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Sleep preferentially consolidates negative aspects of human memory: Well-powered evidence from two large online experiments

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Research suggests that sleep benefits memory. Moreover, it is often claimed that sleep selectively benefits memory for emotionally salient information over neutral information. However, not all scientists are convinced by this relationship [e.g., J. M. Siegel. *Curr. Sleep Med. Rep.*, 7, 15–18 (2021)]. One criticism of the overall sleep and memory literature—like other literature—is that many studies are underpowered and lacking in generalizability [M. J. Cordi, B. Rasch. *Curr. Opin. Neurobiol.*, 67, 1–7 (2021)], thus leaving the evidence mixed and confusing to interpret. Because large replication studies are sorely needed, we recruited over 250 participants spanning various age ranges and backgrounds in an effort to confirm sleep's preferential emotional memory consolidation benefit using a well-established task. We found that sleep selectively benefits memory for negative emotional objects at the expense of their paired neutral backgrounds, confirming our prior work and clearly demonstrating a role for sleep in emotional memory formation. In a second experiment also using a large sample, we examined whether this effect generalized to positive emotional memory. We found that while participants demonstrated better memory for positive objects compared to their neutral backgrounds, sleep did not modulate this effect. This research provides strong support for a sleep-specific benefit on memory consolidation for specifically negative information and more broadly affirms the benefit of sleep for cognition.

sleep | emotion | memory

Significance

Recent research has called into question whether sleep improves memory, especially for emotional information. However, many of these studies used a relatively small number of participants and focused only on college student samples, limiting both the power of these findings and their generalizability to the wider population. Here, using the well-established emotional memory trade-off task, we investigated sleep's impact on memory for emotional components of scenes in a large online sample of adults ranging in age from 18 to 59 y. Despite the limitations inherent in using online samples, this well-powered study provides strong evidence that sleep selectively consolidates negative emotional aspects of memory and that this effect generalizes to participants across young adulthood and middle age.

In this special issue, which is devoted to sleep's role in brain and cognitive function, it seems prudent to address head-on an issue that plagues not only sleep research (1, 2) but also research more generally. Problems with statistical power and generalizability of findings cast doubt on even some of the most foundational research findings, leading to a replication crisis in cognitive neuroscience, psychology, medicine, and other fields (3). Sleep research is not immune to these problems (4, 5). Therefore, it is now necessary to conduct large studies that move beyond homogeneous college participant samples to confirm key results, such as the essential role that sleep is believed to play in memory consolidation. Such studies are needed if we are to believe extant results and extend them to novel areas in our quest to understand the functions of sleep.

Of the many purported functions of sleep, its contribution to memory formation is one of the most important (6). Despite decades of research showing that sleep strengthens memory above and beyond wakefulness (7, 8), sleep's role in memory remains contested (1). Moreover, studies from different laboratories have shown that sleep prioritizes the consolidation of emotional over neutral memories, and to a larger degree than occurs across wake (9–13). However, recent reviews and meta-analyses have been unable to detect such effects when combining multiple studies, experimental designs, and task types (14–16). This raises the question of whether some of the prior results were spurious, arising from methodological flaws or publication bias rather than a true effect. An overreliance on small sample sizes in many experiments is likely a major contributor to conflicting results (2), with studies being underpowered to detect true effects. While it is challenging to recruit large samples for typical laboratory experiments, utilizing online tools to examine the behavioral effect of sleep on memory represents a promising avenue to increase sample size and sample from a broader portion of society (17–19). We turned to this resource to examine, in two well-powered experiments, whether sleep enhances emotional memory in human adults in the largest studies of sleep and emotional memory to date.

Emotion is a key indicator of important elements in our environment. As such, emotionally salient information is better remembered than neutral information. Within a single episode, more salient components of an experience are better remembered than the neutral context in which they occurred, known as an emotional memory trade-off effect

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(20). In a task often used to assess this effect, participants are presented with a series of scenes consisting of an object that is either emotional (e.g., a vicious-looking snake) or neutral (e.g., a harmless-looking chipmunk) on what is an always-neutral background (e.g., a forest scene). When tested, memories of the object and background components are examined separately. Participants typically remember emotionally negative objects better than neutral objects, but at the expense of the backgrounds on which they were presented. Thus, while one would remember the chipmunk and the forest equally well, the snake would be much better remembered than both the forest and the chipmunk.

In our research program, we have frequently shown how this disparity, or "trade-off," between scene aspects increases over time, especially (and perhaps only) if sleep occupies the delay interval (21–26). As such, our prior research suggests that sleep is highly important, if not necessary, for the persistence of emotional selectivity during memory consolidation. Although in our laboratory we have studied the effects of sleep and the emotional memory trade-off in more than 11 studies utilizing various designs (21–33), sample sizes have been limited due to the laboratory-based nature of our experiments. Here, we more than doubled the sample size of not only our previous work in this area but also that of the broader sleep and memory field to robustly estimate and extend the generalizability of sleep's impact on emotional memory.

Emotional memories can be positive as well as negative. However, much of the prior work in the sleep and emotional memory literature has examined only negatively valenced items, perhaps due to the more universally arousing and salient nature of negative items relative to neutral items(34–36). Indeed, prioritization of emotional memories for subsequent sleep-based consolidation is theorized to be governed by salience and arousal cues present during encoding that tag the information for later processing during sleep (37, 38). Prioritizing negative information may even be adaptive, allowing people to apply that learning to prevent and react to future negative scenarios (39, 40). Nevertheless, positive memories can also be highly salient and arousing and can persist in the long-term, similarly to negatively valenced memories, and an emotional memory trade-off does occur for positive objects relative to neutral backgrounds (36, 41). Therefore, in a second experiment, again using a large online sample, we examined whether sleep enhances memory for positive compared to neutral components of complex scenes.

We also addressed the issue of generalizability in the sleep and memory field. Many studies utilize college-student samples, a small subset of society that is typically more homogeneous than society more broadly (42, 43). Because studies reporting a link between sleep and emotional memory typically employ such samples, it is unclear whether we can extrapolate such findings to the wider population. One important dimension of generalizability is how consistent the effects of sleep on emotional memory are across the life span. Aging is characterized by marked changes in sleep quality and physiology, which are implicated in changes in and deterioration of sleep-based memory consolidation (44–52). By older age, there also can be a diminution of negative memory biases and a shift toward positive memory (53, 54), a shift that is also seen in sleep-based memory processing (55). Therefore, it is crucial that a broad age range is considered when asking the question of whether sleep preferentially consolidates emotional information. In the present study, we included young through middle-aged adults (age range 18 to 59 y) since middle-aged individuals constitute a particularly underresearched group (56), even though changes in both sleep and emotional memory processing are already evident by middle age (57, 58). The large sample also allowed us to explore other potential demographic moderators of the sleep–emotional memory relationship, such as biological sex, income, and minority status.

We performed two experiments examining the effect of sleep on the emotional memory trade-off effect. In each experiment, we varied the valence of emotional items that participants were exposed to. In Experiment 1, participants viewed either negative or neutral scenes to investigate whether the original sleep-based enhancement of the emotional memory trade-off effect (21) could be replicated in a large sample. In Experiment 2, we compared positive and neutral scenes to determine if sleep also enhances memory for positive information. With over 250 participants in each study, recruited from a wide sample of participants across the United States, these are, to our knowledge, the largest studies in human adults to compare the effects of sleep and wake on memory generally, let alone emotional memory specifically.

Results

Experiment 1. A total of 280 participants completed both sessions of Experiment 1. Full participant demographics can be found in *SI Appendix*, Table S1. We recruited participants in four age groups (18 to 24, 25 to 35, 36 to 47, and 48 to 59 y old) to adequately sample participants across young and middle adulthood. After obtaining informed consent, participants within each age range were randomly assigned to a sleep ($n = 141$) or wake ($n = 139$) delay condition before participating in two experimental sessions (Fig. 1*A*). In the first session, participants viewed a series of 64 scenes in either the morning or evening. Half of these scenes (32) contained a negative object superimposed on a neutral background, while the other 32 contained a neutral object superimposed on a neutral background. Participants were instructed to rate each scene for its perceived valence and arousal and were not told about the later memory test (Fig. 1*B* and *SI Appendix*, Table S2). Participants rated scenes as significantly more negative [F (1, 263) = 1,408, $P < 0.001$, $\eta p^2 = 0.84$] and significantly more arousing [F (1, 267) = 960, $P < 0.001$, $\eta p^2 = 0.78$]. All other main effects and interactions were nonsignificant (all $P > 0.10$). Age did not correlate with participants' ratings (all $P > 0.09$), demonstrating that valence and arousal ratings did not vary according to time of day or participant age (*SI Appendix*, Table S3 presents full ANOVA tables).

Approximately 12 h later, following a delay containing either subjectively reported nocturnal sleep or daytime wakefulness, participants returned for a second experimental session. Participants in the sleep group self-reported sleeping an average of 7.43 h ($SD = 1.63$). During this session, participants performed a surprise recognition test in which objects and backgrounds were presented separately one at a time (Fig. 1*B*). For each item, participants indicated whether the item 1) was an exact match to a previously viewed component ("same"), 2) shared the same verbal label as a previously viewed component but was not an exact match ("similar"), or 3) was not seen before ("new"). *Overall recognition* was calculated as a corrected recognition score (hits − false alarms), where a hit was scored as responding "same" or "similar" to a same item, and a false alarm was scored as saying "same" to a new item (32). We also calculated a more stringent, corrected *specific recognition* score where a hit constituted responding "same" to a same item. A trade-off magnitude score was created for each recognition score by subtracting the background score from the object score, separately for negative and neutral items (see *Materials and Methods* for full details). Component hit and false alarm rates are displayed in *SI Appendix*, Table S4. Our primary analysis consisted of a 2 (valence: negative, neutral) × 2 (component: object, background) × 2 (delay: sleep, wake) mixed ANOVA.

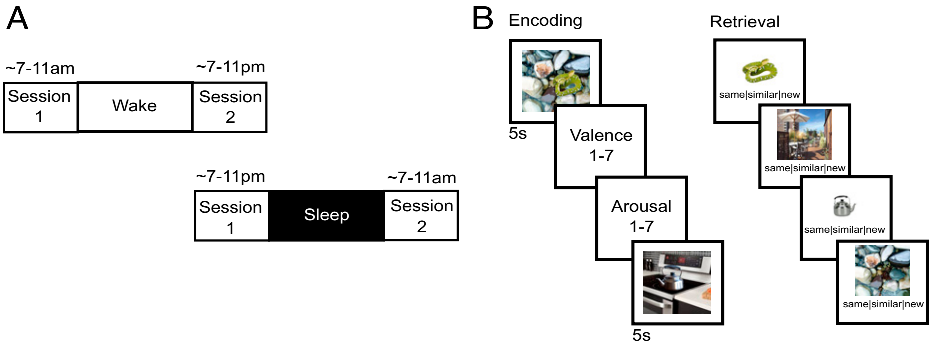

Fig. 1. Experimental design. (*A*) Study timeline. Both experiments followed the same general protocol. After completing a screening survey, participants were randomly assigned to a sleep or wake delay condition. Participants in the Sleep condition completed Session 1 in the evening and Session 2 the following morning. Participants in the Wake condition completed Session 1 in the morning and Session 2 later that evening. In Session 1, participants performed the encoding portion of the emotional memory trade-off task. In Session 2, participants came back to perform the surprise recognition portion. (*B*) Emotional memory trade-off task. During encoding, participants viewed a series of scenes containing an object placed on a background and were asked to rate each scene for its valence and arousal. Each scene appeared on the screen for 5 s, after which participants made their valence and arousal judgments. During recognition, participants viewed scene components individually and one at a time. Some of these components were identical to components of scenes viewed during Session 1, others were similar in visual detail but not an identical match, and others were new images. For each trial, participants had to judge whether the item was the same or similar to a component viewed in Session 1 or if it was a new item.

Critically, we found that sleep selectively enhanced the emotional memory trade-off effect in overall recognition, characterized by a significant three-way interaction between emotion, component, and delay condition [F (1, 278) = 4.12, p_{adj} = 0.043, $\eta p^2 = 0.02$; Fig. 2 and *SI Appendix*, Table S5]. This suggests that participants' memory for negative relative to neutral information varied depending on whether the delay period was filled with sleep or wake. Indeed, follow-up tests found that participants remembered negative objects better after a night of sleep than after a day of wakefulness [t (275) = 2.14, P = 0.034, d = 0.26; Fig. 2], but there were no sleep-wake differences for neutral objects or either paired backgrounds (all $P > 0.310$). This preferential sleep-based enhancement of negative object memory translated into a significantly larger trade-off magnitude score (objects − backgrounds) in the sleep group for negative [t (277) = 2.73, P = 0.007, d = 0.33] but not neutral items [t (277) = 0.47, P = 0.469, d = 0.06; Fig. 3*A*].

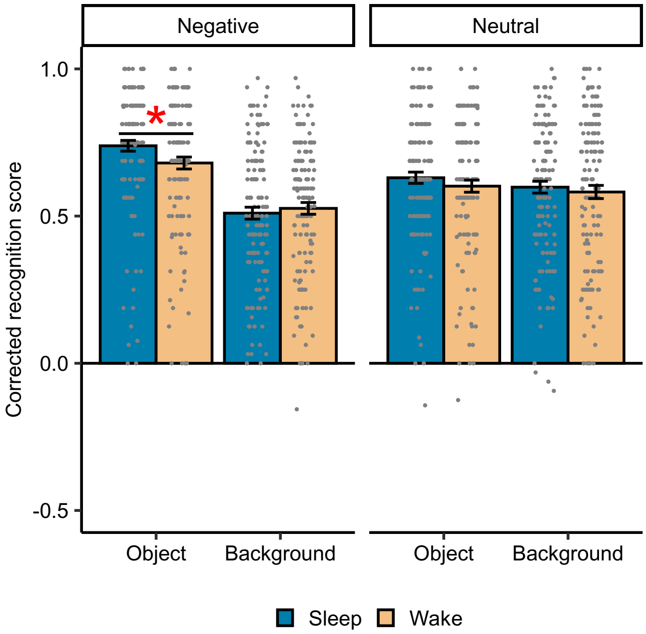

Fig. 2. Sleep enhanced the negative components of memory in a sample of 280 adults ranging in age from 18 to 59 y. Overall corrected recognition memory for objects and backgrounds followed either a sleep or wake delay. Negative objects were remembered better after sleep than after wakefulness. This was the only significant difference. All other sleep-wake differences were not significant. *, $P < 0.05$. Error bars are between-subjects SEMs.

Specific recognition memory followed the same pattern as overall recognition. We again found a significant three-way interaction between emotion, component, and delay condition [F (1, 278) = 6.79, p_{adj} = 0.020, $\eta p^2 = 0.02$] such that the trade-off magnitude was larger for the sleep group than for the wake group for negative [t (278) = 2.00, P = 0.047, d = 0.24] but not neutral items [t (278) = 1.15, P = 0.250, d = 0.14; Fig. 3*B*].

This result confirms that sleep enhanced the emotional memory trade-off effect in a large online sample. Given that generalizability was a key aim here, we next looked in more detail at whether the interaction between sleep and emotional memory trade-off was further moderated by age, sex, income, and minority status. With regard to age, we did not observe a significant four-way interaction between emotion, component, delay, and age [F (3, 272) = 0.14, p_{adj} = 0.935, $\eta p^2 = 0.002$]. Correlations between age and full trade-off magnitude (negative trade-off minus neutral trade-off) were not significant across a wake (r = −0.13, p_{adj} = 0.226) or sleep delay (r = −0.05, p_{adj} = 0.539). We also note that no four-way interaction between emotion, component, delay, and age was observed when age was treated as a binary variable in two broader age bins [younger (18 to 35 y) versus older (36 to 59 y; P = 0.95], and the three-way interaction between emotion, component, and delay remained significant when age was included as a continuous covariate (P = 0.044). As such, we are quite confident that sleep's enhancing effect on the emotional memory trade-off effect is preserved across middle age.

Similarly, the effect of sleep on the emotional trade-off did not vary reliably by biological sex [male or female; F (1, 275) = 4.33, p_{adj} = 0.152, $\eta p^2 = 0.02$], nor did age and sex interactively predict trade-off magnitude in either the sleep [F (3, 132) = 0.294, P = 0.829, $\eta p^2 = 0.007$] or wake [F (3, 131) = 0.788, P = 0.503, $\eta p^2 = 0.01$] conditions. The impact of sleep on the trade-off did not vary reliably by minority status [minority or nonminority; F (1, 276) = 2.45, p_{adj} = 0.238, $\eta p^2 = 0.01$] or income [≥ median income versus < median income; F (1, 257) = 1.19, p_{adj} = 0.368, $\eta p^2 = 0.01$], and income did not correlate with full trade-off magnitude across either a wake (r = −0.18, p_{adj} = 0.079) or sleep delay (r = −0.01, p_{adj} = 0.878).

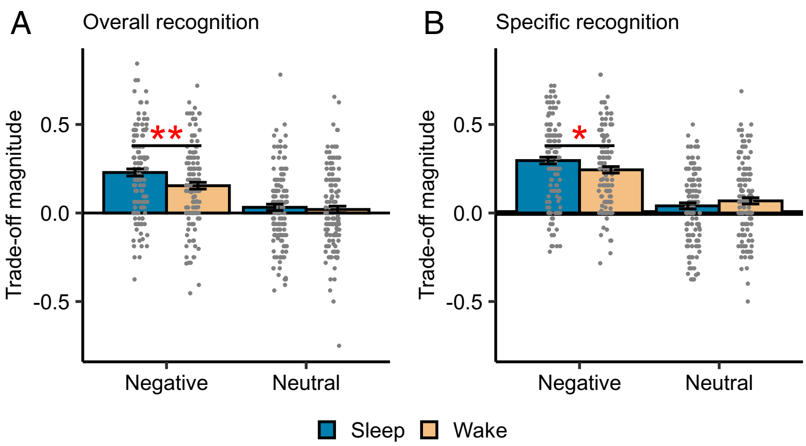

Fig. 3. Magnitude of the trade-off effect (object memory − background memory) following either a sleep or wake delay. We found a significant increase in the negative trade-off magnitude after sleep for both overall and specific recognition memory. Sleep and wake did not differ in the magnitude of the trade-off for neutral items. (*A*) Trade-off magnitude for overall recognition memory. (*B*) Trade-off magnitude for specific recognition memory. **, $P < 0.01$; *, $P < 0.05$. Error bars are between-subjects SEMs.

In summary, Experiment 1 confirmed that sleep improved negative emotional memory in a large online sample. Participants remembered negative objects better after a night of sleep than an equivalent period of time spent awake. Thus, sleep amplified the emotional memory trade-off effect. This effect was found to be consistent across a wide age range and did not vary by sex, income, or minority status. As such, this experiment shows that sleep selectively enhances the negative components of memory, an effect that can be seen in a large sample spanning young through middle age.

Experiment 2. In Experiment 2, we investigated whether sleep would similarly enhance positive memory. In a second large online experiment, we recruited a separate sample of 264 participants (129 sleep, 135 wake), who performed the same experimental protocol as in Experiment 1 except that the negative scenes were replaced with positive scenes. Between sessions, participants in the sleep group self-reported sleeping 7.44 h ($SD = 1.42$). When examining participants' ratings of the scenes during the encoding session, we found a main effect of emotion on valence ratings [$F(1, 243) = 115$, $P < 0.001$, $\eta p^2 = 0.32$] and a significant main effect of emotion on arousal ratings [$F(1, 248) = 159$, $P < 0.001$, $\eta p^2 = 0.39$], with positive scenes being rated as significantly more positive and more arousing than neutral scenes (*SI Appendix*, Table S2). There were no differences in ratings between the sleep and the wake conditions, suggesting that participants' ratings did not vary by the time of day (*SI Appendix*, Table S3). We found that participants' ratings of positive scenes increased with age ($r = 0.18$, $P = 0.006$) such that older adults tended to rate positive scenes more positively, but there were no other correlations between age and valence or arousal measures.

To test whether sleep enhanced positive emotional memory, we again conducted a three-way ANOVA including emotion, component, and delay as factors and controlling for age. Unlike in Experiment 1, we did not find a significant three-way interaction for either overall recognition [$F(1, 262) < 0.01$, $p_{adj} = 0.987$, $\eta p^2 < 0.01$; Fig. 4*A*] or specific recognition [$F(1, 262) = 0.3387$, $p_{adj} = 0.987$, $\eta p^2 = 0.01$]. Similarly, we did not find significant sleep-wake differences in either the positive or neutral overall trade-off magnitudes [$t(256) = 0.13$, $P = 0.902$, $d = 0.02$; $t(257) = 0.11$, $P = 0.910$, $d = 0.01$, respectively; Fig. 4*B*]. The trade-off magnitudes also did not differ for specific recognition [$t(253) = 0.15$, $P = 0.885$, $d = 0.02$ and $t(256) = 0.92$, $P = 0.361$, $d = 0.11$ for positive and neutral trade-off magnitudes, respectively].

We further confirmed that the lack of a difference between the sleep and wake conditions was not due to a lack of trade-off effect overall. The two-way interaction between emotion and component was highly significant [overall: $F(1, 262) = 202.11$, $P < 0.001$, $\eta p^2 = 0.44$; specific: $F(1, 262) = 152.32$, $P < 0.001$, $\eta p^2 = 0.37$]. In fact, when directly comparing the magnitude of the positive memory trade-off effect, regardless of delay condition, in Experiment 2 with the magnitude of the negative memory trade-off effect in Experiment 1, we did not find a statistical difference between the positive and negative trade-off effects [$t(537) = 0.48$, $P = 0.630$, $d = 0.04$].

We next directly compared sleep-associated processing of negative and positive stimuli by running a 2 (emotion: negative, positive) × 2 (delay condition: sleep, wake) ANOVA on trade-off magnitudes across the two experiments. A significant emotion * delay condition interaction [$F(1, 540) = 4.47$, $P = 0.035$, $\eta p^2 = 0.008$] confirmed that the effect of sleep on the emotional memory trade-off existed for negative but not positive stimuli. When compared within delay condition, the negative and positive trade-off effect was equivalent for the sleep group [$t(268) = 1.10$, $P = 0.272$, $d = 0.13$], whereas the negative trade-off was marginally smaller than the positive trade-off in the wake condition [$t(267) = 1.94$, $P = 0.053$, $d = 0.23$]. We then tested whether an effect of sleep on the positive memory trade-off would reveal itself if we restricted our analysis to only the most highly arousing positive items. To do this, we divided positive scenes into either high or low arousal based on a median split of a participant's arousal ratings. We did not see a significant difference in trade-off magnitude between high and low arousal scenes [$F(1, 262) = 0.40$, $P = 0.526$, $\eta p^2 = 0.002$], nor was there a significant interaction between scene arousal and delay condition [$F(1, 262) = 1.74$, $P = 0.19$, $\eta p^2 = 0.007$].

The positive memory trade-off and its relation to delay condition did not interact with age, sex, income, or minority status (all $p_{adj} > 0.34$), suggesting results were generalizable across the whole sample demographic. Together, these results suggest that sleep does not selectively enhance positive emotional memories.

The results of the two experiments together demonstrate that sleep selectively enhances negative, but not positive, emotional memories. Furthermore, the lack of a sleep effect for positive memories was not due to a lack of a positive memory trade-off overall. In fact, the size of the positive trade-off magnitude was

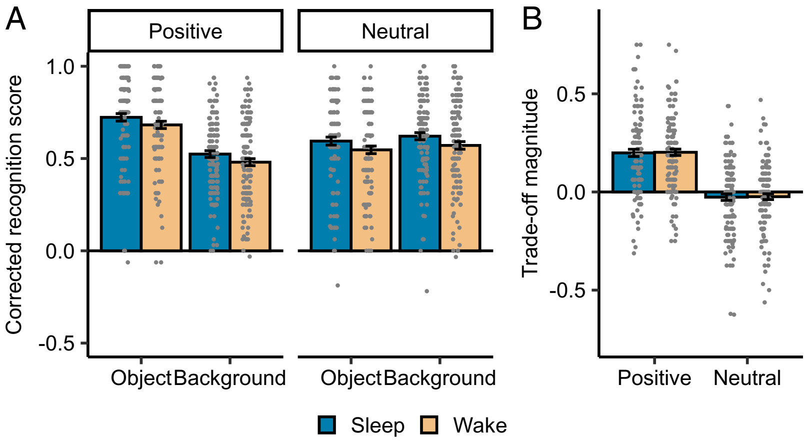

Fig. 4. Sleep does not enhance the positive components of memory. (*A*) Overall recognition memory for objects and backgrounds following either a sleep or wake delay. (*B*) Magnitude of the trade-off effect for positive and neutral items in Experiment 2. Errors bars are between-subjects SEMs.

similar to that of the negative trade-off magnitude in Experiment 1. However, there was no evidence of a sleep-specific enhancement of the positive components of memory in Experiment 2.

Alertness Measures and Subjective Sleep Quality. There were no main effects or interactions between sessions and delay conditions for the psychomotor vigilance test (PVT) reaction time in either experiment (*SI Appendix*, Table S6). As such, our differences between the sleep and wake groups could not be attributed to differences in alertness during either the encoding or recognition portions of the experiment. Subjective sleep quality over the month prior to participation, the three nights prior to the experiment, and during the delay between encoding and retrieval (sleep group only) are displayed in *SI Appendix*, Tables S7–S9. We did not observe any consistent correlations between subjective sleep parameters and the magnitude of the trade-off effect. See *Materials and Methods* for full details of measures obtained.

Discussion

Our results clearly demonstrate that sleep selectively enhances the negative components of memory relative to an equivalent period of time spent awake. These results advance the field of sleep and memory in three important ways. First, this study is the largest-ever replication of sleep's effect on emotional memory in human adults; moreover, it presents direct counterevidence to recent meta-analyses that suggest sleep does not play a role in emotional memory (14–16). Second, our results show that the sleep-specific enhancement of the emotional memory trade-off effect generalizes beyond college student samples and persists into middle age. Finally, we show that sleep and wake do not differ in memory for positive emotional memories, suggesting that sleep's preferential effect is specific to negative emotional memories.

Issues of replicability are a major concern in all areas of psychological research, and sleep and memory is no exception. Recent meta-analyses and reviews have cast doubt on the relationship between sleep and emotional memory, showing that the majority of studies do not suggest a prioritization of emotional information during sleep over and above what occurs across wake (14–16). A major driver of replicability issues is low statistical power, with the risk of spurious findings being higher in small sample studies that also likely overinflate true effect sizes (59, 60). With these issues in mind, the present research represents an important step forward in our understanding of the link between sleep and emotional memory. Confirming our previous laboratory studies using the same task (21–26), we confirmed in a far larger and broader sample that sleep selectively strengthens the negative components of memory, leading to a larger emotional memory trade-off effect than occurs over an equivalent period of wake.

Compared to other investigations of sleep and emotional memory that have utilized different tasks (e.g., 10, 12, 13, 55, 61), the emotional memory trade-off task may be particularly suited to measuring sleep's role in emotional memory processing. Our outcome measures directly compared memory within a single experience (the negative objects compared to their neutral backgrounds) as opposed to discrete stimuli. This represents a more naturalistic task with clear real-world analogues. For example, in eyewitness identification, the presence of a threatening weapon distracts eyewitnesses from characteristics of the perpetrator (i.e., the weapon focus effect). In other words, memory for the negatively salient object (the weapon) is preserved at the expense of other visual details [specific memory for details of the perpetrator's face (62)]. The fact that the trade-off task parallels nuanced memory phenomena in the real world may allow the relative sleep enhancement of negative memory to be clearly demonstrated. Perhaps this is why the majority of studies using the trade-off task, including this one, confirm sleep's selective benefit for negative information (15, 21–26).

Another strength of the current study is its broad population sample. Compared to laboratory studies that generally draw from college-educated young adults in a single location, our online study recruited participants from a much wider range of ages (18 to 59 y), locations across the United States, and education levels. We deliberately chose few inclusion and exclusion criteria in order to further broaden the sample. Replicating the effect of sleep on the emotional memory trade-off effect in this study suggests that the effect generalizes beyond the typical laboratory sample. The effect size for the sleep-wake difference in emotional memory trade-off magnitudes in this sample was smaller ($d = 0.32$) than in previous laboratory studies. This may represent a closer approximation of the actual size of the effect, or it may reflect the cost of decreased experimental control that occurs in online studies. However, the fact that our replication was successful under much less stringent experimental conditions in itself speaks to the strength of the findings. A combination of online research, which can easily facilitate large sample sizes to establish behavioral effects, followed by detailed laboratory work to determine physiological mechanisms would allow the field to move forward in both directions. We do note that this study was primarily interested in generalizability across different ages; thus, some critical areas of inclusion were not addressed. For example, the study population was relatively homogeneous in terms of race and ethnicity, and participants were recruited from just a single country. It will be important in future work to address these disparities.

Although we found a robust effect of sleep on negative emotional memory, Experiment 2 provided no evidence that sleep similarly benefits positive memory. This lack of effect is unlikely to be driven by the size of the emotional memory trade-off, since we did not find that the overall negative and positive trade-off magnitudes differed between the two experiments. One possibility is that different aspects of the emotional experience at encoding underlie the sleep effect. We have argued that at initial exposure, important information is tagged for later processing during sleep (37). Therefore, the initial encoding experience is crucial to eliciting the later sleep effect. Arousal-based neuromodulators such as norepinephrine and cortisol may act as such tags, with arousal during encoding being an important predictor for subsequent consolidation during sleep (63, 64). In the present study, positive scenes were consistently rated as less arousing than negative scenes. As such, the lack of a sleep effect for positive items adds evidence to the idea that emotional memory processing during sleep may be guided by arousal during encoding. However, when we focused our analyses on only the most highly arousing positive images, we still did not detect a significant effect of sleep. Different neural systems underlie the processing of negative and positive emotional experiences (65). Sleep may preferentially act upon the negative system for evolutionary benefit. Selectively honing in on potentially threatening aspects of an experience may allow such experiences to be strongly preserved in memory for future scenarios (66). It is unclear from this study whether encoding both positive and negative items within the same experience would lead to a generalized sleep effect for all emotional items or if one particular valence might “win out,” perhaps guided by arousal and reactivity to the stimuli themselves, as well as personal salience and relevance cues. This will be an important next step for research on emotional memory and sleep.

This study employed the “classic” sleep and memory design of contrasting memory after a day of wakefulness versus a night of sleep. We were motivated to use this design given its widespread use in the literature (e.g. 10, 11, 13, 55, 61) and the fact that the study we aimed to replicate also used this design (21). Although there are several limitations to this approach, we believe that our prior body of work addressed these limitations. First, it is possible that differences in memory performance are due to circadian influence. However, we previously showed that there are no time-of-day differences in memory for the trade-off task after short 30-min delays in the morning or evening (21). Similarly, we found a sleep-enhancing effect on the emotional memory trade-off in afternoon nap studies, where time of training and testing was equivalent across groups (24, 25). Additionally, in the present work, participants were randomly assigned to the sleep or wake condition, so they could not self-select based on circadian preference. PVT scores also show the groups were similarly alert during the evening and morning sessions.

Second, the wake group would have encountered more potentially interfering information during the delay than the sleep group, meaning that the sleep benefit may simply be due to passive protection from interference. While this behavioral-only study cannot identify the exact mechanism(s) underlying the sleep effect, we point to other work from our group using a 24-h delay design, where participants spent an equal amount of time awake and asleep. Negative emotional memory benefits are larger when sleep comes first, compared to when wake occurs first (23). This argues in favor of sleep actively stabilizing memories, making them more resilient from subsequent interference. If sleep merely provided passive protection against interference, then we would expect memory to be equivalent regardless of whether sleep comes soon after learning or after a day of wakefulness. We have also demonstrated that negative emotional memories are strongly positively correlated with time spent in rapid eye movement sleep, but not other sleep stages (indicating a potential overnight sleep mechanism) and, importantly, not with total sleep time (23). Together, these results suggest that aspects of sleep *actively* stabilize emotional aspects of memories. This is not to say that protection from interference plays no role in the sleep effect at all—indeed, we expect that it does. It does argue, however, that in addition to passive protection, sleep also has unique properties that actively promote memory consolidation (37, 67, 68).

Finally, the 12-h interval between encoding and retrieval may not be long enough for some effects to develop. Our previous studies using this task found that the trade-off effect was apparent almost immediately after testing, but got larger over time (23). Sleep benefits can be seen with as little as a 6-h delay (24) and as long as a 24-h delay (23). Whether the sleep-specific enhancement of the trade-off effect persists over even longer delays remains to be seen. Other work, however, has found that the benefits of sleep on emotional memory can be seen years later (69). While it is possible that an effect of sleep on positive memory may have been observed if a longer delay was used, our data cannot speak to such a possibility. We found that the strength of the positive trade-off was marginally stronger across wake compared to the negative trade-off. Although speculative, perhaps the positive components of memory were more strongly encoded than the negative components, which would render these stronger memories less susceptible to decay over time and thus make it harder to see a benefit of sleep.

The question of whether sleep selectively enhances emotional memory over and above wakefulness remains a hotly contested question. Small sample sizes derived mostly from college students remain as limitations in the sleep and memory literature. Here, we tackled both of these limitations head-on. We provide strong evidence that sleep selectively enhances negative emotional experiences. Furthermore, our results broadly support a role for sleep in memory and cognition, lending credence to the necessity of a good night’s sleep.

Materials and Methods

Participants. For both experiments, participants were recruited online via Prolific (https://www.prolific.co). The study was described as an investigation into “emotional reactivity at different times of day” to obscure the later memory test. In order to ensure we obtained similar numbers of participants across a broad age range, participants were recruited in four separate postings that were made visible to the following age brackets: 18 to 24, 25 to 35, 36 to 47, and 48 to 59 y old. After undergoing informed consent, prospective participants filled out a screening survey to determine their eligibility. Inclusion criteria were age between 18 and 59 y, currently residing in the United States, fluent in English, having a Prolific approval rating of at least 85, and free of any diagnosed sleep, psychiatric, or neurological disorders. After filling out the screening form, eligible participants were immediately invited to participate in the main part of the study. Participants assigned to the sleep condition were invited to perform part 1 of the study that same evening (and part 2 the following morning), while wake participants were invited to perform part 1 the next morning and part two later that evening. This exact recruitment and condition assignment procedure was followed for both experiments.

For Experiment 1, a total of 554 eligible participants were recruited. Eligible participants were then randomly assigned to a sleep or wake delay condition. Of those eligible, 280 participants completed both experimental sessions and were included in the final analysis (sleep: 141; wake: 139). A power analysis determined that a sample size of 280 participants yielded 80% power to detect a significant difference between sleep and wake at $P < 0.05$ with an effect size of $d = 0.33$.

For Experiment 2, 533 eligible participants were recruited and randomly assigned to a sleep or wake delay condition. Of these, 264 completed both experimental sessions and were included in the final analysis (sleep: 129; wake: 135).

In all experiments, participants were financially compensated for their time spent completing the screening survey regardless of final eligibility status. Eligible participants then received further payments for completing each experimental session. The study was approved by the University of Notre Dame Internal Review Board. Full participant demographics from all experiments can be found in *SI Appendix*, Table S1.

Materials.

Emotional memory trade-off task. The studied materials consisted of a series of scenes depicting negative ($n = 32$), positive ($n = 32$), or neutral objects ($n = 32$) placed on plausible, always neutral backgrounds 32. Two versions of each scene were created using two similar objects and backgrounds. Online pilot testing in $n = 30$ participants confirmed significant differences between negative, positive, and neutral scenes in terms of subjective valence and arousal ratings. A further 48 objects (16 negative, 16 positive, and 16 neutral) and 32 neutral backgrounds served as new items during the recognition test.

PVT. The PVT is a standardized measure of alertness (70). In the version utilized in the present study, participants were instructed to press the space bar as quickly as possible every time a red dot appeared on their computer screen but were told not to press the button too soon (i.e., before the dot appeared on the screen) (71). The interstimulus interval varied randomly from 1 to 4 s. To reduce participant burden, we used the brief form of the PVT, which lasted for a total of 3 min (72).

Procedure. Fig. 1*A* shows a schematic of the study timeline. The procedure was identical for both experiments, with the exception of which stimuli were used. All participants completed two experimental sessions. Participants assigned to the sleep delay condition performed Session 1 in the evening (between 7 and 11 PM at the participant's local time) and completed Session 2 12 h later the following morning (7 to 11 AM at the participant's local time). Participants in the wake condition performed Session 1 in the morning (7 to 11 AM) and Session 2 12 h later in the evening (7 to 11 PM).

During Session 1, participants first completed a battery of questionnaires to assess subjective sleep and well-being using the Qualtrics survey platform. Participants' sleep quality over the month prior to the experiment was assessed using the Pittsburgh Sleep Quality Index (73), and they retrospectively completed a 3-d sleep diary to characterize their sleep in the days prior to the experiment. They then completed the PVT to assess current alertness levels before performing the encoding portion of the emotional memory trade-off task. During encoding, participants viewed a series of scenes for 5,000 ms each. Participants viewed 64 scenes in total (Experiment 1: 32 negative scenes, 32 neutral scenes; Experiment 2: 32 positive scenes, 32 neutral scenes). For each scene, participants were instructed to rate the scene for its valence and arousal. Valence was rated on a 1 to 7 scale where 1 = very negative, 4 = neutral, and 7 = very positive. Arousal was rated on a second 1 to 7 scale where 1 = highly calming/subduing, 4 = neither calming/subduing nor agitating/exciting, and 7 = high agitating/exciting. After completing Session 1, participants in the wake group were told to refrain from napping during the delay interval. No other specific instructions were given.

When participants returned for Session 2, they completed additional questionnaires before completing a second PVT assessment. Sleep participants completed another sleep diary to measure subjective sleep between experimental sessions. Sleep participants also answered questions relating to their sleep inertia that morning, using a modified version of the sleep inertia questionnaire (74). They then performed an unexpected, self-paced recognition task in which 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 viewed during Session 1, others were the alternate version of the object or background and thus shared the same verbal label but differed in specific visual details, and others were objects or backgrounds that had not been seen during Session 1. Participants saw either the *same* or a *similar* version of a particular item during the recognition test, never both. For each item, participants indicated whether it was an exact match to a previously viewed component (same), similar but not an exact match (similar), or not seen before (new). In Experiment 1, 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 initially paired with a negative object, 16 initially paired with a neutral object), 32 *similar* backgrounds (16 negative, 16 neutral), and 32 *new* backgrounds. The trial count was identical in Experiment 2, except positive stimuli replaced the negative stimuli. The experimental tasks were hosted on the Cognition.run platform (https://www.cognition.run) and were programmed using jsPsych (75).

Analysis. To investigate the effects of sleep and age on memory at the recognition test, we calculated an overall corrected recognition score. For this measure, a "hit" was defined as saying either "same" or "similar" to a same trial, and a false alarm was considered as saying "same" to a new trial (32). We calculated the proportion of hits and false alarms and then subtracted the false alarm rate from the hit rate to obtain an overall corrected recognition score. Consistent with prior studies, this score reflected at least partial memory for the studied scene. That is, for a same item to be identified as either same or similar, participants had to remember that at least a particular type of object or background had been originally studied, because otherwise they would have indicated the item to be new. We also calculated a specific recognition score where hits were defined as saying "same" to a same trial, reflecting precise memory for the studied item. We then subtracted the false alarm rate from the specific recognition hit rate to form a corrected specific recognition score. A corrected recognition score was calculated for each scene component (object, background) and valence (negative, positive, neutral, depending on experiment).

To quantify the magnitude of the trade-off effect (that is, memory for objects relative to the backgrounds they were presented on), we subtracted the corrected recognition score for backgrounds from the corrected recognition score for objects. (separately for negative, positive, and neutral scenes). Here, a positive value would indicate better memory for objects relative to their paired backgrounds, whereas a negative value would suggest better memory for backgrounds relative to their paired objects.

To answer our primary question regarding the effects of sleep on the emotional memory trade-off effect, we performed two 2 (valence: emotional, neutral) × 2 (component: object, background) × 2 (delay: sleep, wake) mixed ANOVAs with either overall or specific corrected recognition scores as the dependent variables. We considered a false discovery rate (FDR)–adjusted $P < 0.05$, with significance adjusted for two tests (overall and specific recognition), to be statistically significant. Follow-up tests were performed as appropriate.

To assess potential moderators of the sleep and emotional memory trade-off effect, we conducted further mixed ANOVAs to investigate whether demographic variables interacted with the sleep and trade-off effect. Specifically, models were run to examine age: 2 (valence) × 2 (component) × 2 (delay) × 4 (age: 18 to 24 y, 25 to 35 y, 36 to 47 y, 48 to 59 y); biological sex: 2 (valence) × 2 (component) × 2 (delay) × 4 (sex: female, male); income: 2 (valence) × 2 (component) × 2 (delay) × 4 (income: ≥ sample median, < sample median); and minority racial status: 2 (valence) × 2 (component) × 2 (delay) × 4 (minority, nonminority). FDR-adjusted $P < 0.05$, with significance adjusted for four tests, was considered to be statistically significant. We also ran Pearson correlations between the magnitude of the full trade-off effect (emotional trade-off minus neutral trade-off) with age and income level, with P values again being adjusted for multiple comparisons using FDR. Uncorrected correlations between full trade-off magnitude and sleep variables are shown in *SI Appendix*, Tables S7–S9.

Data Availability. Anonymized data (i.e., to reproduce reported results) have been deposited in Open Science Framework (10.17605/OSF.IO/24Q6M) (76).

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