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Sleep shapes the associative structure underlying pattern completion in multielement event memory

Nicolas D. Lutz[a,b,1], Estefanía Martínez-Albert[a,b], Hannah Friedrich[a], Jan Born[a,c,d], and Luciana Besedovsky[a,b,1]

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Sleep supports the consolidation of episodic memory. It is, however, a matter of ongoing debate how this effect is established, because, so far, it has been demonstrated almost exclusively for simple associations, which lack the complex associative structure of real-life events, typically comprising multiple elements with different association strengths. Because of this associative structure interlinking the individual elements, a partial cue (e.g., a single element) can recover an entire multielement event. This process, referred to as pattern completion, is a fundamental property of episodic memory. Yet, it is currently unknown how sleep affects the associative structure within multielement events and subsequent processes of pattern completion. Here, we investigated the effects of post-encoding sleep, compared with a period of nocturnal wakefulness (followed by a recovery night), on multielement associative structures in healthy humans using a verbal associative learning task including strongly, weakly, and not directly encoded associations. We demonstrate that sleep selectively benefits memory for weakly associated elements as well as for associations that were not directly encoded but not for strongly associated elements within a multielement event structure. Crucially, these effects were accompanied by a beneficial effect of sleep on the ability to recall multiple elements of an event based on a single common cue. In addition, retrieval performance was predicted by sleep spindle activity during post-encoding sleep. Together, these results indicate that sleep plays a fundamental role in shaping associative structures, thereby supporting pattern completion in complex multielement events.

sleep | episodic memory | pattern completion | consolidation | retrieval

Significance

Real-life events usually consist of multiple elements such as a location, people, and objects that become associated during the event. Such associations can differ in their strength, and some elements may be associated only indirectly (e.g., via a third element). Here, we show that sleep compared with nocturnal wakefulness selectively strengthens associations between elements of events that were only weakly encoded and of such that were not encoded together, thus fostering new associations. Importantly, these sleep effects were associated with an improved recall of the complete event after presentation of only a single cue. These findings uncover a fundamental role of sleep in the completion of partial information and are critical for understanding how real-life events are processed during sleep.

Sleep is known to benefit consolidation of declarative memories (i.e., memories of facts and episodic events), presumably by promoting the redistribution of encoded representations from hippocampal to extra-hippocampal neocortical regions (1, 2). This has been demonstrated particularly for simple associations (e.g., between two elements in classical "paired-associates" learning tasks). However, in real life, events have usually a more complex structure, involving multiple interdependent elements such as the place of an event and people or objects one has interacted with. Also, the strength of associations typically differs between elements of an event, with some elements even being associated only indirectly (e.g., because they occurred at different times of the event). Because of the associative structure interlinking the individual elements, a partial or degraded cue can be sufficient to recover an entire multielement event (3). This property, referred to as pattern completion, constitutes a core function of hippocampal memory processing (4–6). Presently, it is unclear how sleep affects the associative structure of complex multielement events, e.g., whether it differentially affects individual associations depending on the association strength and whether it promotes the ability to retrieve the entire event based on a single element.

Previous studies investigating simple associations suggest a stronger effect of sleep on consolidation of weakly compared with strongly encoded information (7–12). In addition, sleep may not only support consolidation of encoded associations but also of associations between elements that were not directly associated during encoding. Indeed, the sleep-dependent neuronal redistribution of memory representations from hippocampal to neocortical networks has been associated with qualitative changes in the content of the memory (13–18), which might implicate the formation of new connections between elements that were not encoded together. These kinds of novel higher-order associations can be considered evolutionary highly advantageous as they allow for a more complete understanding of the environment, allowing to make more wide-reaching predictions of the world (19, 20). However, very little is known about the role of sleep in this context (21, 22). Finally, sleep may also enhance the interdependency between individual associations by strengthening the hierarchical associative structure, thereby improving processes

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[1]To whom correspondence may be addressed. Email: nicolas.lutz@med.uni-muenchen.de or luciana.besedovsky@med.uni-muenchen.de.

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of pattern completion not only for simple associations but also for complex multielement events (3, 23). Although such knowledge is essential for understanding effects of sleep on complex memories, such as occurring in real life, the specific role of sleep in these aspects is unclear.

In the present study, using a verbal associative learning task comprising events with strongly, weakly, and not-directly encoded associations, we aimed to scrutinize how sleep, compared with a period of nocturnal wakefulness after encoding (followed by a recovery night), affects consolidation of the associative structure and subsequent pattern completion in complex multielement events. We show that sleep vs. wakefulness i) selectively improves the consolidation of weakly encoded associations, ii) strengthens newly formed associations between elements that were not directly associated during encoding, and iii) crucially also that it supports the ability to recollect multiple elements of an event based on a single cue. Collectively, these effects of sleep on the associative structure of multielement events suggest a fundamental role of sleep in pattern completion in complex events, such as occurring in real life.

Results

Fourteen healthy volunteers (seven female) took part in this within-subjects study comprising a Sleep condition and a Wake condition. In both conditions, they engaged in a verbal associative learning task (modified from ref. 3) that was followed by a pre-intervention recall after 30 min. Thereafter, participants either slept (Sleep condition) or stayed awake during the night (Wake condition) in the sleep laboratory. Following the experimental night, they stayed in the laboratory during the following day and left at 10:00 pm to sleep at their home (serving as recovery night in the Wake condition). The next day, participants returned to the laboratory in the evening for a post-intervention recall (Fig. 1*A*).

During the encoding phase, participants studied word pairs derived from individual events, each consisting of four elements (A, B, C, and D): one animal, one location, one object, and one food element (Fig. 1 *B*, *Left*). Events were encoded in a specific temporal pattern (A-B, B-C, C-A, and B-D), leading to three distinct substructures: a closed loop consisting of strong associations between elements A, B, and C; weak associations between

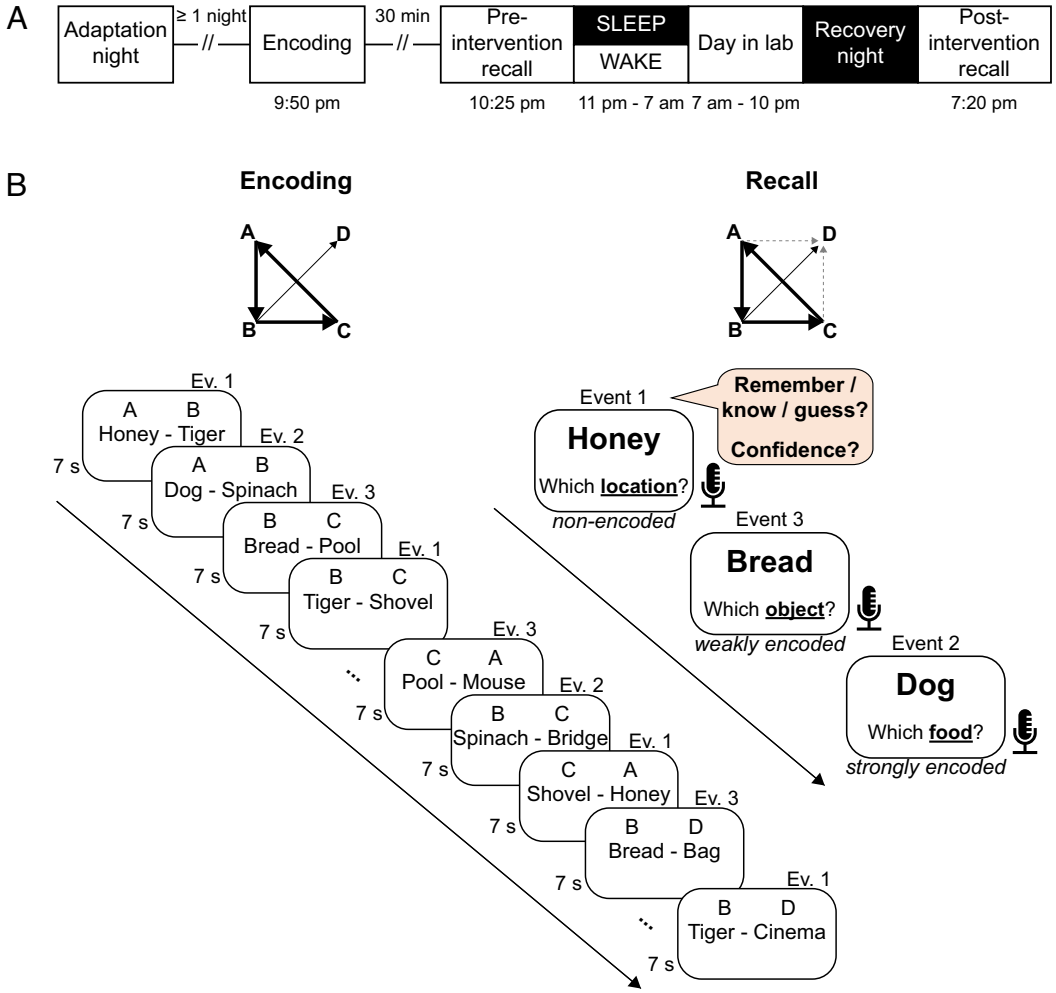

Fig. 1. Experimental design and task. (*A*) Study design. (*B*) *Upper* and *Lower* panels show structures of the multielement events and examples for encoding (*Left*) and recall (*Right*), respectively. Participants encoded 20 events, each consisting of four elements (A, B, C, and D) from four different categories: animals, locations, objects, and foods. The categories were equally distributed across the four elements of the 20 events. During encoding, events were presented sequentially in pairs of words (A-B, B-C, C-A, B-D), leading to three substructures: a closed-loop structure (A-B-C, e.g., Honey–Tiger–Shovel) fostering strong encoding of elements (thick black lines in *Upper* panels), a loop opening (B-D, e.g., Tiger-Cinema) leading to weak encoding (thin black line), and non-encoded associations (A-D and C-D, e.g., Honey–Cinema and Shovel–Cinema; dashed gray lines). Each word pair was presented for 7 s with a 1-s inter-stimulus interval. Note that the letters A, B, C, and D above the encoding examples are shown for illustration purposes only and were not presented to the participants. During the category-specific recall, participants were presented with single previously encoded words and were asked to name the associated word of a specific category. Additionally, we asked them to judge whether their choice reflected episodic remembering, semantic knowing, or random guessing, and to rate their confidence on a 4-point scale. Participants' spoken words were recorded via a headset and their response time was logged via a computer keyboard. Ev., event.

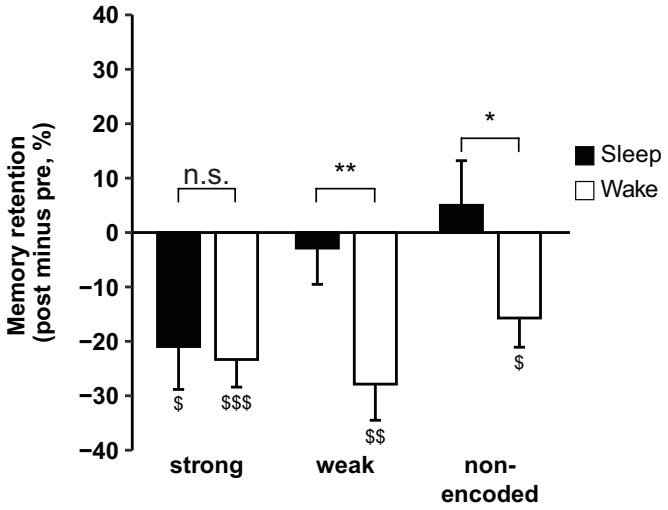

Fig. 2. Memory retention following sleep vs. nocturnal wakefulness. Mean ± SEM of retention performance (change from pre- to post-intervention recall shown as % of the total number of strong, weak, and non-encoded associations) for Sleep (black bars) and Wake conditions (white bars) and the three encoding strengths. $^{**}P < 0.01$; $^{*}P < 0.05$ for the difference between Sleep and Wake conditions. $^{\$\$\$}P < 0.001$; $^{\$\$}P < 0.01$; $^{\$}P < 0.05$ for the change between pre- and post-intervention recalls; n.s., not significant. n = 14.

B and D (induced by the discontinuation of the loop after presentation of element D), and non-encoded associations between A-D and C-D (i.e., these specific word pairs were never presented together). Participants were not informed about this underlying multielement event structure. During recall, participants were shown single previously encoded words and were asked to name the associated word of one given category (Fig. 1 *B*, *Right*). This procedure was always done in the "forward" direction, i.e., in the direction in which the word pairs were encoded (e.g., A-B, not B-A). In addition, participants were asked for each choice to judge whether they explicitly remembered the named associated word, if they knew it (i.e., if they had a feeling of familiarity without being able to remember specific contextual details), or if they had to guess. They were also asked to rate their confidence on a 4-point scale. Associations for an event were presented interleaved with other event associations and participants were not informed that each event consisted of 4 elements.

Sleep Selectively Improves Consolidation of Weak Associations and Strengthens Non-Encoded Associations. Retention of memory (i.e., the difference between pre- and post-intervention recalls) depended on sleep and encoding strength (Sleep/Wake x Encoding strength interaction: $F(2, 26) = 3.69$, $\eta_p^2 = 0.22$, $P = 0.039$; Fig. 2; see *SI Appendix*, Fig. S1 showing results for memory performance on the different encoding strengths and *SI Appendix*, Fig. S2 for additional analyses on individual associations). Post hoc analyses for the different encoding strengths revealed that sleep, compared with wakefulness, specifically promoted retention performance for weak and non-encoded associations but not for strong associations [$t(13) = 3.74$, Cohen's $d = 1.00$, $P = 0.002$, $t(13) = 2.37$, Cohen's $d = 0.63$, $P = 0.034$, and $t(13) = 0.30$, $P = 0.771$, for weak, non-encoded, and strong associations, respectively]. Similar results were obtained for a separate "category-unspecific recall," in which participants were asked to recall all elements of an event associated with one single cue at once (*SI Appendix*, Fig. S3 *A–C*).

Sleep Benefits Joint Remembering of Multiple Elements of an Event. To further investigate the role of sleep in strengthening not only single but also multielement associations, we calculated a measure of "joint remembering" (derived from a measure of full retrieval dependency; see below and refs. 3 and 24), which specifically assesses the probability to retrieve two elements given only a single common cue. Joint remembering occurs if both elements are retrieved correctly. In contrast, "joint forgetting" occurs if neither of the two elements can be remembered correctly (including both incorrect answers and omissions). In our category-specific recall, this approach can be directly applied to element B, which served as direct cue for both C and D (in contrast, A and C only served as a direct cue for B and A, respectively). When calculating joint remembering according to this scheme, we found a significant difference between Sleep and Wake conditions ($Z = 2.58$, $r = 0.690$, $P = 0.010$; Fig. 3 *A*, *Left*), with a reduction in joint remembering from pre- to post-intervention recalls after wakefulness ($Z = 2.76$, $r = 0.738$, $P = 0.006$) but a retention of this ability after sleep ($Z = 0.42$, $P = 0.672$). For joint forgetting, on the other hand, we found a similar increase after sleep and wakefulness, with no significant difference between conditions (Sleep vs. Wake condition: $Z = 0.17$, $P = 0.865$; Sleep condition: $Z = 2.20$, $r = 0.588$, $P = 0.028$; Wake condition: $Z = 2.56$, $r = 0.685$, $P = 0.010$; Fig. 3 *A*, *Right*). To get a full picture of the changes in the associative structure following sleep, we also calculated a measure of "disjoint remembering," which occurs if only one of the two elements can be retrieved correctly. We found a significant difference between conditions ($Z = 2.08$, $r = 0.557$, $P = 0.037$; *SI Appendix*, Fig. S4) with a reduction in disjoint

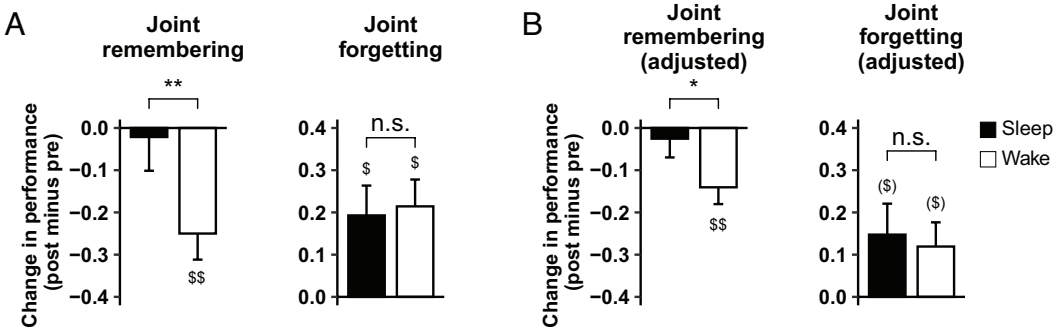

Fig. 3. Change in joint remembering and joint forgetting following sleep vs. nocturnal wakefulness. (*A*) Mean ± SEM of Sleep and Wake conditions for the change (from pre- to post-intervention recall) in joint remembering (i.e., the proportion of events for which both elements C and D were correctly remembered given cue B; *Left*) and joint forgetting (i.e., the proportion of events for which neither of the two elements were correctly remembered; *Right*). (*B*) Mean ± SEM of Sleep and Wake conditions for the change in adjusted joint remembering (*Left*) and adjusted joint forgetting (*Right*) (i.e., corrected for accuracy levels of individual associations; see *Materials and Methods* for details). $^{**}P < 0.01$; $^{*}P < 0.05$ for the difference between Sleep and Wake conditions. $^{\$\$}P < 0.01$; $^{\$}P < 0.05$, $^{(\$)}P < 0.1$ for the change between pre- and post-intervention recalls; n.s., not significant. n = 14.

remembering after sleep (Z = 2.31, r = 0.617, $P = 0.021$) but not after wakefulness (Z = 0.36, $P = 0.720$).

To correct the joint remembering score for accuracy levels of individual associations (3, 25), we additionally calculated an "adjusted joint remembering" measure (see *Materials and Methods* for details). Importantly, we also found a significant difference between Sleep and Wake conditions for this adjusted joint remembering measure (Z = 2.24, r = 0.599, $P = 0.025$), with a significant reduction after wakefulness (Z = 2.65, r = 0.708, $P = 0.008$) but a retention after sleep (Z = 0.21, $P = 0.834$; Fig. 3 *B*, *Left*). For joint forgetting, differences between conditions remained non-significant after applying this correction (Z = 0.51, $P = 0.610$; Fig. 3 *B*, *Right*).

We also found similar results when including the other triplets of the event structure (i.e., A-BD and C-AD, which were retrieved, but not encoded, in a triadic manner), thus considering all four elements of an event (*SI Appendix*, Fig. S5).

We, furthermore, calculated a measure of "full retrieval dependency" according to previous publications (3, 24, 26), which assesses the probability to retrieve or not to retrieve two elements given a single common cue. Hence, this measure includes a combination of joint remembering and joint forgetting. We found a significant difference between Sleep and Wake conditions (Z = 2.08, r = 0.557, $P = 0.037$), with an increase after sleep (Z = 2.31, r = 0.617, $P = 0.021$) but not after wakefulness (Z = 0.36, $P = 0.720$) for the raw dependency measure (*SI Appendix*, Fig. S6, *Left*). However, when calculating dependency in relation to an independent model that assumes complete independence between the associations, this difference was no longer significant (Z = 1.06, $P = 0.289$; see *SI Appendix*, Fig. S6, *Middle*), suggesting that while sleep specifically benefits joint remembering, it does not support full retrieval dependency. Also, comparing dependency in the data with the independent model led to no significant difference (Z = 0.98, $P = 0.325$; see *SI Appendix*, Fig. S6, *Right*), indicating that "open-loop" associative structures as employed in the present study do not show dependency per se.

Sleep Spindles Are Associated with the Retention of Weak Associations and Joint Remembering. Fast (12 to 15 Hz) sleep spindles play a major role in mediating the hippocampal–cortical interplay during sleep-dependent memory consolidation (2). While they have been shown to preferentially consolidate weakly encoded individual associations (27), they are also likely to be involved in strengthening complete associative structures, given their involvement in hippocampal memory reactivation (2), which is also considered a key mechanism of successful pattern completion (5). We therefore investigated whether sleep spindles also predict the strengthening effect of sleep on the associative structure of multielement events (for the overall sleep architecture, see *SI Appendix*, Table S1). Importantly, we found both the performance for memory of weak associations as well as for adjusted joint remembering to correlate with power density in the fast spindle band (r = 0.598, $P = 0.024$ and $\rho = 0.743$, $P = 0.002$, respectively; Fig. 4*A*) and with the amplitude of individual spindles (r = 0.541, $P = 0.046$ and $\rho = 0.654$, $P = 0.011$, respectively; Fig. 4*B*).

Discussion

In the present study, we investigated the effects of sleep on shaping the associative structure of complex multielement events. Our results demonstrate a differential effect of sleep on the consolidation of individual associations, with benefitting effects on weakly and not directly encoded associations but no effect on strong associations. Crucially, these effects were accompanied by an improved ability to jointly remember multiple elements of an event based on a single cue after sleep compared with wakefulness. The consolidation of weak associations as well as the performance for joint remembering were positively associated with sleep spindles during NonREM sleep. Our findings demonstrate that sleep shapes multielement associative structures, thereby supporting pattern completion in complex multielement events, a core hippocampal function essential for recalling complete memories based on a partial cue.

Whereas there is direct evidence for a stabilizing role of sleep in pattern *separation* [i.e., the formation of nonoverlapping orthogonal representations from similar input (28)], so far only indirect hints have been provided for a possible role of sleep in promoting pattern completion: Using the mnemonic similarity task (MST), the same study (28) suggested that, apart from stabilizing pattern separation, sleep may also favor pattern completion based on the finding that sleep shifted participant's ratings of "lure" objects that were highly similar to actually encoded objects from "similar" to "old" (see also ref. 29). However, the MST allows only for a rather restricted assessment of pattern completion conceptualized as diminished pattern separation. Yet, pattern separation and pattern completion are basically separate and independent processes that rely on different neuronal hippocampal mechanisms and operate at different stages of memory processing [encoding vs. retrieval, respectively (30, 31)]. Against this backdrop, the measure of joint remembering (derived from refs. 3 and 24) as assessed in the present study represents, in our view, a highly sensitive and specific measure of pattern completion, because it conceptualizes pattern completion as a process that is required for recovering a whole multielement event in episodic memory based on a partial cue (32). Moreover, the multielement associative learning task we employed attempts to mimic complex real-life events, going beyond classical paradigms using simple paired associates. These events include not only "closed-loop" structures, in which all elements are associated with each other (e.g., A-B, B-C, C-A) but also "open-loop" structures containing elements that were not encoded together (A-D, C-D). The hippocampus appears to be especially important for such complex episodic information, binding together multiple elements with their spatiotemporal context (6, 33, 34). Therefore, our finding that sleep supports joint remembering of multiple elements of an event is consistent with sleep mainly supporting hippocampus-dependent memory processes. In supplementary analyses, this effect was also evident when including the other triplets of the event structure (*SI Appendix*, Fig. S5), suggesting that sleep benefits retrieval of *entire* multielement events. Moreover, the beneficial effect of sleep was specific for joint remembering, whereas joint forgetting showed a general increase over time that was independent of sleep. This suggests an active sleep-dependent effect on remembering complete multielement events but a sleep-independent effect of forgetting complete multielement events over time. The effect of sleep vs. nocturnal wakefulness on joint remembering was still evident after correction for accuracy, showing that this effect was not a simple consequence of sleep improving overall accuracy but that it specifically favors retention of jointly remembered elements. This conclusion is in line with the complementary finding that sleep actually reduced disjoint remembering, which excludes the possibility that the effect of sleep on joint remembering was only a consequence of sleep independently improving the individual associations of an event.

We did not find an effect of sleep on the adjusted measure of full retrieval dependency (which includes processes of both joint remembering as well as joint forgetting). This finding is in line

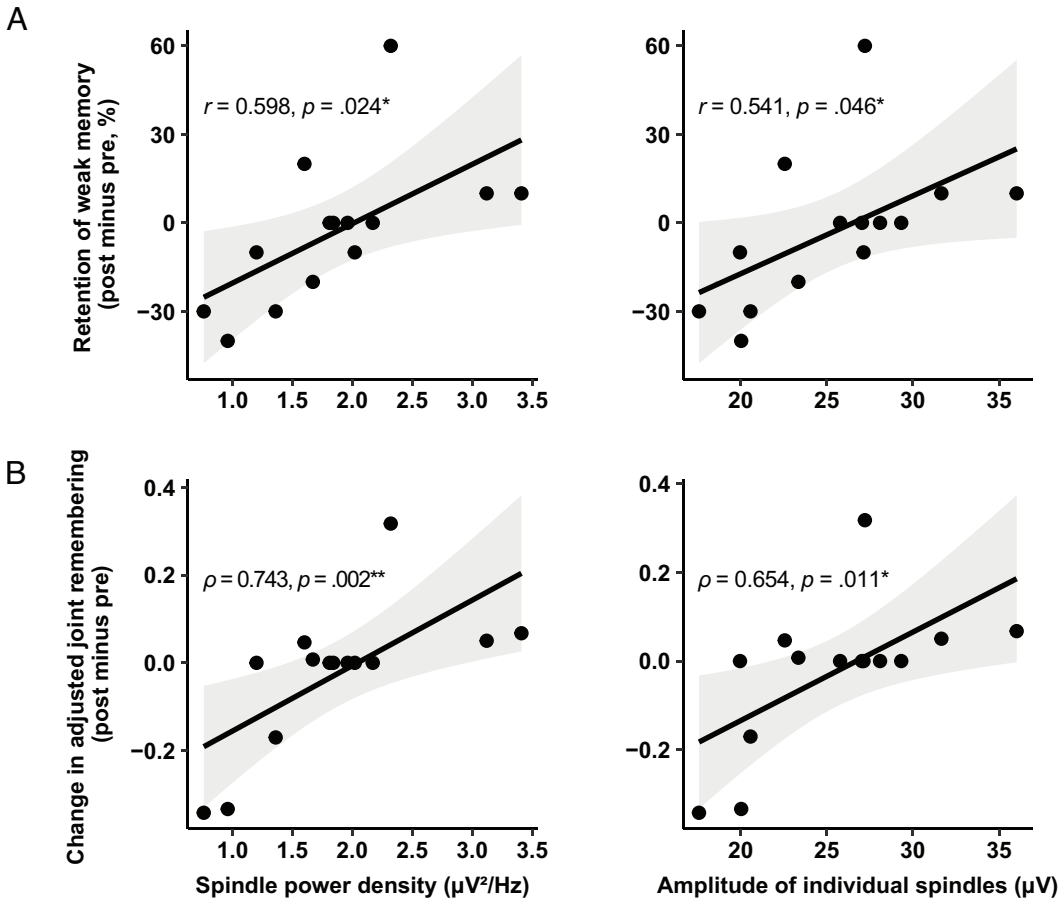

Fig. 4. Correlations of memory performance with fast sleep spindles. Shown are scatter plots including individual data points and 95% CIs (gray shading) for correlations of (*A*) memory of weak associations and (*B*) adjusted joint remembering with spindle power density (*Left*) and spindle amplitude (*Right*) for recordings at central electrodes (average of C3 and C4). Memory performance is indicated as the difference between pre- to post-intervention recalls. n = 14.

with a previous study using this measure in a between-subjects design comparing night-time sleep with daytime wakefulness (23). We also did not find a significant difference between dependency in the data and the independent model. These results are also consistent with previous work, suggesting that "open-loop" (vs. "closed-loop") associative structures do not show dependency per se (e.g., ref. 3). Although the full retrieval dependency measure is very powerful for investigating overall statistical dependency in memory retrieval (including both joint remembering and joint forgetting), we believe that the specific measure of joint remembering is most useful and sensitive to capture the essence of pattern completion as a consistently positively defined ability to remember—and not necessarily to forget—multiple elements of an event based on a partial cue (e.g., ref. 32). The discrepant results for the adjusted joint remembering and full retrieval dependency measures are in line with our finding that sleep specifically benefits processes of joint remembering but not of joint forgetting, suggesting that different processes may underlie these two aspects of memory, at least in open-loop associative structures (see also ref. 35 for a perspective paper supporting this conclusion). Future studies are required to further disentangle the conceptual meanings and physiological bases of these different measures.

Considering individual associations, the beneficial effect of sleep was specific for weakly and not directly encoded associations but was not observed for strongly encoded information. These findings are in line with previous studies suggesting that weakly encoded memories benefit most from mechanisms of sleep-dependent consolidation (7–12). Our findings extend this notion to complex events, meaning that, although all elements are part of one and the same event, not all of these elements benefit from sleep in the same way. In a recent study, Petzka et al. suggested that stronger memories may require higher retrieval difficulty (e.g., by employing a retroactive interference task) to reduce ceiling effects in memory performance for sleep effects to be unveiled (36). However, given that the retrieval performance for strongly encoded associations during pre- and post-intervention recalls was around 68% and 45%, respectively, in our study, ceiling effects are highly unlikely. Our findings appear to be in contrast with two studies that found a specific effect of targeted memory reactivation (TMR) during sleep on strengthening of strongly but not weakly encoded overlapping associations (i.e., associations that share a common cue element) (37, 38). This discrepancy may be explained by the different associative structures and different approaches employed to create strong and weak associations in the studies: Whereas in our study different encoding strengths were established through the associative structure itself (using closed-loop and open-loop components), Oyarzún et al. (37) and Joensen et al. (38) employed different time delays between encoding and an interference task (followed by sleep and a final retrieval test) or different encoding orders between overlapping pairs, respectively, to vary associative strength. In addition, whereas we compared strong vs. weak associations following normal nighttime sleep vs. wakefulness, Oyarzún et al. (37) and Joensen et al. (38) compared different associations following TMR during sleep, with TMR possibly inducing effects distinct from those of spontaneous reactivations in undisturbed sleep conditions.

Not only did we find a beneficial effect of sleep on weakly encoded associations but also on associations that were not directly encoded. Previously, beneficial effects of sleep on transitive inference tasks have been reported in which participants were asked to indicate the relationship between actually encoded "premise" pairs (e.g., A>B, B>C) and not directly encoded "inference" pairs (e.g., A>C; refs. 21 and 22). Unlike in those studies, in our task, participants were not asked to put given information in relation to one another but to spontaneously reproduce this information, which is arguably an even more demanding task. Our findings are in line with two other studies that applied somewhat different designs (23, 39). One possible explanation for this effect of sleep on non-encoded associations is that the inference of associations between not directly encoded pairs may depend on processes of memory abstraction, i.e., the transformation of episodic memories to generalized knowledge or the "gist," which is based on the discovery of commonalities between newly encoded information (40). Such qualitative changes are believed to result from the neuronal redistribution of memories from hippocampal to extrahippocampal, preferentially neocortical, networks during memory consolidation (13, 14) and have previously been suggested to depend on sleep (14–18, 20, 41–44). Although the employed task was not designed to directly investigate processes of gist abstraction, such processes could have played a role for improved inference of not directly encoded associations after sleep compared with wakefulness. However, we only found a numerical, non-significant increase for non-encoded associations from the pre- to the post-intervention recall in the Sleep condition, suggesting that these processes, to the greatest part, occurred already shortly after encoding, and that in these conditions sleep is more likely to maintain rather than to support the new formation of these connections.

Our data also revealed positive correlations of both weakly encoded associations and adjusted joint remembering with sleep spindle activity during NonREM sleep. Sleep spindles are an essential marker for active systems consolidation, which is associated with memory reactivations during sleep (2, 45–48). Reactivations are believed to originate in the hippocampal CA1 subregion, from where they spread into extrahippocampal regions like entorhinal, striatal, and cortical areas to support memory consolidation (2). Indeed, memory consolidation during sleep critically relies on hippocampal function (49, 50). Moreover, involvement of the hippocampus as a binding region for individual elements of an event into coherent "event engrams" has been demonstrated previously (6). Interestingly, the same hippocampal region that is involved in memory reactivations was identified to contribute to pattern completion in humans (51). Thus, in addition to supporting the well-documented correlations between spindles and simple associations, our findings suggest that pattern completion in complex event memory may be linked to spindle-dependent memory reactivations during sleep. However, for more wide-reaching claims on neural correlates of sleep-dependent pattern completion, further studies, e.g., using fMRI, are needed.

As a limitation of the present study, we note that our sample size is relatively small. However, it is based on a power calculation of a related effect as reported in the literature available at the beginning of the study (28), and considering further related studies using similar sample sizes in the field (e.g., refs. 21 and 52–54), the sample size was arguably sufficient to achieve the statistical power necessary for the detection of the presented effects in this proof-of-principle study. A further limitation is that we cannot entirely exclude that the effects on memory performance were a consequence of the lack of sleep rather than an active effect of sleep per se. The strength of our approach is that it controls for time-of-day effects that are independent of sleep and that can bias results of study designs that test participants in the morning vs. the evening. Furthermore, the sleep manipulation in our study was strongly controlled, with participants being observed for an entire 24-h sleep-wake cycle and a 24-h wake-wake cycle with controlled food intake, ambulation, etc. to keep any unspecific effects of sleep deprivation at a minimum. Also, the retrieval took place following a recovery night and there were no significant differences between Sleep and Wake conditions in vigilance and subjective sleepiness at retrieval testing, excluding an unspecific effect of these factors on our findings. Finally, the correlations between sleep spindles and retrieval performance we found in our study further suggest an active role of sleep in this context.

To conclude, we demonstrate here how sleep, in a unique manner, shapes associative structures in complex multielement events, thereby supporting subsequent pattern completion. These effects of sleep can be considered highly adaptive given their role in creating and retrieving more coherent representations of our environment, which allows to make more wide-reaching predictions. Hence, our results unveil a crucial aspect of how sleep can provide an evolutionary advantage. In addition, our findings will likely stimulate new perspectives on how we consolidate and retrieve information embedded in complex multielement events.

Materials and Methods

Participants. Sixteen healthy, young adults (8 female and 8 male) participated in the study (mean age: 23.86 y; range: 19 to 30). The sample size in our experimental design was determined by a statistical power calculation based on an expected large effect size derived from a previous study, which investigated sleep effects on pattern separation but also on an (indirect) measure interpreted as pattern completion (28). To be able to detect a large effect of Cohen's $d = 0.8$ (as a conservative estimate of the large effect sizes of $d \geq 1.10$ derived from this study), a sample size of $n = 12$ is necessary to reach a power of at least 0.8, given $\alpha = 0.05$ and an assumed correlation between conditions of at least $r = 0.6$ [based on an assumed high reliability of the measurements that are based on multiple observations per participant per condition in the present protocol (55)]. In addition, based on previous studies investigating correlations between hippocampus-dependent/episodic memory measures and sleep spindles (e.g., refs. 52–54 and 56), yielding an average effect size of $r = 0.64$, a sample size of $n = 14$ should be sufficient to detect correlations between sleep spindles and episodic memory measures. Of the 16 recruited participants for the present study, one participant had to be excluded from analyses due to being an outlier on several variables, including total sleep time (324.5 min of sleep during the experimental night, which is below our predetermined inclusion criterion of at least 6 h of sleep) as well as sleep and circadian-related actigraphy parameters (sleep efficiency < 70%, sleep latency > 150 min, and wake after sleep onset > 150 min during the night following the sleep/wake intervention; relative amplitude < 0.4 during the 7 d before participating in the experiment). Another participant could not be included in the final analysis due to non-compliance with the experimental procedures, which did not yield useable data. Thus, the final sample size was $n = 14$. Nevertheless, inclusion of data from the outlier participant as well as from another participant examined in the context of pilot tests did not change the results of our study.

Participants did not take any medication (except for oral contraceptives in female participants) and did not report any neurological or psychological disorders. They were asked to refrain from ingesting caffeine (after noon) or alcohol and not take naps during the days of the experimental sessions. All participants gave written informed consent and were paid for participation. The experiment was approved by the ethics committee of the Medical Faculty at the University of Tübingen and conducted in accordance with the Declaration of Helsinki.

Experimental Design and Procedure. The experiment was designed as a within-subjects, cross-over study including a Sleep and a Wake condition, with the order of conditions being counterbalanced (Fig. 1). On the days of the experiment, participants took part in a memory test, including an encoding phase

as well as a first recall 30 min later (pre-intervention recall). This was followed either by night-time sleep (Sleep condition) or by a nocturnal period of wakefulness (Wake condition). Recall performance was tested again 2 d later (post-intervention recall), i.e., after participants had a regular night of sleep at home serving as recovery night in the Wake condition. Because the female hormonal cycle is known to affect sleep-dependent memory processing (e.g., ref. 57), both conditions took place during the same phase of the women's cycle.

Before the experiment proper, participants spent an adaptation night in the sleep laboratory to get accustomed to the laboratory setting. Participants were asked to keep a regular sleep-wake cycle during at least 7 d prior to the experiment. To confirm this, participants filled in a sleep diary and wore an actigraph (MotionWatch 8, *CamNtec*, UK) until the end of the experimental sessions. There was no significant difference between Sleep and Wake conditions for the different actigraphy parameters interdaily stability (i.e., the stability of rest-activity rhythms between different days), intradaily variability (i.e., the fragmentation of rest-activity patterns), or the relative amplitude between the 10 h of maximum activity and the 5 h of lowest activity ($P \geq 0.593$; ref. 58).

Following this 7-d period, participants came to the sleep laboratory for an encoding session at 08:30 pm. After placement of electrodes for polysomnographic recordings and completing a questionnaire on subjective sleepiness [Stanford Sleepiness Scale (59, 60)], the memory task was explained. Encoding took place at 09:40 pm. Following encoding, participants completed again the questionnaire on sleepiness and performed a psychomotor vigilance task (PVT). A first pre-intervention recall was performed 30 min after the encoding session. This was followed by questions on imaginativeness of the word pairs and encoding strategies. They were told not to actively think about the words until the recall takes place. In the Sleep condition, participants were given the possibility to sleep in the sleep laboratory from 11:00 pm to 07:00 am. In the Wake condition, participants spent the same interval in a semi-supine position in bed and engaged in activities like watching series, playing board games, or reading a book. The experimenter continuously monitored if participants were awake during the deprivation night. To ensure that participants did not take daytime naps (especially after sleep deprivation in the Wake condition) and all engaged in similar activities, they spent the following day in the lab, where they got standardized breakfast, lunch, and dinner and were continuously monitored by the experimenter. Participants went home at 10:00 pm to sleep in their own bed (serving as a recovery night in the Wake condition).

Following the night at home, participants returned to the lab at 07:00 pm for a post-intervention recall test. After completing the sleepiness questionnaire and performing the PVT, the post-intervention recall started at 07:25 pm. At the very end of the experiment (after completion of both conditions), participants were asked increasingly specific questions about their knowledge of the multielement event structure (e.g., "Did you notice anything?," "Did you notice a relationship between the encoded words?," "How many elements do you think belong together/form an event?," "Do you think all pairs that were tested during recall were presented together during encoding?"). None of the participants became fully aware of the event structure. In addition, we did not find any significant differences between Sleep and Wake conditions on sleepiness or PVT performance before encoding and recall (all $P \geq 0.082$), indicating that participants were similarly well rested during both sessions.

Memory Task. During encoding, participants studied 80 words, which were displayed consecutively in pairs on a computer screen. These words were derived from 20 events containing four elements (A, B, C, and D) that consisted of one animal, one location, one object, and one food (Fig. 1). Events were encoded in a specific directional pattern (A-B, B-C, C-A, and B-D), leading to three distinct substructures: strong associations derived from a closed-loop structure between A, B, and C, a weak association between B and D (induced by the discontinuation from element D), and non-encoded associations between A-D and C-D. Participants were not informed about this multielement event structure. Each pair was presented for 7 s with 1-s inter-trial-intervals. Pairs belonging to one event were shown with at least two pairs of other events in between. All pairs were presented twice in the same order in two consecutive blocks.

Participants took part in two recall types: a category-specific recall, followed by a category-unspecific recall. In the category-specific recall, participants' specific memory of strong, weak, and non-encoded associations was tested. They were presented with single previously encoded words (e.g., "dog") and asked to name the associated word of one of the four categories (e.g., the word "spinach" of the category "food") into a microphone. Participants had a 10-s time window for their answer. Participants were instructed to make use of this time window if the correct association did not come to mind immediately. They were further instructed to guess rather than say nothing. In addition to their verbal response, we collected participants' reaction times, remember/know/guess judgements (i.e., they were asked whether they explicitly remembered the named associated word, if they had a feeling of familiarity without being able to remember specific contextual details, or if they had to guess), and their confidence ratings on a 4-point scale for each choice. All six associations (i.e., A-B, B-C, C-A, B-D, A-D, and C-D) were tested for each event. Thus, to avoid priming effects due to the recall of other elements, non-encoded associations (i.e., A-D and C-D) were tested first and weak (i.e., B-D) and strong associations (i.e., A-B, B-C, and C-A) were tested in an intermixed order afterward.

In the category-unspecific recall, participants were only presented with words corresponding to element A of the event structure and were asked to name all other words associated with A. We further asked them to indicate words they were unsure of being the correct response.

For the two conditions (Sleep/Wake), we used two parallel versions of each 20 events that were balanced across conditions, as well as two subversions (half of each version) that were balanced across the pre- and post-intervention recalls, respectively. Hence, there were 40 events in total per participant, 20 per condition, and 10 of these events were tested pre-intervention and 10 different events were tested post-intervention. Behavioral data were acquired using MATLAB/Psychtoolbox (RRID:SCR_002881; refs. 61–63).

Data Reduction and Analysis.

Behavioral performance. Reduction and analysis of behavioral data was performed using MATLAB (RRID:SCR_001622). In the category-specific recall, memory performance was analyzed based on correct answers for strong associations (A-B, B-C, and C-A), weak associations (B-D), and non-encoded associations (A-D and C-D). To estimate the ability to retrieve multiple elements of an event together, we calculated a measure of "joint remembering" (derived from refs. 3, 24, and 26 as the proportion of events in which C and D were both correctly retrieved given a single cue B. This measure reflects the direction of encoding and retrieval (from B to C and from B to D). We also calculated a measure of "joint forgetting," reflecting the proportion of events in which C and D were both incorrectly retrieved, either by wrong answers or omissions. To get a complete picture, we additionally calculated a measure of "disjoint remembering," reflecting the proportion of events in which only one element (e.g., C) but not the other (e.g., D) could be retrieved correctly.

To correct for accuracy levels of individual associations, we also calculated an "adjusted joint remembering" measure, i.e., we divided the raw joint remembering score by the product of accuracy for individual associations (i.e., $(p(C \mid B) + 0.5) * (p(D \mid B) + 0.5)$). The addition of a constant of 0.5 was done to account for zero frequencies that lead to undefined values (see, e.g., ref. 25).

We extended these analyses also to include the other triplets of the event structure, which were retrieved (but not encoded) together (i.e., A-BD and C-AD) (*SI Appendix*).

In the category-unspecific recall, participants were presented with the cue A and memory performance was analyzed based on correct answers for B, C, and D, respectively. Since in this recall, A was the cue and B, C, and D were to be retrieved, joint remembering and joint forgetting were calculated including all elements in the direction of recall (A-BCD).

Finally, we also calculated a measure of "full retrieval dependency" according to refs. 3 and 24, which takes into account performance for both joint remembering and joint forgetting (i.e., the proportion of events in which C and D were both correctly or both incorrectly retrieved given a single cue B). To correct for individual accuracy levels, this measure was also calculated in relation to an "independent model" (i.e., by calculating the difference between dependency in the data and the independent model), as previously established (3, 24, 25).

Retention performance after the sleep/wake manipulation was calculated as the change in the percentage of remembered associations (word pairs or entire events, respectively) from pre- to post-intervention recall.

Sleep recordings. Polysomnographic recordings were obtained and digitized at a sampling rate of 500 Hz using a BrainAmp MR plus system (Brain Products, Germany). Electroencephalography (EEG) was recorded from six locations (F3 and F4, C3 and C4, and O1 and O2, according to the international 10–20 system) and

referenced online against the mean of the two mastoids (A1, A2). Additionally, the electrooculogram (EOG), electromyogram (EMG, electrodes positioned on the chin), and electrocardiogram were recorded with bipolar montages. All data were stored unfiltered. For analysis, filters were applied to the EEG and EOG at a frequency of 0.16 Hz (high-pass) and 30 Hz (low-pass) as well as to the EMG at a frequency of 5.31 Hz (high-pass) and 90 Hz (low-pass). In addition, a notch filter was applied at 50 Hz. Sleep scoring was performed offline and manually based on 30-s epochs, in accordance with standard criteria (64).

Sleep spindle detection was performed using an algorithm implemented in SpiSOP (RRID:SCR_015673). The frequency of fast spindles (mean center frequency: 13.34 Hz) was determined for each participant based on individual power spectra across all electrodes for sleep stages S2, S3, and S4. Spindle detection was performed for central electrodes (average of C3 and C4). Based on our previous findings (65), our analyses focused on power density in the fast spindle band and fast spindle amplitude (i.e., the mean amplitude of discrete fast spindle events, measured from trough to peak).

Statistical analysis. To examine the effect of sleep vs. wakefulness on memory performance, we focused on retention performance (i.e., the difference between performance in the post-intervention recall minus performance in the pre-intervention recall) and performed repeated-measures ANOVA including the factors Sleep/Wake (Sleep vs. Wake condition) and Encoding strength (strong vs. weak vs. non-encoded associations) or Association type (A–B vs. A–C vs. A–D), for category-specific and category-unspecific recalls, respectively. These analyses were followed by post hoc *t* tests to compare differences between Sleep and Wake conditions and between pre- and post-intervention recalls for Sleep and Wake conditions separately. To examine the effects of sleep vs. wakefulness on joint remembering, joint forgetting, disjoint remembering, and full retrieval dependency measures, we calculated Wilcoxon rank-sum tests comparing Sleep and Wake conditions as well as pre-and post-intervention recalls for Sleep and Wake conditions separately. We used non-parametric tests for all of these related measures, even for those that were normally distributed, to keep comparability between them. However, results for parametric tests were equivalent. To investigate associations between sleep spindles and memory performance, we used Pearson's or Spearman's correlations for normally and non-normally distributed data, respectively. Repeated-measures ANOVAs were used with Greenhouse–Geisser correction of degrees of freedom where applicable. Two-tailed tests were chosen for all statistical analyses. A P value < 0.05 was considered significant. Statistical analyses were performed in R (R Project for Statistical Computing, RRID:SCR_001905).

Data, Materials, and Software Availability. All data relevant to the conclusions of this paper have been deposited in Open Science Framework (https://osf.io/y5zb7/) (66).

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Author affiliations: [a]Institute of Medical Psychology and Behavioral Neurobiology, University of Tübingen, Tübingen 72076, Germany; [b]Institute of Medical Psychology, LMU Munich, Munich 80336, Germany; [c]Werner Reichardt Centre for Integrative Neuroscience, University of Tübingen, Tübingen 72076, Germany; and [d]German Center for Diabetes Research, Institute for Diabetes Research and Metabolic Diseases of the Helmholtz Center Munich at the University Tübingen, Tübingen 72076, Germany

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