Sleep deprivation increases rates of forgetting in episodic memory. Yet, whether an extended lack of sleep alters the qualitative nature of forgetting is unknown. We compared forgetting of episodic memories across intervals of overnight sleep, daytime wakefulness, and overnight sleep deprivation. Item-level forgetting was amplified across daytime wakefulness and overnight sleep deprivation, as compared to sleep. Importantly, however, overnight sleep deprivation led to a further deficit in associative memory that was not observed after daytime wakefulness. These findings suggest that sleep deprivation induces fragmentation among item memories and their associations, altering the qualitative nature of episodic forgetting.

Why are some memories remembered and others forgotten? Retroactive interference accounts of forgetting argue that learning and mental activity that occurs after encoding contributes to memory loss (Wixted 2004). Consistent with this view, rates of forgetting are typically reduced across sleep relative to wakefulness (Jenkins and Dallenbach 1924; Newman 1938; Barrett and Ekstrand 1972; Plilhal and Born 1997; Gais et al. 2006; Tucker et al. 2006; Tamminen et al. 2010; Payne et al. 2012; Atherton et al. 2016; Cairney et al. 2018a,b), as sleep shelters new memories from competing information.

Given that forgetting is reduced by sleep, it is unsurprising that extended periods of sleep deprivation give rise to severe impairments in memory recall (Maquet et al. 2003; Gais et al. 2006; Tempesta et al. 2015, 2017; Harrington et al. 2018). In humans, empirical studies of sleep deprivation and memory often require participants to learn new information in the afternoon/evening, and then remain awake across the entire night (Maquet et al. 2003; Gais et al. 2006; Harrington et al. 2018). Hence, under these conditions, newly formed memories are subjected to a combination of retroactive interference and proactive interference (from events that occur prior to the encoding phase; Underwood 1957), leading to a substantial decline in recall accuracy.

To date, studies of sleep deprivation and memory have typically assessed forgetting for single items (e.g., images or words; Gais et al. 2006; Tempesta et al. 2015; Harrington et al. 2018). Episodic memory retrieval, in contrast, is critically dependent on the ability to recall associations between disparate features of prior experience (Tulving 1985). In recent work, pairwise event associations between locations, people, and objects were forgotten to a greater extent across daytime wakefulness than overnight sleep (Joensen et al. 2019). Yet, regardless of the postencoding delay (sleep or wake), forgetting invariably occurred in an all-or-none manner; when one element of an event (e.g., location) was remembered, the other elements of the same event (person and object) were also more frequently remembered than forgotten. Hence, although wakefulness increased overall rates of forgetting, it did not induce fragmentation among the memories that survived.

Sleep deprivation is known to amplify forgetting in episodic memory, but whether a protracted lack of sleep also leads to an irregular fragmentation of episodic representations has yet to be established. On account of the interference posed by waking activities occurring both before and after the critical learning episode (a deleterious combination of proactive and retroactive interference), sleep deprivation might open the door to fragmented forms of memory loss and, ultimately, alter the qualitative nature of forgetting.

Across two experiments, we investigated the impacts of sleep deprivation, as compared to sleep and routine daytime wakefulness, on memory for items and their associations. In Experiment 1, 27 healthy adults (10 male; mean ± SD age = 20.85 ± 3.29 yr) entered a within-subjects crossover design (sleep vs. wake, Fig. 1A). Conditions were separated by 1 wk and condition order was counterbalanced. Participants encoded adjective-object and adjective-scene pairs in the morning (08:00) or evening (20:00; Fig. 1B). The encoding phase included an immediate baseline test (T1), in which recognition memory ("old" or "new" judgments) for the adjectives was assessed. When an adjective was judged to be "old," memory for the associated image category (object or scene) was also assessed. After T1, participants entered a 12 h delay of unsupervised daytime wakefulness (morning encoding) or overnight sleep at home (evening encoding). Participants were asked to refrain from caffeine and alcohol during this interval, and, if in the wake condition, refrain from napping. Adherence to these restrictions was confirmed via questionnaire. Participants in the sleep condition provided subjective estimations of hours slept (mean ± SD = 7.78 ± 0.90 h). Following the delay, participants were retested (T2). Whereas adjective forgetting between T1 and T2 reflects item memory loss, category forgetting reflects associative memory loss, or memory fragmentation, as memory for the base item persists.

Experiment 2 (n = 28; 4 male; mean ± SD age = 19.43 ± 1.32 yr) followed identical procedures to Experiment 1, with the exception...
that retesting (T2) always took place in the morning following a night of sleep or total sleep deprivation. In both conditions, participants rose by 08:00 on the morning of the first session (~12 h before encoding) and remained awake throughout the day (confirmed via wristwatch actigraphy). Resultantly, by T2 of the sleep deprivation condition, participants had been awake for ~24 h. Across both experiments, we predicted that overnight sleep deprivation (vs. sleep and routine daytime wakefulness) would amplify adjective and category forgetting.

Sleep-deprived participants were monitored by a researcher throughout the overnight period. They were permitted to play games, watch movies and read. In the sleep condition, participants slept in a sleep laboratory and were monitored with polysomnography (Embla N7000; sampling rate = 200 Hz); permitting investigation of potential relationships between sleep stages and forgetting. Electrodes for electroencephalography (EEG) were attached at eight standardized locations: F3, F4, C3, C4, P3, P4, O1, and O2, each referenced to the contralateral mastoid (A1 or A2). Electrooculography (EOG) and electromyography (EMG) electrodes were also attached. Sleep data were segmented into 30 sec epochs and scored as wake, N1, N2, N3, or REM sleep in accordance with standardized criteria (see Supplemental_Table_S1.docx; Iber et al. 2007).

In both experiments, a follow-up test (T3) was administered 2 d after T2 (~10:00) to assess item and associative memory loss following opportunities for recovery sleep. Participants completed the Stanford sleepiness scale (Hoddes et al. 1972) and a psychomotor vigilance test (Gagnepain et al. 2017) at each test phase (see Supplemental_Analysis_S1.docx and Supplemental_Table_S2.docx).

All behavioral tasks were implemented on a PC with MATLAB 2017a and Psychtoolbox 3.0.13 (Brainard 1997). At encoding, participants viewed 60 adjective-object pairs and 60 adjective-scene pairs in a randomized, intermixed order. Adjectives were selected from a database of 14,000 English lemmas (Warriner et al. 2013). Objects and scenes were selected from standardized image batteries (Lang et al. 2005; Marchewka et al. 2014) and online resources. Because previous work has suggested that negative affect can circumvent the impacts of sleep loss on item-level forgetting (Sterpenich et al. 2007; Vargas et al. 2019), we also investigated whether the effects of sleep deprivation on associative memory were modulated by emotion. The objects and scenes were therefore evenly subcategorized as negative or neutral. Assignment of images to negative and neutral subcategories was validated by an independent sample of healthy adults (n = 51, 4 male; mean ± SD age = 19.96 ± 5.29 yr). Emotional ratings (1 = highly negative, 5 = neutral, 9 = highly positive) were significantly lower for negative images (mean ± SEM = 2.98 ± 0.09) than neutral images (mean ± SEM = 5.61 ± 0.06; t(50) = 26.00, P < 0.001, d = 3.64). All adjectives were emotionally neutral.

Each encoding trial began with a 1.5 sec fixation period. A randomly selected adjective was then displayed above a randomly selected object or scene image for 5 sec. Participants were instructed to visualize the adjective and image interacting, and then to indicate via keyboard press whether the mental image they generated was realistic or bizarre (to facilitate deep encoding; Craik and Lockhart 1972). To ensure that participants were able to differentiate between image categories, they were then asked to indicate whether the presented image was an object or scene. Image categorization performance was very high (both experiments: mean ± SEM = 96.83 ± 0.62%), and there were no differences in categorization accuracy between the sleep and wake conditions in Experiment 1 (t(26) = 0.43, P = 0.67) or Experiment 2 (t(27) = 1.14, P = 0.26). Each adjective-image pair was presented once, and participants were required to make each of their responses within 10 sec.

A hierarchical approach was used at each test phase, permitting a distinction between item memory (adjectives) and associative memory (images associated with adjectives). T1 included 180 adjectives: 120 targets presented at encoding and 60 foils. Each trial began with a 1.5 sec fixation period, after which a randomly selected adjective was displayed for 5 sec. Participants were instructed to indicate whether the adjective was “old” (they recognized the adjective from encoding) or “new” (they did not recognize the adjective) within 10 sec. They were also able to indicate uncertainty by pressing “?”. This ensured that participants were reasonably confident in their “old”/“new” responses and discouraged guessing. Note that inclusion of the “uncertain” response at adjective recognition precluded calculation of the sensitivity index (d’) for item memory. Uncertainty data and analyses are available in Supplemental_Table_S3.docx and Supplemental_Analysis_S2.docx, respectively.

For each “old” response, participants indicated whether the image associated with that adjective at encoding was an object or scene, or pressed “?” if they were uncertain. After each “object” or “scene” response, participants provided a brief typed description...
of the image (e.g., “Pewter Mug” for Fig. 1C; see Supplemental_Analysis_S3.docx). For “new” or “uncertain” responses to adjectives, participants moved immediately to the next trial. The procedures for T2 and T3 were identical to those of T1, except that a new set of foil adjectives were used in each test.

Drawing on data from Experiment 1, we first investigated whether item memories were forgotten to a greater extent across a day of wakefulness relative to a night of sleep. To address this question, we isolated adjectives that were correctly recognized at the immediate test (T1) and then calculated the proportion of these adjectives that were forgotten (incorrect or “uncertain” responses) at the delayed test (T2). As expected, the resultant item loss proportion scores were higher after wakefulness than sleep [F(26) = 2.44, P = 0.02, d = 0.47; Fig. 2A]. Behavioral data is displayed in Table 1.

Turning to Experiment 2, we next examined whether overnight sleep deprivation also increased item forgetting relative to sleep. Indeed, when participants were deprived of sleep they exhibited a trend for the Delay*Experiment interaction suggested that the effect of wakefulness on fragmentation scores was more prevalent after sleep deprivation than daytime wakefulness, F(1,26) = 3.93, P = 0.05, η² = 0.14, but this effect was not modulated by delay condition F(1,26) = 0.86; Emotion*Delay interaction: F(1,26) = 0.44; Fig. 2A]. Hence, although item forgetting was increased after a day of wakefulness (vs. overnight sleep), the waking delay had no impact on memory fragmentation. The fragmentation scores were unaffected by image emotion [Emotion main effect: F(1,26) = 0.03, P = 0.86; Emotion*Delay interaction: F(1,26) = 0.74, P = 0.40].

Unsurprisingly, the overall effect of wakefulness on item forgetting was highly significant [F(1,53) = 25.72, P < 0.001, η² = 0.33], whereas general rates of item forgetting were comparable between experiments [F(1,53) = 1.73, P = 0.19].

The overall effect of wakefulness on item forgetting was highly significant [F(1,53) = 25.72, P < 0.001, η² = 0.33], whereas general rates of item forgetting were comparable between experiments [F(1,53) = 1.73, P = 0.19].

Next, we investigated whether sleep deprivation induced fragmentation among item memories and their associations. To probe this question, we first isolated adjectives that were correctly recognized at T1 and T2, and for which the associated image category (object or scene) was correctly retrieved at T1. We then calculated the proportion of these adjectives for which the image category was forgotten (incorrect or “uncertain” responses) at T2. The resultant fragmentation scores for Experiments 1 and 2 were submitted to separate 2 (Delay: Sleep/Wake) × 2 (Image Emotion: Negative/Neutral) repeated-measures ANOVAs.

In Experiment 1, fragmentation scores were comparable after daytime wakefulness and overnight sleep [F(1,26) = 0.15, P = 0.71; Fig. 3A]. Hence, although item forgetting was increased after a day of wakefulness (vs. overnight sleep), the waking delay had no impact on memory fragmentation. The fragmentation scores were unaffected by image emotion [Emotion main effect: F(1,26) = 0.03, P = 0.86; Emotion*Delay interaction: F(1,26) = 0.74, P = 0.40].

Strikingly, however, fragmentation scores in Experiment 2 were significantly higher after sleep deprivation than sleep [F(1,27) = 10.23, P = 0.004, η² = 0.28; Fig. 3B]. Thus, in contrast to routine daytime wakefulness (Experiment 1), overnight sleep deprivation appeared to induce fragmentation among item memories and their associations. Negative images were associated with greater fragmentation than neutral images [F(1,27) = 4.45, P = 0.04, η² = 0.14], but this effect was not modulated by delay condition [F(1,27) = 0.05, P = 0.83].

Consistent with the view that memory fragmentation was more prevalent after sleep deprivation than daytime wakefulness, a 2 (Delay: Sleep/Wake) × 2 (Experiment: One/Two) mixed ANOVA (collapsed across image emotion) revealed a significant Delay*Experiment interaction [F(1,53) = 4.16, P = 0.05, η² = 0.07]. The overall effect of wakefulness on fragmentation scores was significant [F(1,53) = 6.59, P = 0.01, η² = 0.11], whereas general rates of fragmentation were comparable between experiments [F(1,53) = 0.62, P = 0.44]. Sleep duration (mean ± SEM) was 430.20 ± 6.45 min in the sleep condition of Experiment 2. There were no

Table 1. Memory performance at T1, and losses at T2 and T3

|                | T1                | T2                | T3                | T1                | T2                | T3                |
|----------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
| **A**          |                   |                   |                   |                   |                   |                   |
| Sleep          | 68.58 (±2.46)     | 16.58 (±1.79)     | 18.71 (±1.77)     | 69.61 (±2.77)     | 17.55 (±1.75)     | 16.06 (±1.89)     |
| Wake*          | 67.10 (±2.54)     | 20.56 (±2.14)     | 21.42 (±2.55)     | 71.10 (±2.62)     | 26.64 (±2.60)     | 19.37 (±1.74)     |
| **B**          |                   |                   |                   |                   |                   |                   |
| Sleep          | 62.88 (±2.85)     | 17.43 (±2.37)     | 12.31 (±1.52)     | 63.79 (±2.76)     | 15.30 (±2.46)     | 13.29 (±2.21)     |
| Negative       | 63.35 (±2.51)     | 18.44 (±2.76)     | 10.77 (±1.60)     | 65.46 (±2.96)     | 11.26 (±1.82)     | 9.50 (±1.91)      |
| Neutral        | 65.82 (±2.92)     | 19.48 (±1.65)     | 13.80 (±1.93)     | 65.34 (±2.47)     | 21.17 (±2.26)     | 16.09 (±3.27)     |
| Wake*          | 63.85 (±2.98)     | 17.83 (±1.66)     | 10.72 (±1.64)     | 66.98 (±2.67)     | 17.92 (±3.02)     | 14.31 (±2.67)     |

A. Left columns: Item memory performance at T1. Middle and right columns: Item memory losses at T2 and T3, respectively. B. Left columns: Associative memory performance at T1. Middle and right columns: Associative memory losses (memory fragmentation) at T2 and T3, respectively. Note that item/associative memory losses at T2 are calculated relative to T1, whereas item/associative memory losses at T3 are calculated relative to T2.

*For Experiment 2, “Wake” refers to the sleep deprivation condition. Data are shown as percentages (mean ± SEM).
significant correlations between item or associative forgetting and time (min) spent in any stage of sleep (all \( P > 0.05 \)).

In Experiment 2, alertness levels at T2 were reduced in the sleep deprivation (vs. sleep) condition, as indicated by the Stanford sleepiness scale and psychomotor vigilance test (see Supplemental Analysis S1.docx). The foregoing findings might thus be explained by between-condition differences in tiredness (and/or associated stress) on retrieval performance at T2. To address this possibility, we asked whether the effects of sleep deprivation on item forgetting and memory fragmentation observed at T2 were maintained 2 d later at T3 (when between-condition differences in tiredness were eliminated). Item loss proportion scores calculated between T1 and T3 (the proportion of correctly recognized adjectives at T1 that were forgotten at T3) were indeed higher in the sleep deprivation (vs. sleep) condition than were retention scores calculated between T2 and T3 (the proportion of correctly retrieved image categories at T2 that were forgotten at T3), but the effect was observed when comparing the wake and sleep conditions in Experiment 1 \([t(26) = 2.05, P = 0.05, d = 0.47]\). Note that the same effect was observed when comparing the wake and sleep conditions in Experiment 2 \([t(27) = 2.50, P = 0.02, d = 0.47]\). To compute fragmentation scores between T1 and T3 in Experiment 2, we first isolated adjectives that were correctly recognized at T1 and T3, and for which the associated image category was correctly retrieved. Then, we calculated the proportion of these adjectives for which the image category was forgotten at T3. Importantly, fragmentation scores were higher in the sleep deprivation (vs. sleep) condition \([F(1,27) = 8.71, P = 0.01, \eta^2 = 0.24]\). As before, a main effect of Emotion emerged \([F(1,27) = 5.47, P = 0.03, \eta^2 = 0.17]\), but there was no Emotion*Delay interaction \([F(1,27) = 1.60, P = 0.22]\).

Taken together, our findings suggest that the memory deficits associated with sleep deprivation were not simply due to excessive tiredness or stress at T2. It is nevertheless possible that high stress levels during consolidation contributed to a long-lasting fragmentation of memory.

We next investigated whether postlearning wakefulness or sleep deprivation (vs. sleep) led to an additional item forgetting at T3 (and/or associated stress) on retrieval performance at T2. Item loss proportion scores calculated between T2 and T3 (the proportion of correctly recognized adjectives at T2 that were forgotten at T3) were comparable between the wake and sleep conditions in Experiment 1 \([t(26) = 1.22, P = 0.23]\). However, sleep deprivation (vs. sleep) led to a trend toward additional item forgetting in Experiment 2 \([t(27) = 1.89, P = 0.07, d = 0.36]\). Fragmentation scores calculated between T2 and T3 (the proportion of correctly retrieved image categories at T2 that were forgotten at T3, when the base adjective was correctly recognized at T2 and T3) were applied to a 2 (Delay: Sleep/Wake) × 2 (Emotion: Negative/Neutral) repeated-measures ANOVA. However, no significant effects emerged in Experiment 1 \([\text{Emotion}: F(1,26) = 2.17, P = 0.15; \text{Delay}: F(1,26) = 0.25, P = 0.62; \text{Emotion} \times \text{Delay}: F(1,26) = 0.32, P = 0.58]\) or Experiment 2 \([\text{Emotion}: F(1,27) = 2.05, P = 0.16; \text{Delay}: F(1,27) = 1.52, P = 0.23; \text{Emotion} \times \text{Delay}: F(1,27) = 0.36, P = 0.55]\).

Finally, we examined item and associative memory performance at T1 to ensure that the above effects were driven by between-condition differences at baseline. Item memory performance was calculated as the proportion of “old” adjectives that were correctly identified as “old.” No differences were observed between the sleep and wake conditions in Experiment 1 \([t(26) = 0.79, P = 0.44]\) or Experiment 2 \([t(27) = 0.85, P = 0.41]\). Associative memory performance was calculated as the proportion of correctly identified “old” adjectives for which the associated image category was also correctly retrieved. A 2 (Delay: Sleep/Wake) × 2 (Emotion: Negative/Neutral) repeated-measures ANOVA revealed no significant effects in Experiment 1 \([\text{Emotion}: F(1,26) = 0.32, P = 0.57; \text{Delay}: F(1,26) = 0.59, P = 0.45; \text{Emotion} \times \text{Delay}: F(1,26) = 0.80, P = 0.38]\) or Experiment 2 \([\text{Emotion}: F(1,27) = 1.49, P = 0.23; \text{Delay}: F(1,27) = 0.58, P = 0.45; \text{Emotion} \times \text{Delay}: F(1,27) < 0.001, P = 0.99]\).

Taken together, our findings suggest that sleep deprivation prompts a qualitative change in the nature of episodic forgetting. In Experiment 1, a routine day of wakefulness increased item-level forgetting relative to a night of sleep, but had no impact on associative memory when the base items survived. In Experiment 2, by contrast, overnight sleep deprivation (vs. sleep) not only increased item-level forgetting, but also increased associative memory loss when the base items remained unscathed. Hence, sleep deprivation appears to induce fragmentation among episodic representations that are typically forgotten in an all-or-none manner (Joensen et al. 2019).

Proactive and retroactive interference are thought to contribute to forgetting (Underwood 1957; Wixted 2004). Hence, a combination of these two sources of interference could have particularly deleterious effects on memory performance. In the sleep deprivation condition of Experiment 2, the encoding session was bookended by 12 h waking intervals (see Fig. 1A), providing scope for both proactive and retroactive interference. In the wake condition of Experiment 1, by contrast, encoding and retesting took place in the morning and following evening, respectively, meaning that the novel adjective-image associations were subject to proactive interference. Across both experiments, sleep occurred soon after the evening encoding phase and seemingly ameliorated the impacts of proactive interference.

Wakeful experience is associated with a net increase in synaptic strength (De Vivo et al. 2017; Spano et al. 2019). A putative synaptic renormalization during sleep serves to globally downscale synaptic weights and, consequently, improve signal-to-noise ratios for synapses that were strongly potentiated as a result of prior learning (Tononi and Cirelli 2006). It has been suggested that this renormalization process constitutes an “efficient and smart” means of avoiding runaway potentiation and, importantly, separating meaningful information from unwanted interference (Tononi and Cirelli 2014). Amplified and fragmented forgetting following sleep deprivation could therefore be driven by excessive synaptic potentiation, which results from wakeful interference occurring before and after learning together with an absence of sleep-associated synaptic renormalization. Yet, it should be noted that time in N3—the sleep stage primarily implicated in synaptic renormalization (Tononi and Cirelli 2006, 2014)—was not correlated with item or associative memory performance in Experiment 2 of the current study.
Previous work has suggested that emotionally salient memories are more resistant to the effects of sleep deprivation than neutral memories (Sterpenich et al. 2007; Vargas et al. 2019). In the current study, by contrast, the impacts of sleep deprivation on memory fragmentation were comparable for negative and neutral images. This discrepancy may relate to the nature of the affective representation under scrutiny. Whereas previous studies have investigated the effects of sleep deprivation on central aspects of emotional memory (Sterpenich et al. 2007; Vargas et al. 2019), our findings relate to affective associations, which might be more susceptible to deterioration with sleep loss.

Interestingly, memory fragmentation was generally greater for negative than neutral images in Experiment 2, which is consistent with earlier work (Bisby and Burgess 2013; Bisby et al. 2016), and the view that negative emotional content disrupts coherence among episodic representations (Bisby et al. 2018). Because the adjective stimuli used in this study were emotionally neutral, we could not determine how the emotional properties of item memories influence the susceptibility of their associations to sleep deprivation, although this is an interesting question for future research.

In conclusion, our findings suggest that sleep deprivation not only amplifies item-level forgetting, but induces fragmentation among item memories and their associations. Such fragmented memory loss might be due to a combination of proactive and retroactive interference, leading to severe and irregular impairments in episodic memory retrieval. More broadly, our findings offer novel insights into the cognitive impairments posed by insufficient sleep; an issue that is particularly pertinent when considering the prevalence of chronic sleep deprivation (Bonnet and Arand 1995; Stranges et al. 2012; Liu et al. 2016), which is arguably an issue that is particularly pertinent when considering the view that negative emotional content disrupts coherence among episodic representations (Bisby et al. 2018).

Data access

Study data are freely available via the following link: https://osf.io/s35f9/.

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References

Atherton KE, Nobre AC, Lazar AS, Wulff K, Whittaker RG, Dhawan V, Lazar ZI, Zeman AZ, Butler CR. 2016. Slow wave sleep and accelerated forgetting. Cortex 84: 80–89. doi:10.1016/j.cortex.2016.08.013

Barrett TR, Ekstrand BR. 1972. Effect of sleep on memory: III. Controlling for time-of-day effects. J Exp Psychol 82: 321–327. doi:10.1037/0096-6212.82.2.321

Bisby JA, Burgess N. 2013. Negative affect impairs associative memory but not item memory. Learn Mem 20: 21–27. doi:10.1101/lm.032409.113

Bisby JA, Horner AJ, Horslyc BD, Burgess N. 2016. Opposing effects of negative emotion on amygdalar and hippocampal memory for items and associations. Soc Cogn Affect Neurosci 11: 981–990. doi:10.1093/scan/nsw028

Bisby JA, Horner AJ, Bush D, Burgess N. 2018. Negative emotional content disrupts the coherence of episodic memories. J Exp Psychol Gen 147: 243–256. doi:10.1037/pspa0000356

Bonnet MH, Arand DL. 1995. We are chronically sleep deprived. Sleep 18: 908–911. doi:10.1093/sleep/18.10.908

Brainard DH. 1997. The psychophysics toolbox. Spatial Vis 10: 433–436. doi:10.1163/156858997X00357

Cairney SA, Guittonen AAV, El Marj N, Staresina BP. 2018a. Memory consolidation is linked to spindle-mediated information processing during sleep. Curr Biol 28: 948–954. doi:10.1016/j.cub.2018.01.087

Calmey SA, Lindsay S, Paller KA, Gaskell MG. 2018b. Sleep preserves original and distorted memory traces. Cortex 99: 39–44. doi:10.1016/j.cortex.2017.10.005

Craig FM, Lockhart RS. 1972. Levels of processing: a framework for memory research. J Verb Learn Verb Behav 11: 671–684. doi:10.1016/S0020-5371(72)80001-X

De Vivo L, Bellesi M, Marshall W, Bushong EA, Ellisman MH, Tononi G, Cirelli C. 2017. Ultrastructural evidence for synaptic scaling across the wake/sleep cycle. Science 355: 507–510. doi:10.1126/science.aah5982

Gagnepain P, Hubert J, Anderson MC. 2017. Parallel regulation of memory and emotion supports the suppression of intrusive memories. J Neurosci 37: 6423–6441. doi:10.1523/JNEUROSCI.2732-16.2017

Gais S, Lucas B, Born J. 2006. Sleep after learning aids memory recall. Learn Mem 13: 259–262. doi:10.1101/lm.132106

Harrington MO, Nedergaard KM, Durrant SJ. 2018. The effect of sleep deprivation on emotional memory consolidation in participants reporting depressive symptoms. Neurobehav Learn Mem 152: 10–19. doi:10.1016/j.nlm.2018.04.013

Hobbs E, Dement W, Zarcone V. 1972. The development and use of the Stanford sleepiness scale (SSS). Psychophysiology 9: 150.

Iber C, Ancoli-Israel S, Cherson A, Quan SF. 2007. The AASM manual for the scoring of sleep and associated events, terminology, and technical specifications. American Academy of Sleep Medicine. Westchester, IL: Jenkins KG, Dallenbach KM. 1924. Obliviscence during sleep and waking. Am J Psychol 35: 605–612. doi:10.2307/1414040

Joensen BH, Gaskell MG, Horner AJ. 2019. United we fall: all-ornothing forgetting of complex episodic events. J Exp Psychol Gen 10.1037/ xge0000648.

Lang PJ, Bradley MM, Cuthbert BN. 2005. International affective picture system (IAPS): technical manual and affective ratings. University of Florida, Gainesville, FL.

Liu Y, Wheaton AG, Chapman DP, Cunningham TJ, Lu H, Croft JB. 2016. Prevalence of Healthy Sleep Duration among Adults—United States, 2014. MMWR Morb Mortal Wkly Rep 65: 137–141. doi:10.15585/mmwr mmw6506a1

Maquet P, Schwartz S, Passingham R, Frith C. 2003. Sleep-related consolidation of a visuomotor skill: brain mechanisms as assessed by functional magnetic resonance imaging. J Neurosci 23: 1432–1440. doi:10.1523/JNEUROSCI.3404-03.2003

Marchewka A, Zawralski Ł, Jednoróg K, Grabowska A. 2014. The Nencki Affective Picture System (NAPS): introduction to a novel, standardized, wide-range, high-quality, realistic picture database. Behav Res Methods 46: 596–610. doi:10.3787/s13428-013-0379-1

Newman EB. 1938. Forgetting of meaningful material during sleep and waking. Am J Psychol 52: 65–71. doi:10.2307/1416661

Payne JD, Tucker MA, Ellenbogen JM, Wamsley EJ, Walker MP, Schacter DL, Stickgold R. 2012. Memory for semantically related and unrelated declarative information: the benefit of sleep, the cost of wake. PLoS One 7: e33079. doi:10.1371/journal.pone.0033079

Pihlal W, Born J. 1997. Effects of early and late nocturnal sleep on declarative and procedural memory. J Cogn Neurosci 9: 534–547. doi:10.1162/jocn.1997.9.4.534

Spano GM, Banning SH, Marshall W, De Vivo L, Bellesi M, Loschky SS, Tononi G, Cirelli C. 2019. Sleep deprivation by exposure to novel objects increases synapse density and axo-spine interface in the hippocampal CA1 region of adolescent mice. J Neurosci 39: 6613–6625. doi:10.1523/JNEUROSCI.080-19.2019

Sterpenich V, Albouy G, Boly M, Vandewalle G, Darsaud A, Boly M, Dang-Vu TT, Desseilles M, D’Argembeau A, Gais S, et al. 2007. Sleep-related hippocampo-cortical interplay during emotional memory recollection. PLoS Biol 5: 2709–2722. doi:10.1371/journal.pbio.0050282

Swanson S, Tigue W, Gómez-Olivé FX, Thorogood M, Kandala N-B. 2012. Sleep problems: an emerging global epidemic? Findings from the INDEPTH WHO-SAGE study among more than 40,000 older adults from 8 countries across Africa and Asia. Sleep 35: 1173–1181. doi:10.5665/sleep.2012

Tamminen J, Payne JD, Stickgold R, Wamsley EJ, Gaskell MG. 2010. Sleep spindle activity is associated with the integration of new memories and existing knowledge. J Neurosci 30: 14356–14360. doi:10.1523/JNEUROSCI.3028-10.2010

Tempesta D, De Gennaro L, Natale V, Ferrara M. 2015. Emotional memory processing is influenced by sleep quality. Sleep Med 16: 862–870. doi:10.1016/j.sleep.2015.01.024

Tempesta D, Soci C, Vello Iolo G, De Gennaro L, Ferrara M. 2017. The effect of sleep deprivation on retrieval of emotional memory: a behavioural study using film stimuli. Exp Brain Res 235: 3059–3067. doi:10.1007/s00221-017-5043-z

www.learnmem.org
Tononi G, Cirelli C. 2006. Sleep function and synaptic homeostasis. Sleep Med Rev 10: 49–62. doi:10.1016/j.smrv.2005.05.002
Tononi G, Cirelli C. 2014. Sleep and the price of plasticity: from synaptic and cellular homeostasis to memory consolidation and integration. Neuron 81: 12–34. doi:10.1016/j.neuron.2013.12.025
Tucker MA, Hitrota Y, Wamsley EJ, Lau H, Chaklader A, Fishbein W. 2006. A daytime nap containing solely non-REM sleep enhances declarative but not procedural memory. Neuronbiol Learn Mem 86: 241–247. doi:10.1016/j.nlm.2006.03.005
Tulving E. 1985. Elements of episodic memory. Oxford, UK.
Underwood BJ. 1957. Interference and forgetting. Psychol Rev 64: 49–60. doi:10.1037/h0044616
Vargas I, Payne JD, Muench A, Kuhlman KR, Lopez-Duran NL. 2019. Acute sleep deprivation and the selective consolidation of emotional memories. Learn Mem 26: 176–181. doi:10.1101/lm.049312.119
Warriner AB, Kuperman V, Brysbaert M. 2013. Norms of valence, arousal, and dominance for 13,915 English lemmas. Behav Res Methods 45: 1191–1207. doi:10.3758/s13428-012-0314-x
Wixted JT. 2004. The psychology and neuroscience of forgetting. Annu Rev Psychol 55: 235–269. doi:10.1146/annurev.psych.55.090902.141555

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