Research Article

Sleep Facilitates Consolidation of Emotional Declarative Memory

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ABSTRACT—*Both sleep and emotion are known to modulate processes of memory consolidation, yet their interaction is poorly understood. We examined the influence of sleep on consolidation of emotionally arousing and neutral declarative memory. Subjects completed an initial study session involving arousing and neutral pictures, either in the evening or in the morning. Twelve hours later, after sleeping or staying awake, subjects performed a recognition test requiring them to discriminate between these original pictures and novel pictures by responding "remember," "know" (familiar), or "new." Selective sleep effects were observed for consolidation of emotional memory: Recognition accuracy for* know *judgments of arousing stimuli improved by 42% after sleep relative to wake, and recognition bias for* remember *judgments of these stimuli increased by 58% after sleep relative to wake (resulting in more conservative responding). These findings hold important implications for understanding of human memory processing, suggesting that the facilitation of memory for emotionally salient information may preferentially develop during sleep.*

Over the past decade, a rich diversity of studies have offered converging evidence that sleep plays a critical role in memory processing and brain plasticity (M.P. Walker & Stickgold, 2006). These findings demonstrate that sleep, and its varied stages, contribute importantly to latent processes of both declarative and procedural memory consolidation (for review, see M.P. Walker & Stickgold, 2004). Aspects of the relationship between declarative episodic memory and sleep have, however, been

questioned on the basis of earlier studies that were equivocal—some confirming a role for sleep, others refuting it (e.g., Chernik, 1972; Empson & Clarke, 1970; Meienberg, 1977; Zimmerman, Stoyva, & Metcalf, 1970; Zimmerman, Stoyva, & Reite, 1978)—and this topic remains actively debated.

Supporting the idea that sleep has a beneficial influence on episodic memory, animal models have provided evidence for the role of sleep in hippocampal-dependent tasks. Training on such tasks is known to trigger alterations in sleep-stage characteristics (e.g., Ambrosini et al., 1993; Hennevin & Hars, 1987; Mandai, Guerrien, Sockeel, Dujardin, & Leconte, 1989; Smith, Young, & Young, 1980), and posttraining sleep deprivation induces consolidation impairments at retest (e.g., Beaulieu & Godbout, 2000; Fishbein, Kastaniotis, & Chattman, 1974; Hennevin & Hars, 1987; Shiromani, Gutwein, & Fishbein, 1979; Smith & Kelly, 1988; Smith & Lapp, 1986). These results indicate that sleep is not simply correlated with learning, but causal to it.

Independent of the field of sleep and learning, an established literature now demonstrates that memory processing can be modulated by the emotional strength of the material being learned (for review, see McGaugh, 2004). These studies show that memories associated with the evocation of emotion, as defined either by valence (positive/negative) or by arousal (high/low), are encoded and persist more strongly than memories lacking affective tone (Kensinger, 2004). McGaugh (2004) has suggested that these beneficial effects are due to the combined influence of amygdala and hippocampal structures, and mediated by neurohormonal and neuromodulator changes. Most relevant to the topic of off-line memory consolidation are the findings showing that the effects of emotion on memory retention increase as the delay between encoding and testing increases across hours or days (Kleinsmith & Kaplan, 1963; Levonian, 1972; Sharot & Phelps, 2004; E.L. Walker & Tarte, 1963), suggesting that emotion influences slow, time-dependent consolidation processes.

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Despite these parallel lines of evidence, few studies have investigated the interactive effect of sleep and emotion on consolidation. Wagner, Gais, and Born (2001) showed that late-night sleep, rich in rapid eye movement (REM) sleep, selectively favors retention of previously learned emotional texts relative to neutral texts. However, in this study, emotion was not specified in terms of either valence or arousal, and so it remains unclear which component of emotion governed these effects. No study to date has examined the effects of specific components of affect (i.e., arousal and valence) on overnight memory consolidation, nor has any study specifically investigated whether a period of daytime wake and an equivalent time period across a night containing sleep result in similar effects on consolidation of episodic memory (either neutral or emotional).

Finally, an important distinction in memory recollection has been demonstrated using the remember/know (R/K) procedure (Tulving, 1985). A *remember* (R) judgment indicates that recollection evokes a specific episode in which the stimulus was previously experienced. In contrast, a *know* (K) judgment indicates that a stimulus is thought to have been previously experienced (i.e., is familiar), but that the specific event details are not recollected. These two kinds of judgments may be mediated by somewhat different medial temporal lobe structures (Rugg & Yonelinas, 2003). To date, no study has investigated whether the effects of a night of sleep on memory consolidation are the same for R and K judgments, nor has this paradigm been used to examine the interactive effects of sleep and emotion on episodic memory.

In the current study, we investigated the consolidation of arousing and neutral episodic memory across 12-hr periods containing either a night of sleep or an equivalent period of time awake, examining whether these effects varied between R and K responses. Furthermore, we determined whether sleep influenced not only the accuracy of memory recognition, but also memory bias (selection criterion), for R and K judgments of emotionally arousing and neutral pictures.

Our study was driven by the hypothesis that sleep-dependent modulation of episodic memory would be particularly prominent for emotionally arousing stimuli. We predicted this for two main reasons. First, the strong emotional tone of mental activity occurring during sleep (often referred to as dream mentation), particularly during REM (Hobson, Pace-Schott, & Stickgold, 2000), has long encouraged speculation about selective sleep-dependent emotional memory processing. Second, a commonly reported consequence of a lack of sleep is dysregulation of emotion and mood (Dinges et al., 1997; Lingenfelser et al., 1994; Wesnes et al., 1997; Zohar, Tzischinsky, Epstein, & Lavie, 2005), indicating that sleep plays a role in the modulation of emotional processing and reactivity. In addition, recent studies have demonstrated that the strengths of associative memories are altered in a state-dependent manner during different sleep stages (Stickgold, Scott, Rittenhouse, & Hobson, 1999; M.P. Walker, Liston, Hobson, & Stickgold, 2002), which indicates that sleep may preferentially favor enhancement of more weakly

defined memory traces—in the current experimental context, memories associated with K responses, rather than R responses.

METHOD

The experiment was approved by the local human studies committee and in accordance with the principles of the Declaration of Helsinki.

Participants
The subjects ($N = 14$; 8 females; mean age = 22.9 years, $SD = 2.3$) reported no prior history of drug or alcohol abuse and no neurological, psychiatric, or sleep disorders. They agreed to be drug, alcohol, and caffeine free for 24 hr prior to and during the study period. All subjects maintained a standard sleep schedule for 1 week prior to the study. The amount of overnight sleep obtained was documented with sleep logs and averaged 7.4 hr ($SD = 1.1$) per night.

Experimental Protocol and Task
Subjects performed an emotional memory task involving an initial study period followed 12 hr later by a recognition test. The task was administered twice—once with the 12-hr period spanning a night of sleep (sleep phase) and once with the 12-hr period extending across the day (wake phase). Different stimulus sets were used for the two phases. The phases were counterbalanced, so that half the subjects experienced the wake phase first and the other half experienced the sleep phase first. The two phases were always separated by a 1-week interval.

The stimuli were pictures selected from the International Affective Picture System (IAPS), a series of picture slides with standardized emotional ratings (Lang, 1997). We selected two sets of stimuli that were matched in their visual characteristics (e.g., image luminance and content, such as human faces) and thematic content (objects, places, scenes), allowing for a repeated measures within-subjects experimental design.

Each stimulus set contained 300 picture slides, and each slide had a specified arousal strength, from 1 (most arousing) to 9 (least arousing) and valence strength, also from 1 (most unpleasant) to 9 (most pleasant; Lang, 1997). During the study session, subjects viewed 180 of the stimuli on a 17-in. CRT monitor at full width and height. Half of the stimuli were classified as arousing ($M = 3.6$, $SD = 0.70$), and the other half as neutral ($M = 5.6$, $SD = 0.59$); valence scores were equivalent for the arousing ($M = 4.9$, $SD = 1.8$) and neutral ($M = 5.2$, $SD = 1.7$) categories. During the recognition test, all 180 pictures from the study session were presented, randomly intermixed with 120 new pictures that were similarly balanced in arousal and valence. We selected the stimuli and designed the testing procedure (e.g., number of stimuli, ratio of old to new pictures, affect strength) in such a way that performance would be at neither floor nor ceiling levels.

Each study trial began with the presentation of a fixation crosshair (500 ms), followed by the target picture (1,500 ms) and then a blank screen (2,500 ms), after which the next trial began. Subjects were asked to view the picture stimuli knowing there would be a recognition test later. On each trial, they pressed a button on a computer keyboard to indicate whether the picture scene was judged to be indoors or outdoors. In addition, 10 alertness-control trials were randomly intermixed throughout; on these trials, the screen displayed a "1" or "0," instead of a picture, and subjects were asked to press the corresponding key on the computer keyboard during the blank-screen period. These trials were added both to maintain subjects' attention, preventing their habituation to the repetitive picture stimuli, and to provide a built-in measure of response alertness at evening and morning sessions, so that possible circadian influences could be examined.

In the 300 trials of the subsequent recognition test, an event sequence similar to that from the study phase was followed: Each trial began with a fixation crosshair (500 ms), which was followed by a picture stimulus (1,500 ms) and then a blank screen. However, the next trial did not begin until subjects made a key-press response indicating that they (a) consciously recollected seeing the specific picture from the prior study session (*R judgment*), (b) knew that the picture was presented in the prior study phase but could not recollect any contextual information about its previous occurrence (*K judgment*), or (c) thought the picture was new (*N judgment*). Subjects were given brief practice before testing proper. During this practice, they followed directions to complete nine example trials involving equal numbers of R, K, and N judgments. On practice trials, the stimuli were clipart cartoon pictures (chosen so they would not cause interference with the experimental stimuli); instructions on the R/K/N distinction were presented before each response to clarify these examples.

RESULTS

Recognition trials were classified according to whether R, K, or N judgments were correct or incorrect, and from these classifications, we calculated both recognition accuracy (d'—a measure of discriminability) and memory bias (C—an index of conservative vs. liberal response tendency), according to signal detection theory (Macmillan & Creelman, 1991). Table 1 presents a summary of the responses in the sleep and wake conditions.

Recognition Accuracy (d')

K Judgments

With the sleep and wake conditions combined, K judgments showed a significant difference between recognition accuracy for arousing pictures and recognition accuracy for neutral pictures (Fig. 1a). The direction of this difference was in accord with the results of previous research: Arousing stimuli exhibited a 30% advantage in recognition accuracy over neutral stimuli at the 12-hr recognition test, $d' = 0.93$ vs. 0.71, $t(13) = 2.45$, $p = .029$, $p_{rep} = .91$, $d = 0.36$.

However, when we performed an analysis of variance comparing the results across the four combinations of stimulus type (arousing or neutral) and condition (sleep or wake), differences emerged, $F(3, 52) = 3.17$, $p = .03$, $p_{rep} = .90$ (Fig. 1a). For arousing stimuli, recognition accuracy was significantly greater in the sleep condition than in the wake condition, $t(13) = 3.23$, $p = .006$, $p_{rep} = .96$, $d = 1.79$; a night of sleep produced a striking 42% memory advantage compared with a period of daytime wake ($d' = 1.09$ vs. 0.77). Although recognition accuracy for neutral stimuli was also better following sleep than wake ($d' = 0.78$ vs. 0.64, respectively), this difference was not significant, $t(13) = 1.00$, $p = .33$, $p_{rep} = .62$, $d = 0.18$.

Therefore, the advantage for arousing over neutral stimuli in the combined analysis was derived almost entirely from superior recognition memory for arousing stimuli in the sleep condition, and not the wake condition. Indeed, recognition accuracy for emotionally arousing stimuli in the wake condition was not significantly different from recognition accuracy for neutral stimuli in either the wake condition, $t(13) = 1.22$, $p = .24$, $p_{rep} = .69$, $d = 0.67$, or the sleep condition, $t(13) < 1$. These results demonstrate a selective influence of sleep on consolidation of emotionally arousing memory.
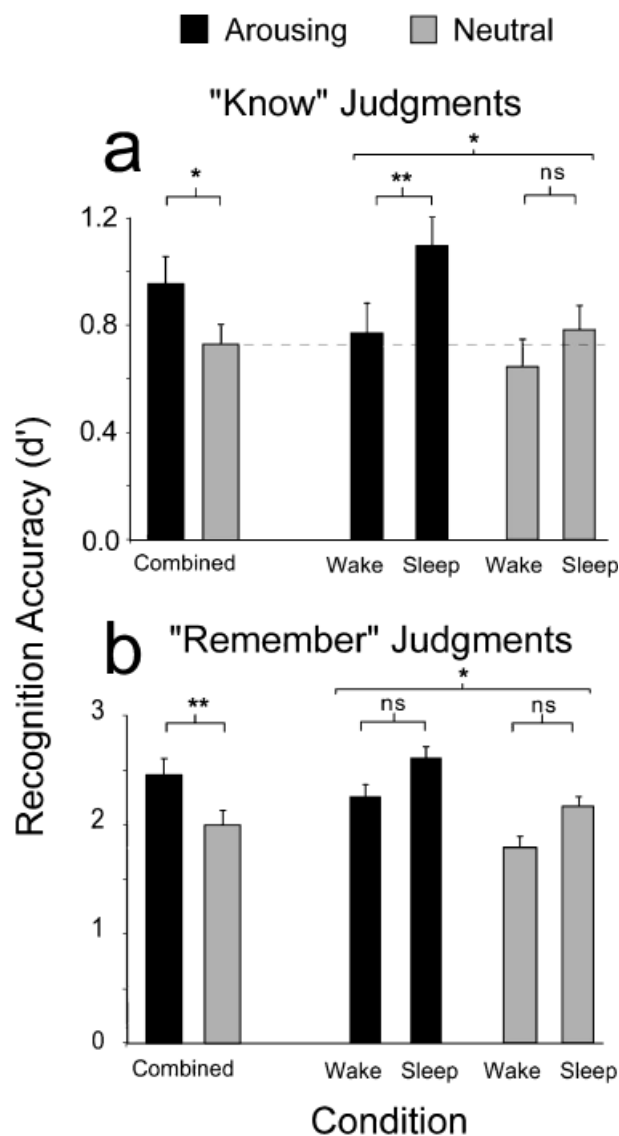
R Judgments

For R judgments, with sleep and wake conditions combined, there was again a difference between recognition memory for emotional and neutral pictures (Fig. 1b), with performance accuracy being 23% better for arousing stimuli than for neutral

TABLE 1

Mean Number of Hits, False Alarms, Correct Rejections, and Misses in the Sleep and Wake Conditions

Condition	Hits		False alarms		Correct rejections	Misses
	K	R	K	R		
Sleep	27.7 (11.0)	101.8 (36.7)	13.1 (7.3)	2.9 (1.3)	103.9 (8.1)	52.6 (29.1)
Wake	27.0 (12.1)	104.5 (33.2)	17.7 (9.9)	8.9 (8.7)	92.6 (17.6)	50.7 (27.7)

Note. Hits and false alarms are broken down into *remember* (R) and *know* (K) judgments. Standard deviations are given in parentheses.

Fig. 1. Recognition accuracy (d') for (a) *know* (K) judgments and (b) *remember* (R) judgments of arousing and neutral stimuli. Results for the sleep and wake conditions combined are shown on the left; the graphs on the right present results for the two conditions separately, showing results of significance tests comparing the sleep and wake conditions for each stimulus type (lower brackets) and comparing the four combinations of condition and stimulus type (upper brackets). The dashed line is for comparison with neutral memory level for the combined sleep and wake conditions. Error bars indicate standard errors of the means. Significant differences between conditions and stimulus types are indicated by asterisks, *$p < .05$, **$p < .01$.

stimuli at the 12-hr test ($d' = 2.46$ vs. 2.00), $t(13) = 5.95$, $p < .001$, $p_{rep} < .98$, $d = 3.30$.

Significant differences were also observed in an analysis of variance comparing results for the four combinations of stimulus type and condition, $F(3, 52) = 3.75$, $p = .01$, $p_{rep} = .95$ (Fig. 1b). In contrast to the K judgments, which showed consistently better performance in the sleep condition for both stimulus types, the R judgments showed no significant differences between the sleep

and wake conditions, either for arousing stimuli, $t(13) = 1.72$, $p = .10$, $p_{rep} = .81$, $d = 0.95$, or for neutral stimuli, $t(13) = 1.66$, $p = .11$, $p_{rep} = .80$, $d = 0.92$. These data indicate that the 12-hr day and overnight periods similarly benefited recognition accuracy for R judgments in both the emotional memory and the neutral memory categories.

Memory Bias (*C*)

K Judgments

We also investigated changes in the modulation of memory bias. With the sleep and wake conditions combined (Fig. 2a), K judgments showed a significant difference in recognition bias between arousing and neutral pictures, with higher scores (more conservative responding) for neutral relative to arousing stimuli ($C = 0.83$ vs. 0.72), $t(13) = 2.32$, $p = .037$, $p_{rep} = .89$, $d = 1.29$.

In an analysis of the four combinations of stimulus type and condition, no significant differences in recognition bias emerged ($F < 1$). Comparisons between the sleep and wake conditions confirmed this, showing no significant differences for either arousing stimuli ($t < 1$) or neutral stimuli, $t(13) = 1.42$, $p = .17$, $p_{rep} = .75$, $d = 0.79$.
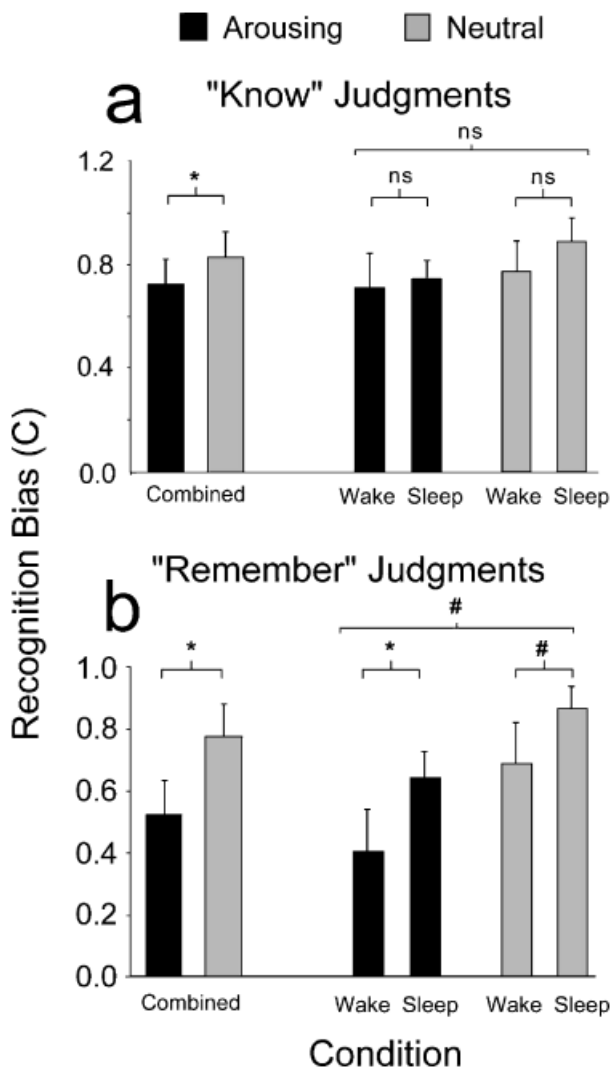
R Judgments

With the sleep and wake conditions combined, R judgments again showed a significantly higher bias score for neutral than for arousing stimuli ($C = 0.77$ vs. 0.52), $t(13) = 6.52$, $p < .001$, $p_{rep} > .98$, $d = 3.61$ (Fig. 2b).

Further differences emerged in an analysis across the four combinations of stimulus type and condition, $F(3, 52) = 2.56$, $p = .06$, $p_{rep} = .86$. For arousing stimuli, bias score was 58% higher (more conservative) in the sleep condition than in the wake condition ($C = 0.64$ vs. 0.40), $t(13) = 3.15$, $p = .007$, $p_{rep} = .95$, $d = 1.75$. For neutral stimuli, performance in the sleep condition showed a similar directional shift to more conservative tendencies ($C = 0.86$ in the sleep condition vs. 0.68 in the wake condition), and although this difference was significant, it was proportionally smaller (25%) than the difference for arousing stimuli, $t(13) = 2.12$, $p = .054$, $p_{rep} = .87$, $d = 1.18$.

Therefore, although K judgments showed no bias differences between the sleep and wake conditions for either arousing or neutral stimuli, R judgments did reveal a selective shift of the response criterion after a period of sleep, and this shift was most dramatic for emotionally arousing stimuli.

Reaction Times and Alertness

Reaction times for the alertness-control trials embedded in the initial study sessions showed no significant differences between the sleep (evening) and wake (morning) conditions (sleep condition: $M = 910$ ms, $SD = 52$; wake condition: $M = 897$ ms, $SD = 72$; $t < 1$). Reaction times for the R, K, and N responses during the later recognition tests (Table 2) similarly showed no

Fig. 2. Recognition bias (C) for (a) *know* (K) judgments and (b) *remember* (R) judgments of arousing and neutral stimuli. Results for the sleep and wake conditions combined are shown on the left; the graphs on the right present results for the two conditions separately, showing results of significance tests comparing the sleep and wake conditions for each stimulus type (lower brackets) and comparing the four combinations of condition and stimulus type (upper brackets). Error bars indicate standard errors of the means. Significance of the differences between conditions and stimulus types is indicated, #*p* < .06, **p < .05.

significant differences between the sleep (morning test) and wake (evening test) conditions (*p* > .11), even when arousing and neutral stimuli were analyzed separately (*p* > .18). This lack

of a diurnal reaction time difference between the sleep and wake conditions was supported by scores on the Stanford Sleepiness Scale, a standard measure of subjective alertness that was administered at each study and test session. These scores also showed no significant difference between the conditions (sleep condition: *M* = 2.3, *SD* = 0.8; wake condition: *M* = 2.6, *SD* = 1.0; *t* < 1).

DISCUSSION

The current study investigated differences in memory processing of emotionally arousing stimuli relative to neutral stimuli across a night of sleep and an equivalent period of daytime wake. To our knowledge, these are the first findings that demonstrate (a) a dissociation of emotional memory consolidation across wake and sleep, resulting in the selective overnight enhancement of memory accuracy for arousing material (by more than 40% for K judgments), and (b) an overnight increase in memory bias for R judgments, resulting in a shift toward less indiscriminate responding, particularly for emotionally arousing stimuli.

One possible explanation for these effects on memory processing is that they simply reflect circadian influences on mechanisms of recollection. However, we find this explanation to be inadequate for several reasons. First, if there were circadian influences that, for example, favored recollection in the morning rather than the evening, this effect should have been observed for both arousing and neutral memories, which was not the case. Second, even if a circadian effect were selective for arousing stimuli (a notion for which there is currently no evidence), the effect should have been observed for both types of recollection (i.e., R and K responses), which again was not the case. Instead, selective effects of the sleep condition were seen for recognition accuracy of K responses to arousing (but not neutral) stimuli, whereas an increase in memory bias scores was observed only for R responses. Third, reaction time measures for the alertness-control trials during the study phase, and for R, K, and N responses in the later test session, showed no significant differences between the evening and morning sessions. Fourth, the subjective ratings of alertness likewise did not differ at these evening and morning times.

An alternative explanation for the sleep-specific effects is that the lack of interference normally present during waking activ-

TABLE 2

Mean Reaction Times (in Milliseconds) on the Recognition Test in the Sleep (Morning Session) and Wake (Evening Session) Conditions

	Hits		False alarms		Correct rejections	Misses
Condition	K	R	K	R		
Sleep	1,116 (491)	999 (167)	1,209 (453)	972 (410)	1,078 (322)	1,088 (306)
Wake	1,190 (432)	1,107 (194)	1,070 (564)	1,111 (358)	1,150 (243)	1,129 (249)

Note. Standard deviations are given in parentheses. K = *know* judgments; R = *remember* judgments.

ities results in a passive rather than proactive state, favoring consolidation at night. We find this explanation unsatisfying as well, for several reasons. First, the lack of overnight interference should result in global consolidation benefits for both arousing and neutral memories. However, sleep benefits were seen only for arousing stimuli. Indeed, one might predict that arousing stimuli, being more emotional and potent than neutral stimuli, should be less susceptible to interference across the day, and therefore should show retention levels similar to those following a night of sleep. Instead, the opposite was found; the greatest difference in memory between the sleep and wake conditions was observed for emotional stimuli. Second, if a lack of interference was responsible for the benefits observed in the sleep condition, R and K responses should have benefited equally across the night; instead, only K responses showed the consolidation benefit for recollection accuracy for arousing stimuli, and only R responses showed the enhancement of memory bias.

Given these considerations, we believe the most parsimonious explanation for these findings is that sleep itself actively influences specific components of emotional memory consolidation, enhancing recollection accuracy for K responses and memory bias for R responses. We now consider each of the main experimental findings in more detail.

Overnight Enhancement of Recognition Accuracy

With the sleep and wake conditions combined, arousing stimuli demonstrated significantly enhanced levels of recognition accuracy, relative to neutral stimuli, over the 12-hr delay. These findings are consonant with a plethora of studies demonstrating that emotional experiences undergo a latent process of amplified consolidation over time (McGaugh, 2004). However, separate analyses of the data in the sleep and wake conditions produced a marked dissociation for K judgments. Specifically, there was a selective enhancement of emotionally arousing memory across a night of sleep, resulting in a 42% advantage in recognition accuracy. Most remarkable of all, this selective overnight enhancement appeared to be responsible for almost all the advantage seen for arousing over neutral stimuli in the combined analysis, as recognition memory in the wake condition did not differ significantly between arousing stimuli and neutral stimuli.

The overnight enhancement of affective memory is in line with our original hypothesis and consistent with the view that emotional information is selectively consolidated across sleeping periods (Power, 2004b; Wagner et al., 2001). These findings suggest that the beneficial influence of affect on memory consolidation and long-term retention previously reported across hours or days in both animals (McGaugh, 2004) and humans (Kleinsmith & Kaplan, 1963; Levonian, 1972; Sharot & Phelps, 2004; E.L. Walker & Tarte, 1963) is an enhancement that preferentially develops during sleep, rather than over time per se.

The specificity of this sleep effect may also clarify and help resolve previous conflicts regarding sleep and consolidation of declarative memory (M.P. Walker & Stickgold, 2004). Inconsistent findings regarding sleep-dependent consolidation of episodic memory may in part be due to inadequately separating emotionally arousing from neutral materials, and thereby obscuring the overnight enhancement specific to affective memory representations.

Although further work is necessary to determine the underlying basis of this effect, we speculate that sleep, and especially REM sleep, may be a brain state that is particularly amenable to consolidation of emotional memories because of its unique biology. Levels of limbic and forebrain acetylcholine (ACh) are markedly elevated during REM sleep (Vazquez & Baghdoyan, 2001)—reportedly quadruple the levels seen during deep non-REM sleep and double those measured in quiet waking (Marrosu et al., 1995). Considering the known importance of ACh in the long-term consolidation of emotionally arousing experiences (McGaugh, 2004), this procholinergic REM state may result in a selective facilitation of affective memory representations similar to that observed following experimental manipulations of ACh (Power, 2004a). At the neurophysiological level, these neurochemical changes may be reflected in or caused by known changes in synchronized oscillatory activity between amygdala and hippocampal regions during REM (Pare, Collins, & Pelletier, 2002). Cooperation between these structures is understood to play a fundamental role in the modulation of affective experiences (Pare et al., 2002). Thus, it is possible that synchronous activity within these circuits during REM sleep modulates plastic changes essential to consolidation of emotional memories.

Overnight Enhancement of Memory Bias

Although K judgments showed no difference in memory bias between the sleep and wake conditions, R judgments did show such a difference. In this case, the night of intervening sleep specifically shifted the response criterion, leading to a more conservative (higher) C score relative to the wake condition. Furthermore, this overnight effect was more pronounced for arousing than for neutral stimuli, resulting in a 58% increase in bias relative to the wake condition. These findings suggest that for R judgments, overnight sleep produces less indiscriminate responding, potentially by strengthening confidence judgments for remembered stimuli (i.e., in the present study, subjects' certainty in R judgments increased). Indeed, it is impressive that despite the more conservative response bias (reduced tendency to respond "old") in the sleep condition, memory accuracy (d') for both arousing and neutral stimuli was equally good in the sleep and wake conditions.

How might sleep modulate this bias enhancement? The procholinergic state of REM sleep has been shown to facilitate access to weak associative memories (Stickgold et al., 1999) and to enhance flexible, creative processing of recently acquired information (M.P. Walker et al., 2002). It is also of note that

diseases (e.g., Alzheimer's disease) that exhibit low levels of cortical ACh are associated with abnormally liberal (low) recognition bias (Fuld, Katzman, Davies, & Terry, 1982), which suggests that the process of memory bias can be neurochemically mediated. Although anatomical models of memory bias are currently lacking, we offer the hypothesis that the bias enhancement triggered by sleep is the product of a REM-associated increase in hippocampal ACh. Given that R judgments have been argued to depend more exclusively on hippocampal circuits than K judgments do (Rugg & Yonelinas, 2003), and given that the greatest increase in ACh during REM has been reported to be in hippocampal regions (Marrosu et al., 1995), it would make sense that any overnight enhancement of bias would develop preferentially for R judgments. Therefore, stimuli that have been consolidated overnight are associated with a stronger level of confidence judgment upon recognition, and this greater confidence is reflected in more discriminate (conservative) responding.

Conclusion

In summary, we have demonstrated that the consolidation of emotional memory is selectively facilitated during sleep, as indicated by preferential enhancement of both recognition accuracy and bias overnight. These findings may offer important insights into affective clinical disorders exhibiting abnormalities of sleep and memory processing (e.g., posttraumatic stress disorder and major depression), which instead of being viewed as co-occurring factors, may now be considered more causally related to the disorders.

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