. P., Tremblay, J., Robertson, K., Nader, K., & Pitman, R. K. (2008). Effect of post-retrieval propranolol on psychophysiologic responding during subsequent script-driven traumatic imagery in post-traumatic stress disorder. *Journal of Psychiatric Research, 42,* 503–506. doi:10.1016/j.jpsychires.2007.05.006

Carrier, M., & Pashler, H. (1992). The influence of retrieval on retention. *Memory & Cognition, 20,* 633–642. doi:10.3758/BF03202713

Debiec, J., LeDoux, J. E., & Nader, K. (2002). Cellular and systems reconsolidation in the hippocampus. *Neuron, 36,* 527–538. doi:10.1016/S0896-6273(02)01001-2

Dudai, Y. (2004). The neurobiology of consolidation, or, how stable is the engram? *Annual Review of Psychology, 55,* 51–86. doi:10.1146/annurev.psych.55.090902.142050

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. doi:10.1101/lm.486107

Hupbach, A., Gomez, R., Hardt, O., & Nadel, L. (2007). Reconsolidation of episodic memories: A subtle reminder triggers integration of new information. *Learning & Memory, 14,* 47–53. doi:10.1101/lm.365707

Hupbach, A., Hardt, O., Gomez, R., & Nadel, L. (2008). The dynamics of memory: Context-dependent updating. *Learning & Memory, 15,* 574–579. doi:10.1101/lm.1022308

Karpicke, J. D., & Roediger, H. K. (2008). The critical importance of retrieval for learning. *Science, 319,* 966–968. doi:10.1126/science.1152408

Kindt, M., Soeter, M., & Vervliet, B. (2009). Beyond extinction: Erasing human fear responses and preventing the return of fear. *Nature Neuroscience, 12,* 256–258. doi:10.1038/nn.2271

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). *International Affective Picture System (IAPS): Technical manual and affective ratings.* Gainesville, FL: National Institute of Mental Health Center for the Study of Emotion and Attention.

Lee, J. L. C., Di Ciano, P., Thomas, K. L., & Everitt, B. J. (2005). Disrupting reconsolidation of drug memories reduces cocaine-seeking behavior. *Neuron, 47,* 795–801. doi:10.1016/j.neuron.2005.08.007

McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psychological Review, 102,* 419–457.

McGaugh, J. L. (2000). Memory - A century of consolidation. *Science, 287,* 248–251. doi:10.1126/science.287.5451.248

Milekic, M. H., & Alberini, C. M. (2002). Temporally graded requirement for protein synthesis following memory reactivation. *Neuron, 36,* 521–525. doi:10.1016/S0896-6273(02)00976-5

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. doi:10.1126/science.160.3827.554

Myers, K. M., & Davis, M. (2002). Systems-level reconsolidation: reengagement of the hippocampus with memory reactivation. *Neuron, 36,* 340–343.

Nadel, L., & Moscovitch, M. (1997). Memory consolidation, retrograde amnesia and the hippocampal complex. *Current Opinion in Neurobiology, 7,* 217–227.

Nader, K. (2003). Memory traces unbound. *Trends in Neuroscience, 26,* 65–72. doi:10.1016/S0166-2236(02)00042-5

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. doi:10.1038/35021052

Przybyslawski, J., Roullet, P., & Sara, S. J. (1999). Attenuation of emotional and nonemotional memories after their reactivation: Role of β adrenergic receptors. *Journal of Neuroscience, 19,* 6623–6628.

Sara, S. J. (2000). Retrieval and reconsolidation: Toward a neurobiology of remembering. *Learning & Memory, 7,* 73–84. doi:10.1101/lm.7.2.73

Schiller, D., Monfils, M.-H., Raio, C. M., Johnson, D. C., LeDoux, J. E., & Phelps, E. A. (2009). Preventing the return of fear in humans using reconsolidation update mechanisms. *Nature, 463,* 49–53. doi:10.1038/nature08637

Schwabe, L., & Wolf, O. T. (2009). New episodic learning interferes with the reconsolidation of autobiographical memories. *PLoS ONE, 4,* e7519. doi:10.1371/journal.pone.0007519

Squire, L. R. (1999). Memory and hippocampus: a synthesis from findings with rats, monkeys, and humans. *Psychological Review, 99,* 195–231.

Suzuki, A., Josselyn, S. A., Frankland, P. W., Masushige, S., Silva, A. J., & Kida, S. (2004). Memory reconsolidation and extinction have distinct temporal and biochemical signatures. *The Journal of Neuroscience, 24,* 4787–4795. doi:10.1523/JNEUROSCI.5491-03.2004

Walker, M. P., Brakefield, T., Hobson, J. A., & Stickgold, R. (2003). Dissociable stages of human memory consolidation and reconsolidation. *Nature, 425,* 616–620. doi:10.1038/nature01930

Wang, S.-H., de Oliveira Alvares, L., & Nader, K. (2009). Cellular and systems mechanisms of memory strength as a constraint on auditory fear reconsolidation. *Nature Neuroscience, 12,* 905–913. doi:10.1038/nn.2350

Wickelgren, W. A. (1965). Acoustic similarity and retroactive interference in short-term memory. *Journal of Verbal Learning and Verbal Behavior, 4,* 53–61. doi:10.1016/S0022-5371(65)80067-6

Received March 28, 2011
Revision received May 5, 2011
Accepted July 26, 2011 ■