Research Article

Sleep Preferentially Enhances Memory for Emotional Components of Scenes

Jessica D. Payne,[1,2] **Robert Stickgold,**[2] **Kelley Swanberg,**[1] **and Elizabeth A. Kensinger**[3]

[1]*Department of Psychology, Harvard University;* [2]*Harvard Medical School Department of Psychiatry at Beth Israel Deaconess Medical Center; and* [3]*Department of Psychology, Boston College*

ABSTRACT—*Central aspects of emotional experiences are often well remembered at the expense of background details. Previous studies of such memory trade-offs have focused on memory after brief delays, but little is known about how these components of emotional memories change over time. We investigated the evolution of memory for negative scenes across 30 min, 12 daytime hours spent awake, and 12 nighttime hours including sleep. After 30 min, negative objects were well remembered at the expense of information about their backgrounds. Time spent awake led to forgetting of the entire negative scene, with memories of objects and their backgrounds decaying at similar rates. Sleep, in contrast, led to a preservation of memories of negative objects, but not their backgrounds, a result suggesting that the two components undergo differential processing during sleep. Memory for a negative scene develops differentially across time delays containing sleep and wake, with sleep selectively consolidating those aspects of memory that are of greatest value to the organism.*

Sleep plays an important role in memory consolidation. Although most studies to date have focused on procedural memory (Stickgold, 2005), emerging evidence suggests that sleep benefits episodic memory as well (Born, Rasch, & Gais, 2006). In behavioral studies of word recognition and word-pair association (Gais, Lucas, & Born, 2006), sleep following learning has been shown to improve performance relative to

Address correspondence to Jessica D. Payne, Department of Psychology, Harvard University, 33 Kirkland St., Room 884, Cambridge, MA 02138, e-mail: jdpayne@bidmc.harvard.edu, or to Elizabeth A. Kensinger, Department of Psychology, Boston College, 140 Commonwealth Ave., Chestnut Hill, MA 02467, e-mail: elizabeth.kensinger.1@bc.edu.

waking control conditions, and to increase resistance to interfering information (Ellenbogen, Hulbert, Stickgold, Dinges, & Thompson-Schill, 2006). Training on such episodic memory tasks has been shown to modify the architecture of subsequent sleep stages (Gais, Molle, Helms, & Born, 2002) and to promote the reactivation of neural ensembles during posttraining sleep—effects that often correlate with memory improvement (Peigneux et al., 2004). Moreover, performance on hippocampally dependent tasks is frequently impaired following posttraining sleep deprivation (Smith & Rose, 1996), which suggests that sleep may be necessary for memory consolidation. These studies strongly suggest that sleep contributes to the consolidation of episodic memories, perhaps through slow, off-line processes that stabilize memories.

Episodic memory performance can be enhanced by emotional arousal, and, interestingly, this effect is often greater after longer ($\geq$ 24 hr) retention delays than after shorter ones (Kleinsmith & Kaplan, 1963; Sharot & Yonelinas, 2007; Walker & Tarte, 1963). These findings demonstrate that emotion can influence slow, off-line memory-consolidation processes, and suggest that these processes may be sleep dependent.

Despite the current interest in emotion and memory, researchers are still learning how emotional memories evolve over time, and only two studies have examined changes in emotional memories across periods of wake and sleep (Hu, Stylos-Allan, & Walker, 2006; Wagner, Gais, & Born, 2001). As a consequence, little is known about how such memories are changed by time spent in different brain states.

In their study of sleep and emotional memory, Wagner et al. (2001) found that memory for negative arousing narratives was facilitated after 3 hr of late-night sleep, which is rich in REM (rapid eye movement) sleep.[1] As REM sleep intensely activates

[1]The majority of non-REM slow-wave sleep occurs in the first half of the night, whereas the majority of REM sleep occurs in the second half.

the limbic system, particularly the amygdala, and is the stage of sleep in which most emotional dreaming occurs, this was the predicted result. Yet it remained to be determined whether a full (7–8 hr) night of sleep would also benefit emotional memories.

Hu et al. (2006) examined the impact of a full night of sleep on memory for negative arousing and neutral pictures, using both *remember* and *know* measures of recognition memory. A night of sleep improved memory accuracy for negative arousing pictures relative to an equivalent period of daytime wakefulness, but only for *know* judgments. Moreover, memory bias changed across a night of sleep relative to a period of wakefulness, such that participants became more conservative when making *remember* judgments, especially for emotionally arousing pictures. These findings demonstrate that sleep's influence can be observed following a full night of sleep and provide further evidence that sleep may facilitate memory for emotionally salient information.

Both of these studies suggest a role for sleep in processing and consolidating memory for emotional experiences. We thought an important next step was to examine exactly which aspects of memories of emotional events are influenced by sleep. This question is an important one because memories of emotional events are not preserved as precise replicas of original experience. Rather, central, emotional information is often remembered at the expense of background details (Payne, Nadel, Britton, & Jacobs, 2004; Reisberg & Heuer, 2004). A real-world example of this trade-off is the *weapon-focus effect*, wherein victims vividly remember an assailant's weapon but have little memory for other important aspects of the scene (Stanny & Johnson, 2000). This divergence in memory for central and peripheral aspects of emotional events reflects, at least in part, differential encoding of these two components of the scene. But it is also possible that these elements undergo qualitatively different processing subsequent to encoding.

At present, it is unclear how the components of emotional memories are processed and stored, whether they change over time or remain the same, and whether periods of sleep affect their consolidation differently than periods spent awake. Emotional scenes could be stored as intact units, undergoing some forgetting over time but retaining the same relative vividness for central and peripheral components. Alternatively, the components of the scene could undergo differential processing and storage, perhaps with a selective emphasis on what is most salient and worthy of remembering. In the study reported here, we asked how the consolidation process influences memories for negative emotional scenes, and whether the distinctive brain state of sleep leads to a unique pattern of memory retrieval.

We presented participants with pictures of neutral or negatively arousing objects (e.g., a dead body) on neutral backgrounds (e.g., a sidewalk), and later tested their memory separately for the objects and backgrounds. This task reveals an "emotional trade-off" following brief (30-min) delays (Kensinger, Garoff-Eaton, & Schacter, 2007). Whereas negative emotional objects are better remembered than neutral ones, neutral backgrounds associated with these negatively arousing objects are remembered more poorly than similar backgrounds presented with neutral objects. Our goal was to investigate the development of memory for these two scene components across time delays of 30 min, 12 daytime hours spent awake, and 12 nighttime hours including a night of sleep.

METHOD

Participants

Eighty-eight students from Boston College and Harvard University participated for payment. They were randomly assigned to one of four conditions: wake-delay condition (24 participants), sleep-delay condition (24 participants), morning 30-min condition (20 participants), and evening 30-min condition (20 participants). Participants in the wake-delay condition viewed the stimuli at 9 a.m. and were tested 12 hr later at 9 p.m.; they did not nap between sessions. Participants in the sleep-delay condition viewed the stimuli at 9 p.m. and were tested 12 hr later, after a full night (7–8 hr) of sleep, at 9 a.m. the following morning. The two baseline circadian control groups viewed the stimuli at 9 a.m. (morning 30-min condition) or 9 p.m. (evening 30-min condition) and were tested just 30 min later. All participants were native English speakers with normal or corrected-to-normal vision. No participant reported a history of psychiatric or sleep disorders or was taking medications that affect the central nervous system or sleep architecture.

Materials

The scenes portrayed negative arousing or neutral objects placed on plausible neutral backgrounds. For each of 64 scenes (e.g., a car on a street), we created eight different versions by placing each of two similar neutral objects (e.g., two images of a car) and each of two related negative objects (e.g., two images of a car accident) on each of two plausible neutral backgrounds (e.g., two images of a street). An additional 32 scenes served as lures on a recognition memory test (Fig. 1). Participants in a previous study had rated the objects and backgrounds for valence and arousal, using 7-point scales (Kensinger, Garoff-Eaton, & Schacter, 2006). All negative objects had received arousal ratings of 5 to 7 (with high scores signifying an exciting or arousing image) and valence ratings lower than 3 (with low scores signifying a negative image). All neutral items (objects and backgrounds) had been rated as nonarousing (arousal values lower than 4) and neutral (valence ratings between 3 and 5).

Procedure

Participants studied a set of 64 scenes (32 with a neutral object and 32 with a negative object, all on neutral backgrounds) for 5 s each, and then indicated on a 7-point scale whether they would approach or move away from the scene if they encountered it in real life. This task was used to maximize encoding. The studied
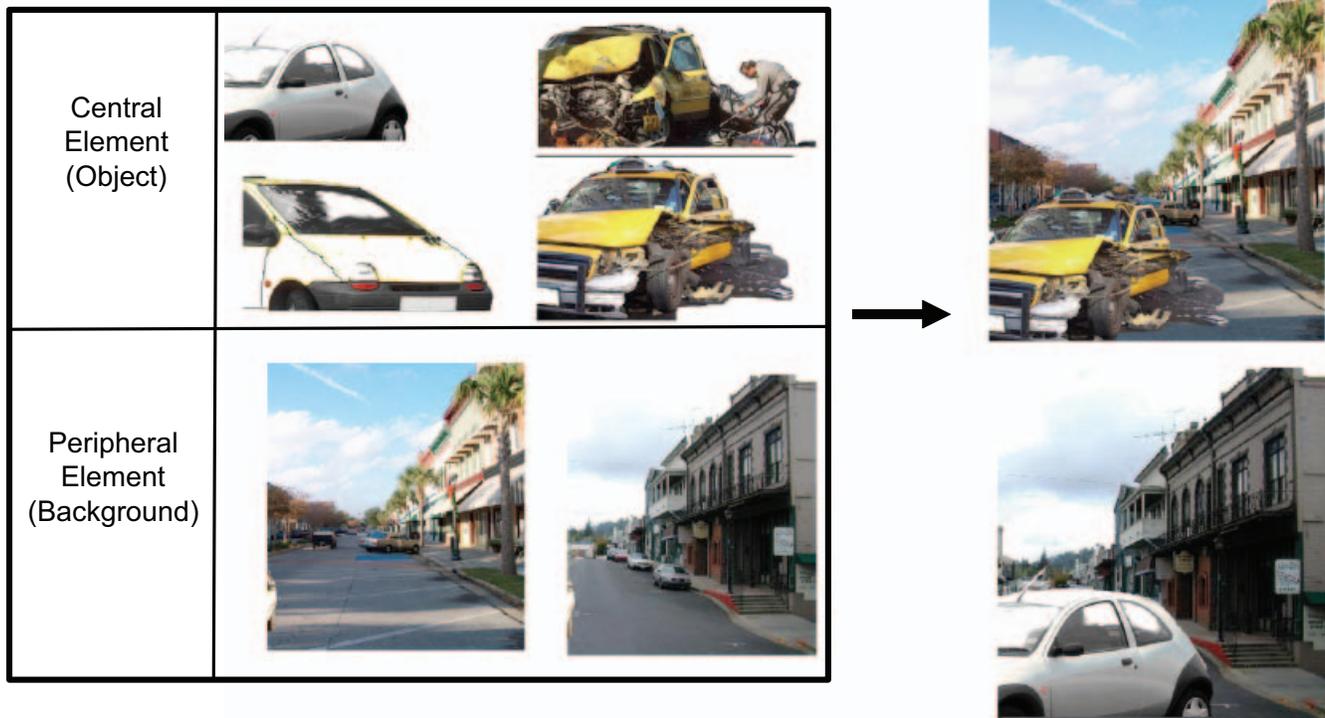
Fig. 1. Examples of the scenes presented to subjects. Eight versions of each scene were created by combining each of four similar objects (two neutral objects, two negative and arousing emotional objects) with each of two plausible neutral backgrounds. In this example, the two neutral central objects are cars, and the two negative central objects are cars damaged in an accident; the neutral backgrounds are street scenes. Two of the eight versions of the completed scene are shown.

version of each scene (of the eight possible versions) was counterbalanced across participants.

After the delay period, participants performed an unexpected, self-paced recognition task. During this task, objects and backgrounds were presented separately and one at a time. Some of these objects and backgrounds were identical to the scene components that had been studied (e.g., the *same* car accident), others were the alternate version of the object or background and therefore shared the same verbal label but differed in specific visual details (e.g., a *similar* car accident), and others were objects or backgrounds that had not been studied (*new*). Participants never saw both the *same* and the *similar* version of an item at test. Each object or background was presented with a question (e.g., "Did you see a monkey?"). If the answer to the question was "yes," participants pressed one button to indicate that the object or background was an exact match to a studied component ("same") or a second button to indicate that it was not an exact match ("similar"). If the answer to the question was "no," they pressed a third button.[2]

The recognition task included 32 *same* objects (16 negative, 16 neutral), 32 *similar* objects (16 negative, 16 neutral), 32 *new*

objects (16 negative, 16 neutral), 32 *same* backgrounds (16 previously shown with a negative object, 16 previously shown with a neutral object), 32 *similar* backgrounds (16 previously shown with a negative object, 16 previously shown with a neutral object), and 32 *new* backgrounds.

Data Analysis

To permit a direct replication of Kensinger et al. (2007), we calculated an *overall recognition* score by adding the number of "same" and "similar" responses to *same* items. This measure was used to determine whether we had replicated the trade-off at 30 min and whether it extended to 12 hr. For all other analyses, however, we separated this measure into specific and general recognition memory for scene components. This was key, because previous studies suggest that sleep preferentially promotes memory for general over detailed information (Gómez, Bootzin, & Nadel, 2006; Hu et al., 2006; Payne et al., 2007). Following the procedures of previous studies in which participants made a same-similar distinction at retrieval (e.g., Garoff, Slotnick, & Schacter, 2005; Kensinger et al., 2007), we scored a response as *specific recognition* of visual details when a subject correctly responded "same" to a *same* item, but as *general recognition* without specific details when a subject responded "similar" to a *same* item. Because "similar" responses were constrained by the number of "same" responses (i.e., subjects

---

[2]We asked questions using text to limit the scope of "similar" responses. For example, remembering a church seen during encoding might lead a subject to score a picture of a mosque shown at test as similar. Asking "Did you see a mosque?" would force a negative response.

responded "similar" only when they did not remember the visual details), we computed the general recognition score as the proportion of "similar" responses after exclusion of "same" responses (similar/[1 − same]). This calculation parallels that used for "independent know" calculations in the remember/ know procedure (Rajaram, 1993; Tulving, 1985; Yonelinas & Jacoby, 1995) and accounts for the fact that the two response types were mutually exclusive.

Specific and general recognition scores were computed separately for central objects (negative or neutral) and for the peripheral neutral backgrounds (studied with either a negative or a neutral object). By comparing memory after a short (30-min) delay with memory after a 12-hr delay spent awake and with memory after a 12-hr delay including sleep, we could examine how the passage of time, with and without sleep, influenced memory.

Because the false alarm rate ("same" or "similar" responses to *new* items) was low (less than 5% for "same" responses to *new* items and less than 20% for "similar" responses to *new* items) and did not differ between groups (all $ps > .16$), we report uncorrected recognition scores, except in the Other Analyses section.

RESULTS

Circadian Effects

We first examined whether circadian effects influenced memory performance on this task, but we found no evidence of such influences. No measure of memory performance differed between the morning and evening 30-min-delay groups (see Table 1). We therefore combined data from these two groups in the analyses reported in the following sections. Standard measures of

TABLE 1

Mean Proportion of Items Correctly Recognized in the Morning and Evening 30-Min Conditions

Memory type and scene component	Group				Difference	
	Morning		Evening			
	M	SEM	M	SEM	t(38)	p
Overall recognition						
Negative objects	.83	.03	.86	.02	0.81	.42
Negative backgrounds	.69	.03	.65	.03	0.92	.36
Neutral objects	.74	.03	.76	.03	0.52	.61
Neutral backgrounds	.76	.03	.75	.03	0.20	.84
General recognition						
Negative objects	.57	.07	.63	.06	0.71	.49
Negative backgrounds	.53	.05	.40	.06	1.8	.08
Neutral objects	.49	.04	.57	.05	1.1	.26
Neutral backgrounds	.48	.05	.49	.06	0.20	.84
Specific recognition						
Negative objects	.72	.04	.71	.03	0.34	.72
Negative backgrounds	.42	.03	.43	.04	0.18	.85
Neutral objects	.60	.04	.55	.04	1.0	.31
Neutral backgrounds	.58	.04	.57	.03	0.25	.80

subjective alertness, acquired using the Stanford Sleepiness Scale (Hoddes, Zarcone, Smythe, Phillips, & Dement, 1973), also were not significantly different between the morning and evening 30-min-delay groups (2.4 ± 0.20 vs. 2.3 ± 0.24; $p = .58$). These findings strongly suggest that diurnal differences in cognitive performance, or general levels of alertness, do not account for the memory differences we found between the sleep-delay and wake-delay groups.

The Emotional-Memory Trade-Off and Its Persistence Over Time

Our first objective was to confirm the existence of the emotional-memory trade-off at 30 min and, more critically, to determine whether it would remain pronounced after 12 hr (across the combined sleep- and wake-delay conditions). We therefore conducted a 2 (valence: negative, neutral) × 2 (scene component: object, background) × 2 (delay: 30 min, 12 hr combined) mixed analysis of variance (ANOVA) on overall recognition ("same" plus "similar" responses), after Kensinger et al. (2007). This analysis revealed a main effect of delay, $F(1, 86) = 27.8$, $p < .0001$, $\eta_p^2 = .25$; memories for both scene components were better after 30 min than after 12 hr. Critically, there was a significant interaction between valence and scene component, $F(1, 86) = 68.7$, $p < .0001$, $\eta_p^2 = .44$, which confirmed the existence of the trade-off. These factors did not interact with the delay variable, however. Thus, the trade-off was present at both 30 min and 12 hr (see Fig. 2). Although objects and backgrounds were recognized at similar rates within the neutral scenes, objects were significantly better recognized than backgrounds within the negative scenes, $t(39) = 6.3$, $p < .0001$, and $t(47) = 7.7$, $p < .0001$, for the 30-min delay and 12-hr delay, respectively. Moreover, although memory was significantly better for negative than for neutral objects after both delays, $t(39) = 3.9$, $p < .0001$ (30-min delay), and $t(47) = 5.0$, $p < .0001$ (12-hr delay), memory for backgrounds that had contained these negative objects was impaired relative to memory for backgrounds that had contained neutral objects, $t(39) = 3.9$, $p < .0001$ (30-min delay), and $t(47) = 4.5$, $p < .0001$ (12-hr delay).

Specific recognition ("same" responses) also showed the critical Valence × Scene Component interaction, $F(1, 86) = 150.3$, $p < .0001$, $\eta_p^2 = .64$, as did general recognition (similar/[1 − same]), $F(1, 86) = 10.6$, $p = .002$, $\eta_p^2 = .11$. These findings confirm and extend the well-documented trade-off in memory for the central and peripheral components of emotional scenes after brief time delays (Kensinger et al., 2007).

Sleep Versus Wake

Given the growing literature on sleep and memory consolidation, our main goal was to determine whether a period of sleep would affect the consolidation of these scenes differently than a period of wake. Because Hu et al. (2006) found that sleep benefited emotional memory for "know" but not "remember" responses,
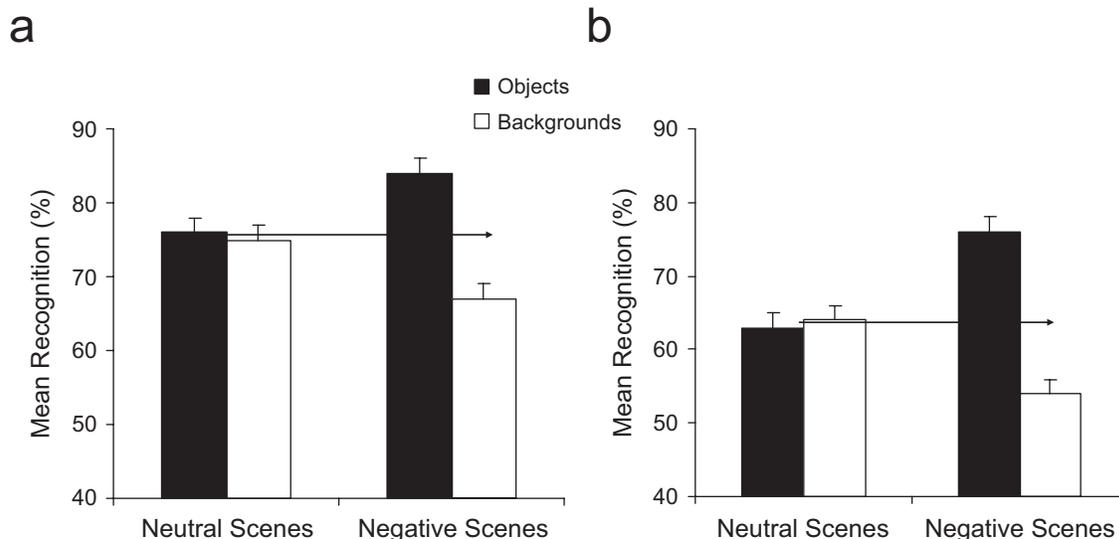
Fig. 2. Mean overall recognition memory for objects and backgrounds in neutral and negative emotional scenes. Results are shown for subjects tested (a) after 30 min (morning and evening groups combined) and (b) after 12 hr (wake-delay and sleep-delay groups combined). The arrows represent the average recall for objects and backgrounds in the neutral condition. Overall recognition was calculated as the total number of ''same'' and ''similar'' responses to *same* items (after Kensinger, Garoff-Eaton, & Schacter, 2007). Note that because the y-axes reflect overall recognition scores, these graphs are not directly comparable with those in Figure 3, which splits memory into general and specific recognition.

and because other work in our laboratory suggests that sleep preferentially promotes memory for general information over memory for specific information (Payne et al., 2007), we focus on general recognition memory (similar/[1 − same]) for all analyses concerning sleep.

A 2 (condition: sleep, wake) × 2 (valence: negative, neutral) × 2 (scene component: object, background) mixed ANOVA on general recognition revealed interactions between condition and valence, $F(1, 46) = 13.1$, $p = .001$, $\eta_p^2 = .20$; between condition and scene component, $F(1, 46) = 7.6$, $p = .008$, $\eta_p^2 = .14$; and, most important, among the three factors, $F(1, 46) = 4.7$, $p = .03$, $\eta_p^2 = .10$ (see Figs. 3a and 3b). Negative, but not neutral, objects were better remembered after sleep than after wake, $F(1, 46) = 11.5$, $p = .001$, $\eta_p^2 = .20$. In contrast, sleep offered no benefit for backgrounds, regardless of whether they were presented with negative or neutral objects (Valence × Condition interaction, $p > .10$). Thus, although memory for negative objects was enhanced by sleep relative to wake (68% vs. 44%), memory for their accompanying backgrounds was unchanged by sleep (38% vs. 38% in the sleep and wake conditions, respectively). The same pattern emerged in analyses of specific recognition memory, but the three-way interaction did not reach significance ($p > .1$, n.s.; see Figs. 3c and 3d).

Changes in Memory Relative to the 30-Min Baseline
To determine how memories changed over time, we next analyzed general recognition performance across wake and sleep relative to performance after 30 min by subtracting performance at 30 min from performance at 12 hr. A 2 (condition: sleep, wake) × 2 (valence: negative, neutral) × 2 (scene component:

object, background) mixed ANOVA revealed significant two-way interactions between condition and valence, $F(1, 46) = 11.6$, $p = .001$, $\eta_p^2 = .20$, and between condition and scene component, $F(1, 46) = 7.6$, $p = .008$, $\eta_p^2 = .14$, as well as a significant three-way interaction, $F(1, 46) = 4.7$, $p = .035$, $\eta_p^2 = .09$. Referring back to Figure 3b, one can see that for neutral scenes, general recognition of objects was similar to general recognition of backgrounds in each of the three delay groups (30-min delay, wake delay, sleep delay; all $ps > .1$, n.s.), and that there was little change in memory for neutral scenes over time, whether spent awake or asleep. The pattern for specific recognition memory for neutral scenes was similar, except that both object and background recognition were significantly reduced at 12 hr relative to 30 min (both $ps < .05$; see Fig. 3d).

By contrast, change in memory for negative-scene components was distinctly different across periods of wake and sleep. Time spent awake led to a clear deterioration in general recognition memory, and this decline was present for both objects and their backgrounds (16% and 9% deterioration after a 12-hr wake delay, relative to a 30-min delay; see Fig. 3a). Sleep, however, produced a divergence in memory for objects and backgrounds within negative scenes. Whereas memory for backgrounds containing negative objects was again reduced by 9% after a 12-hr delay including sleep, relative to the 30-min delay (a reduction similar to that seen after 12 hr of wake), memory for negative objects showed a nonsignificant 8% *increase* after sleep. Critically, memory for negative objects was significantly better after sleep than after wake; this was true for both general recognition (68% vs. 44%), $t(46) = 3.4$, $p = .001$, and for specific recognition (68% vs. 58%), $t(46) = 2.7$, $p = .01$.
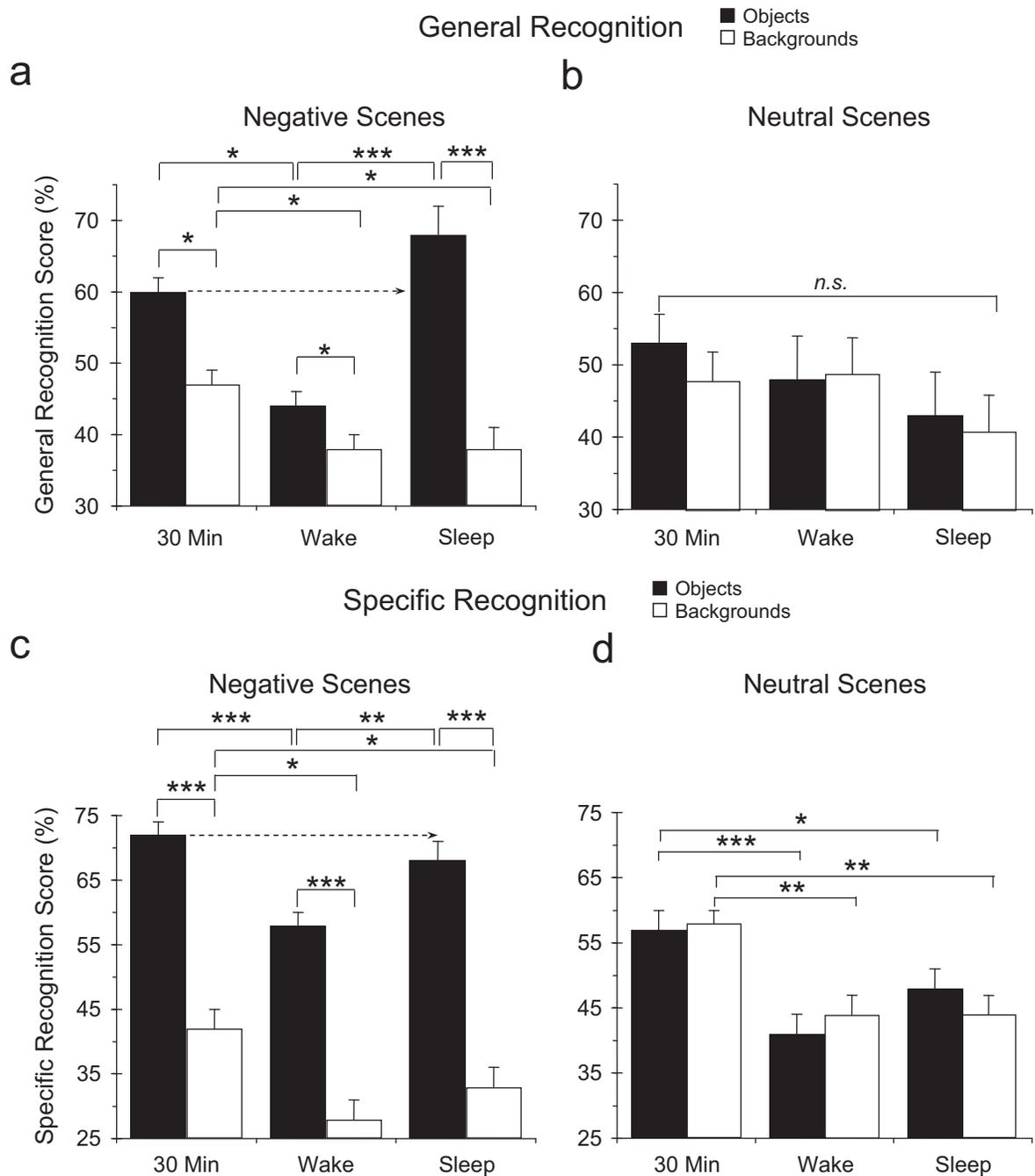
Fig. 3. Mean recognition memory for objects and backgrounds in the three delay conditions: 30 min, wake delay, and sleep delay. Separate graphs show results for (a) general recognition for negative scenes, (b) general recognition for neutral scenes, (c) specific recognition for negative scenes, and (d) specific recognition for neutral scenes. The dotted arrows highlight the difference in memory for negative arousing objects between the 30-min condition and the 12-hr sleep condition. Significant differences are denoted by asterisks, $*p < .05$, $**p \leq .01$, $***p \leq .001$.

These results suggest that, rather than preserving memory for the entire negative scene, sleep selectively preserved memory for the scene's negative emotional center.

Other Analyses
As expected, given the low rates of false alarms in all conditions, correcting for false alarms did not change the pattern of findings for overall, general, or specific recognition. For example, when general recognition scores were corrected for false alarms ("similar" responses to *new* stimuli/(1 − ["same" responses to *new* stimuli]), the critical 2 (condition: sleep, wake) × 2 (object valence: negative, neutral) × 2 (scene component: object, background) ANOVA still revealed significant interactions between condition and valence, $F(1, 46) = 13.0$, $p = .001$,

$\eta_p{}^2 = .19$; between condition and scene component, $F(1, 46) = 8.2$, $p = .006$, $\eta_p{}^2 = .14$; and among the three factors, $F(1, 46) = 4.6$, $p = .04$, $\eta_p{}^2 = .10$.

DISCUSSION

Emotional episodic memories are often complex, with multiple components. This study provides important insights into how such memories develop over time. First, we replicated the emotional-memory trade-off after 30 min (Kensinger et al., 2007). Negatively arousing objects are better remembered than neutral objects, whereas their backgrounds are more poorly remembered than the backgrounds associated with neutral objects. But what happens to these memories with further processing, as they begin the process of long-term consolidation? We have demonstrated that the disparity between negative objects and their backgrounds persists or even grows across 12 hr, and that these memory components develop differently across sleep and wakefulness.

Although 12 hr of wake produced similar forgetting of both components of negative scenes, relative to a 30-min delay, sleep led to a divergence of the two memory components. Rather than conferring a general benefit on memory for negative scenes in their entirety, sleep promoted memory for central emotional objects only; sleep's benefit did not extend to the backgrounds in which the emotional objects were embedded. As a result, the disparity in general recognition between emotional objects and their backgrounds more than doubled after 12 hr including sleep, compared with after either a 30-min delay or 12 hr spent awake (see Fig. 3a)—an increase that was entirely due to maintenance of emotional-object memory. This result is consistent with the possibility that the individual components of the scene become "unbound" during sleep, allowing sleep to selectively preserve only what is calculated to be most salient and perhaps most worthy of remembering.

These results add to a growing literature demonstrating that sleep benefits the consolidation of emotional over neutral information. Wagner and his colleagues demonstrated a benefit of sleep for emotional, but not neutral, narratives, and showed that this benefit lasts for years (Wagner et al., 2001; Wagner, Hallschmid, Rasch, & Born, 2006). Hu et al. (2006) showed a similar sleep benefit for emotional over neutral photographs. Together, these findings suggest that sleep plays a role in consolidation of emotional memories that exceeds any benefit it has for neutral memories.

Intriguingly, sleep did not benefit neutral memory in any of these studies, which is curious given the literature on sleep-based consolidation of neutral episodic memories (see Payne, Ellenbogen, Walker, & Stickgold, 2008, for a review). It may be that mixed presentation of neutral and emotional stimuli biases processing toward enhancing only the emotional information, whereas blocked presentation would produce benefits of sleep for both neutral and emotional information. Although this possibility remains to be tested, we note that mixed and pure presentation of stimuli lead to very different patterns of memory retrieval in other paradigms (e.g., Hadley & McKay, 2006; Schmidt, 1994). Moreover, in the present study, sleep exerted its strongest effects on general, rather than specific, memory. This pattern is consistent with the findings of Hu et al. (2006) and Payne et al. (2007), and suggests that sleep may preferentially promote memory for gist over memory for detail.

Although we believe that sleep itself produced these unique patterns of memory consolidation, two alternative explanations deserve consideration. The first is that memory was simply better in the morning than in the evening. However, if this were the case, differences in memory for the negative scenes should have emerged between the two 30-min groups (morning and evening), and the same circadian influence should have operated equally on negative and neutral memories. Neither pattern was observed. Moreover, the discrepancy between memory for negative objects and memory for their backgrounds not only was greater after a period of sleep than after a period of wakefulness, but also was greater after a period of sleep than after a much shorter 30-min delay in the morning ($Fs > 3$, $ps < .05$). Finally, there were no differences between morning and evening subjective ratings of alertness in the 30-min-delay groups. Together, these points suggest that circadian influences cannot account for our findings.

Our findings also could reflect a lack of interference during sleep (Wixted, 2004). But in this case, sleep should have provided a global consolidation benefit to memories for both objects and backgrounds and for both negative and neutral stimuli. Yet only memory for negative objects benefited from sleep. One could argue that during sleep, memory interference continued unabated for backgrounds and neutral objects, while being completely absent for negative objects. But interference did not show such effects during wake. Furthermore, if the findings were due to a lack of interference during sleep, memory for negative objects should have been better after a 30-min delay (a time interval allowing very little interference) than after a 12-hr delay including sleep, given that participants in the latter condition were awake for 2.5 hr on average after their training at 9 p.m. and for at least 30 min prior to their test at 9 a.m. the following morning. That is, subjects in the sleep-delay condition had 3 hr of waking interference between training and test, yet their memory for negative objects was actually nonsignificantly better after 12 hr with sleep than was the negative-object memory of subjects who were tested after just 30 min awake. We therefore feel that interference alone cannot satisfactorily explain our findings.

Although interference likely did contribute to deterioration in the wake condition, we believe our results are most parsimoniously explained by an active role for sleep in the consolidation of emotional memories (Ellenbogen, Payne, & Stickgold, 2006). By an "active" role, we mean that sleep-specific neural processes contribute directly to memory consolidation. These could

include neurophysiological processes (e.g., 1- to 4-Hz slow waves, slow oscillations at a frequency below 1 Hz, or 12- to 16-Hz sleep spindles) and neurochemical processes related to the fluctuations in aminergic and cholinergic neurotransmitters seen across the wake-sleep cycle (Payne et al., 2008).

To our knowledge, these are the first findings to demonstrate (a) that the emotional-memory trade-off persists over time, and (b) that the individual components of emotional-scene memories evolve differently across time spent asleep and time spent awake. Thus, these findings provide important insights into the evolution of emotional memories over time, and suggest a unique role for sleep in their consolidation.

REFERENCES

Born, J., Rasch, B., & Gais, S. (2006). Sleep to remember. *Neuroscientist*, *12*, 410–424.

Ellenbogen, J.M., Hulbert, J.C., Stickgold, R., Dinges, D.F., & Thompson-Schill, S.L. (2006). Interfering with theories of sleep and memory: Sleep, declarative memory, and associative interference. *Current Biology*, *16*, 1290–1294.

Ellenbogen, J.M., Payne, J.D., & Stickgold, R. (2006). The role of sleep in declarative memory consolidation: Passive, permissive, active, or none? *Current Opinion in Neurobiology*, *16*, 716–722.

Gais, S., Lucas, B., & Born, J. (2006). Sleep after learning aids memory recall. *Learning & Memory*, *13*, 259–262.

Gais, S., Molle, M., Helms, K., & Born, J. (2002). Learning-dependent increases in sleep spindle density. *Journal of Neuroscience*, *22*, 6830–6834.

Garoff, R.J., Slotnick, S.D., & Schacter, D.L. (2005). The neural origins of specific and general memory: The role of the fusiform cortex. *Neuropsychologia*, *43*, 847–859.

Gómez, R.L., Bootzin, R.R., & Nadel, L. (2006). Naps promote abstraction in language-learning infants. *Psychological Science*, *17*, 670–674.

Hadley, C.B., & MacKay, D.G. (2006). Does emotion help or hinder immediate memory? Arousing vs. priority-binding mechanisms. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *32*, 79–88.

Hoddes, E., Zarcone, V., Smythe, H., Phillips, R., & Dement, W.C. (1973). Quantification of sleepiness: A new approach. *Psychophysiology*, *10*, 431–436.

Hu, P., Stylos-Allan, M., & Walker, M. (2006). Sleep facilitates consolidation of emotional declarative memory. *Psychological Science*, *17*, 891–898.

Kensinger, E.A., Garoff-Eaton, R.J., & Schacter, D.L. (2006). Memory for specific visual details can be enhanced by negative arousing content. *Journal of Memory and Language*, *54*, 99–112.

Kensinger, E.A., Garoff-Eaton, R.J., & Schacter, D.L. (2007). Effects of emotion on memory specificity: Memory trade-offs elicited by negative visually arousing stimuli. *Journal of Memory and Language*, *56*, 575–591.

Kleinsmith, L.J., & Kaplan, S. (1963). Paired-associate learning as a function of arousal and interpolated interval. *Journal of Experimental Psychology*, *65*, 190–193.

Payne, J.D., Ellenbogen, J.M., Walker, M.P., & Stickgold, R. (2008). The role of sleep in memory consolidation. In J. Byrne (Series Ed.) & H.L. Roediger (Vol. Ed.), *Learning and memory: A comprehensive reference: Vol. 2. Cognitive psychology of memory* (pp. 663–685). Oxford, England: Elsevier.

Payne, J.D., Nadel, L., Britton, W.B., & Jacobs, W.J. (2004). The biopsychology of trauma and memory. In D. Reisberg & P. Hertel (Eds.), *Emotion and memory* (pp. 76–128). Oxford, England: Oxford University Press.

Payne, J.D., Propper, R., Huang, L., Walker, M.P., Schacter, D.L., & Stickgold, R. (2007, May). *Sleep on it to get the gist: Memory associations across the night*. Paper presented at the annual meeting of the Association for Psychological Science, Washington, DC.

Peigneux, P., Laureys, S., Fuchs, S., Collette, F., Perrin, F., Reggers, J., et al. (2004). Are spatial memories strengthened in the human hippocampus during slow wave sleep? *Neuron*, *44*, 535–545.

Rajaram, S. (1993). Remembering and knowing: Two means of access to the personal past. *Memory & Cognition*, *21*, 89–102.

Reisberg, D., & Heuer, F. (2004). Memory for emotional events. In D. Reisberg & P. Hertel (Eds.), *Emotion and memory* (pp. 3–41). Oxford, England: Oxford University Press.

Schmidt, S.R. (1994). Effects of humor on sentence memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *20*, 953–967.

Sharot, T., & Yonelinas, A.P. (2007). Differential time-dependent effects of emotion on recollective experience and memory for contextual information. *Cognition*, *106*, 538–547.

Smith, C., & Rose, G.M. (1996). Evidence for a paradoxical sleep window for place learning in the Morris water maze. *Physiology and Behavior*, *59*, 93–97.

Stanny, C.J., & Johnson, T.C. (2000). Effects of stress induced by a simulated shooting on recall by police and citizen witnesses. *American Journal of Psychology*, *113*, 359–386.

Stickgold, R. (2005). Sleep-dependent memory consolidation. *Nature*, *437*, 1272–1278.

Tulving, E. (1985). Memory and consciousness. *Canadian Psychologist*, *26*, 1–12.

Wagner, U., Gais, S., & Born, J. (2001). Emotional memory formation is enhanced across sleep intervals with high amounts of rapid eye movement sleep. *Learning & Memory*, *8*, 112–119.

Wagner, U., Hallschmid, M., Rasch, B., & Born, J. (2006). Brief sleep after learning keeps emotional memories alive for years. *Biological Psychiatry*, *60*, 788–790.

Walker, E.L., & Tarte, R.D. (1963). Memory storage as a function of arousal and time with homogeneous and heterogeneous lists. *Journal of Verbal Learning and Verbal Behavior*, *2*, 113–119.

Wixted, J.T. (2004). The psychology and neuroscience of forgetting. *Annual Review of Psychology*, *55*, 235–269.

Yonelinas, A.P., & Jacoby, L.L. (1995). The relation between remembering and knowing as bases for recognition: Effects of size congruency. *Journal of Memory and Language*, *34*, 622–643.