When Sleep-Dependent Gist Extraction Goes Awry: False Composite Memories are Facilitated by Slow Wave Sleep

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Abstract

Contemporary evidence suggests that sleep contributes to the extraction of gist from previously encoded experiences, a process that relies on compressed memory replay. While the functional significance of the time compression is not fully understood, a recent 'temporal scaffolding' model suggested that compression allows associating encoded events that happened in disparate times, a critical feature when extracting gist of a temporal nature. We examined this hypothesis using a novel behavioral paradigm. Subjects were first presented with word pairs that could form a new composite word if combined (e.g., car, pet --> carpet), and then tested on whether they falsely recognize seeing the composite word. When subjects napped in between exposure and testing, false memories of composite words increased, with reaction times for false recognition correlating to time spent in slow wave sleep. These results confirm the functional role of time compression in memory replay, supporting the temporal scaffolding model.

Keywords: Sleep; Memory Replay; Gist Extraction; False Memories; Temporal Scaffolding

Introduction

Numerous studies over the last two decades support the notion that sleep facilitates memory consolidation (Rasch & Born, 2013). There is now compelling evidence from human and rodent studies that during one particular sleep stage, Slow Wave Sleep (SWS), recently encoded memories are replayed in the hippocampus as part of a hippocampal-cortical dialogue (Wilson & McNaughton, 1994; Diba & Buzsaki, 2007). Theoretical models suggest this replay may contribute to the strengthening of common features within those memories while eroding their idiosyncratic elements, effectively leading to the extraction of "gist" and their integration within general knowledge structure in the cortex (McCelland, McNaughton, & O'reilly, 1995; Lewis & Durrant, 2011).

Perhaps the most striking example of gist extraction is exemplified by demonstrations that SWS can support insightful discovery of hidden rules. In these studies, subjects were presented with a sequence of stimuli and asked to respond to each stimulus as quickly and accurately as possible by following a simple rule (Fischer, Drosopoulos, Tsen, & Born, 2006; Wagner, Gais, Haider, Verleger, & Born, 2004). Unknown to subjects, a hidden temporal structure governed the series of presentations such that, if discovered, it could improve performance significantly. Following sleep, subjects were more likely to discover the hidden rule and improve performance compared to subjects that stayed awake, an effect that was correlated with the time spent in SWS (Wilhelm, Rose, Imhof, Rasch, Büchel, & Born, 2013; Yordanova, Kolev, Verleger, Bataghva, Born, & Wagner, 2012). While sleep-dependent discovery of hidden rules fits the general theory of gist extraction during sleep, the particular mechanism, and its relation to SWS, remain unclear. Recently, a 'temporal scaffolding' model was proposed to account for the effects of sleep on insightful processes (Lerner 2017a, 2017b; Lerner et al., 2019). The model suggests a key property of memory replay that allows for these effects to emerge: its time-compressed nature. In particular, hippocampal memory replay is known to occur in an accelerated form, up to twenty times the speed of the original experience (at least in rodents; Rasch & Born, 2013). When encoded sequences of events are reactivated in this accelerated manner, Hebbian learning mechanisms can associate events that were otherwise too temporally distant from each other to fall within the typical neural learning timescale (50-200ms for Hebbian mechanisms; August & Levy, 1999). Consequently, discovery of hidden rules that relies on the detection of temporal structure within sequential stimuli should, according to the model, be particularly prone to facilitation by SWS.

One surprising prediction of this model is that temporal associations resulting from time-compressed replay during sleep might also hurt memory, not just facilitate it. If two distinct events are replayed in a compressed timescale one after the other during SWS, this may lead to their assimilation into one single memory following the consolidation process, even if such assimilation is unwarranted. In particular, such phenomena might occur if the two events have a special meaning when compiled together, thus signaling to the cortex to maintain the combined meaning rather than the separated memories (a gist extraction of sorts, albeit one that occurs under the wrong circumstances). An example of this theoretical process can be demonstrated by presenting a subject with two consecutive words, such as *car* and *pet*, which could be combined into a composite (or compound) word: *carpet*. Due to the temporal scaffolding mechanism, the proximal but distinct events of seeing *car* and *pet* might be integrated following sleep to become a false memory of seeing *carpet*.

In the current study, we tested this hypothesis by exploring how an afternoon nap affects the probability of falsely recognizing composite words whose components were previously encountered, as if they were actual memories. Since memory replay during SWS is known to occur predominantly in a forward manner (i.e., replay of encoded events proceeds in the same order as the original experience, albeit in accelerated form; Diba & Buzsaki, 2007), we predicted that sleep would facilitate false memories of composite words whose components were presented sequentially in the forward direction (e.g., car -> pet), but not of those presented backwards (pet->car), or when the components were presented in totally separate trials. Confirming that SWS facilitates the formation of such false memories substantially supports the idea that accelerated forward replay plays a part in gist extraction

Methods

Participants

Forty young adults (ages 18-24, n=19 females) from Rutgers University and the New Jersey Institute of Technology participated in this study for monetary compensation. Subjects were recruited via protocol flyers, in-class announcements and on-campus active recruitment. All subjects were screened for exclusion criteria, which included personal or family history of sleep problems, neurological or psychiatric disorders, drug or alcohol abuse, and/or intake of medications that have any effect on sleep. Furthermore, all recruited subjects had normal or corrected vision/hearing and were fluent in English. Subjects were also asked not to increase daily caffeine and to abstain from caffeine and alcohol before testing. All participants provided informed consent in line with the procedures approved by the Institutional Review Board of Rutgers University.

Sleep Monitoring

We recorded sleep using the Zmachine ® Insight device (Model DT-200; General Sleep Corporation), a sleep monitoring apparatus designed for use in clinical and home environments, and has been shown to reliably detect sleep stages at a level comparable to Polysomnography (Wang et al., 2016). It consists of three self-applicable, single-use, disposable electroencephalography (EEG) sensors, two located on the mastoids (signal electrodes) and one on the back of the neck (ground electrode). The machine detects and records three sleep stages, in addition to wake stage: light sleep (combined Stages N1 and N2), SWS, and Rapid Eye Movement (REM) sleep for each 30-second epoch of sleep. Following the completion of each subject testing, the collected data was transferred from the device's micro SD card to a secure desktop computer for further analysis.

Behavioral Task

Stimuli We compiled three groups of word pairs, 6 pairs per group, such that the words of each pair, if combined together, create a "composite" word (e.g., *car, pet* --> *carpet*; *under, stand* --> *understand*). Words of each pair were selected such that they were not semantically related to each other, nor were they related to the composite word they create together. In addition, we compiled a group of 32 non-composite words. The average length and frequency of the composite words (i.e., the combination of the two components together) in each of the three groups, as well as each single word in the non-composite group, was roughly equal, with M=~7.5 letters and M=~18,000 occurrences for length and frequency, respectively (Frequency data was based on the database found in: https://corpus.byu,.du/coca/)

Based on these four groups, two word-pair lists were created for the "exposure" phase of the experiment. The first exposure list was comprised of the following: (1) 'Forward' composite items: the word pairs of the first composite group appearing in the order that corresponds to the composite word (e.g., *car, pet*); (2) 'Backward composite items: the word pairs of the second composite group appearing in the reverse order to the one corresponding to the composite word (e.g., *stand, under*); (3) 'Separate composite items: each of the two words of the third composite group paired with random words from the non-composite group (e.g., *honey, moon*, forming the composite word *honeymoon*, were paired with *pharmacy, sad*, to create the pairs *pharmacy, honey* and *moon, sad*); (4) the remainder of the words from the non-composite group, randomly paired. The total number of items (pairs) in the list was 34, and their order within the list was pseudo-randomized with the restriction that items containing words that belonged to the same word-pair of the Separate composite group would not appear sequentially. The second exposure list was identical to the first, except that the Forward and Backward composite items were switched such that the first group composed the backward items and the second group composed the forward items. The order of the items within the list was switched as well, such that the location of the forward and backward pairs was similar in the two lists.

We next created two testing lists, matching the two exposure lists. The first testing list contained all 18 composite words made of the Forward, Backward and Separate composite items, as well as 24 additional non-composite words from the exposure list, and 6 totally new, non-composite words (48 items in total, half of which are old). The totally new words were chosen such that the average length and frequency of the new and old words across the testing list remained roughly equal. The order of these words within the list was chosen pseudo-randomly. The second testing list was identical to the first, except that the location of the forward and backward composite words was switched to match the first testing list.

Composite Word task The behavioral task included an exposure session and a testing session, separated by an intermission during which subjects were either allowed to sleep or remained awake (see Figure 1). The objective of the exposure session was to allow subjects to encode the components of the composite words consecutively, without driving their attention to their composite nature (by using a distracting task). The testing session included a surprise memory test, where subjects' tendency to incorrectly recognize the composite words as words they have been exposed to earlier was examined.

Figure 1: The behavioral task used in the study. During an exposure session, subjects saw two colored words in succession and were asked to indicate whether the words appeared in the same or different color. Unknown to subjects, some of those word pairs could be concatenated to create a third, unrelated word. Following an intermission during which some of the subjects took a 90 minute nap and some remained awake, they received a surprise memory test requiring to indicate whether a series of presented words are new or appeared in the earlier exposure session. Some of those words were the composite words whose components were previously displayed.

Exposure Session In each trial of the exposure session, subjects were presented with two consecutive words. Each of the words appeared in one of 3 colors: red, green, or blue. Subjects were required to indicate whether the two words appeared in the same or different colors by pressing one of two buttons on the keyboard. The two words presented in each trial were taken from the items in the exposure list, with half of the subjects receiving the first list and the other half – the second list. To facilitate the probability that Forward and Backward composite items will be combined in memory during sleep, word pairs belonging to these two conditions were always presented in the same color. Other word pairs were presented in either the same or different colors, and the total number of 'same' and 'different' trials was counterbalanced across the session. Subjects were not informed that some of the word pairs could construct a composite word if combined.

Testing Session During the testing session, subjects were presented with single words appearing on the screen one at a time. After each word presentation, subjects were required to indicate whether they recognize seeing this word in the first session or not, by pressing one of two buttons on the keyboard. These words could either be old words appearing in the first session, composite words whose components appeared as single words in the first session, or totally novel words. Subjects that received the 1st exposure list also received the 1st testing list, and subjects receiving the 2nd exposure list also received the 2nd testing list. Following the testing session, subjects were administered a post-experimental questionnaire, designed to determine if they explicitly recognized the existence of composite words in either of the sessions. The questionnaire was designed as a series of questions of escalating details, which avoided revealing the hidden structure of the task unless subjects came up with it by themselves. Three subjects who explicitly recognized the presence of composite words during the exposure session were removed from the study.

Procedure Subjects first arrived to the lab to collect the sleep-monitoring device and were given detailed instructions on how to use it. They then monitored their sleep at home for two nights to allow them to adapt to sleeping with the device on their scalp, and to allow the sleep stage detection algorithm of the device to accommodate to the subjects' individual EEG patterns. After two nights, subjects returned to the lab at the afternoon to begin the experiment, which included the 2 sessions of behavioral measurements, exposure and testing, separated by a 120-minute intermission. The experiment was ran in a quiet room using a MacBook Air (v.2014) laptop, with subjects situated in a convenient distance of 30cm from the screen. Subjects first received detailed instructions on screen regarding the task. Each trial of the exposure session began with the presentation of small white fixation cue appearing on a black screen for 500ms. The screen then remained black for 1500ms until the presentation of the first word for 500ms. After an Inter Stimulus Interval of 100ms, the second word appeared for 500ms, followed by a black screen that remained until the subject's response. Following the response, the next trial initiated. Five practice trials preceded the exposure, using different word pairs. Practice trials were similar to the exposure trials, with the exception that subjects received feedback immediately after responding (a smiley face for a correct response and a sad face for an erroneous response), which replaced the fixation cue. Following the exposure session, subjects put on the sleep monitoring device and went into the intermission period during which they were allowed to take a nap for 90 minutes in a designated sleep testing room (Sleep group; N = 19) or watched a non-stimulating movie in the same testing room (Wake group; N = 18). Following the intermission (which lasted 2 hours for both groups, to allow half an hour of wake time for the Sleep group to eliminate sleep inertia), subjects underwent the testing session. Subjects received instructions on screen regarding the memory recognition test before starting the task. Each testing trial consisted of a word appearing on the screen in white, until the subject's response. After responding, the screen remained black for 1000ms, after which the next word appeared, and so on until the end of testing.

Data Analysis For each subject, we assessed the performance of each of the four critical experimental conditions (Forward composite items, Backward composite items, Separate composite items, Novel items) using two behavioral measures, Error Rate and Normalized Error Reaction Time (RT). Error rates were defined as the total number of erroneous responses in each condition, divided by the number of trials in that condition (an error was defined as responding "Old"). Normalized Error RTs were defined as the mean RTs for wrongly identified items divided by the total mean RT, for each condition (calculated after removal of outlier RTs, defined as values above or below 3 standard deviations from an individual's mean, across conditions). We used the normalized RT measure rather than raw RTs because pilot data collected prior to the experiment suggested that between-subject individual differences in RTs were substantially higher than within-subject differences in this task, potentially blurring the effects of interest. We expected that the more false memories an individual has, the higher will the error rate and the lower will the Normalized Error RT be (based on a common interpretation of RTs as indicating confidence in the responses; Wiedemann & Kahana, 2016). We compared these two measures between the Sleep and Wake groups, and within the groups themselves, using Bonferroni-corrected independent and paired t-tests, respectively. In addition, for the Sleep group, we also correlated these measures across subjects with the individual time spent in sleep, and in each sleep stage, during the nap (as well as the percent of time spent in each sleep stage out of total sleep time).

Results

Mean error rate values for each condition and subject group are presented in Figure 2.

Bonferroni-corrected t-tests showed that error rates in recognizing Forward composite items as "Old" were significantly higher for the Sleep group compared to the Wake group ($t(35) = 2.61$, $p < 0.05$). No other condition showed a difference between the groups. Within the Wake group, Bonferroni-corrected pairwise comparisons showed that error rates for the Backward composite items were significantly higher than those of the Separate composite items ($t(17) = 4.19$, $p < 0.004$), as well as higher, on a trend level, than those of the Forward composite and Novel items ($t(17) = 2.91$, $p < 0.06$, and $t(17) = 2.87$, $p < 0.07$. respectively). Within the Sleep group, in contrast, error rates for the Forward and Backward composite items were significantly higher than those of the Separate composite and Novel items (all ps < 0.03), but there was no difference between the Forward and Backward composite items ($p = 0.47$). Repeating the same analysis with Normalized Error RTs, we found no significant effects between or within the groups.

We also compared the error rates of the Sleep and Wake group in the Old words condition (i.e., non-composite words that appeared during the exposure session and for which the correct answer was "Old" and an error response was "New"). There was no difference between the groups in this condition (M = 50.9 and M = 54.2 for the sleep and Wake group, respectively; $p = 0.526$).

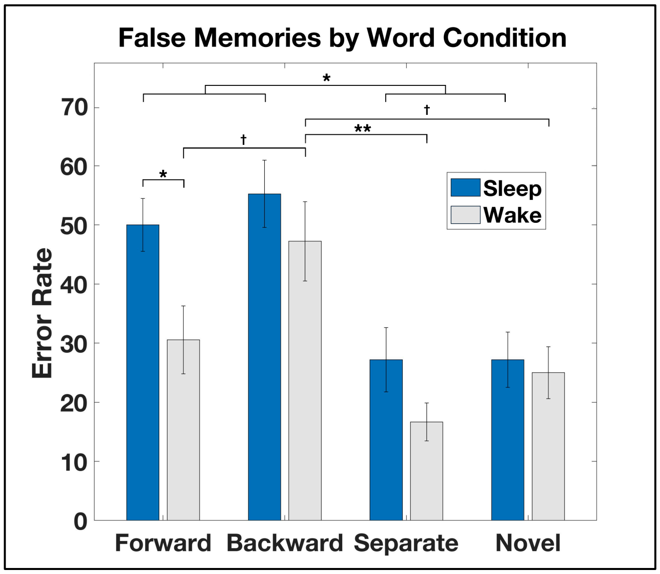

Figure 2: Error rate by word condition for the sleep and wake groups. Subjects who slept exhibited more false memories (higher error rate) for composite words that were presented in the forward direction during training compared to the wake group. ** $p<0.005$; * $p<0.05$; † $p<0.07$. Error bars represent standard error of the mean.

We next examined whether the performance measures were influenced by any of the recorded sleep parameters for subjects in the sleep group (see sleep statistics in Table 1). First, we computed the Pearson correlations between the total time subjects spent in sleep and each of the two performance measures in each of the four experimental conditions (8 comparisons in total). We found a significant correlation of total sleep time with the Normalized Error RT of Forward composite items ($r = -0.6717$, $p = 0.0023$; $p = 0.018$ after correcting for 8 multiple comparisons). No other correlation was significant.

Table 1: Recorded sleep statistics. TST = Total Sleep Time.

Sleep Measure	Mean (std)
TST (minutes)	40.41 (22.3)
N1/N2 (minutes)	23.97 (13.0)
% N1/N2 out of TST	66.46 (23.7)
SWS (minutes)	11.32 (13.1)
% SWS out of TST	19.59 (21.6)
REM (minutes)	5.10 (5.8)
% REM out of TST	13.92 (18.1)

Next, to investigate the contribution of particular sleep stages, a multiple regression analysis was carried out for each condition, with the performance measure of interest as the dependent variable and time in each recorded sleep stage (N1/N2, SWS, REM) as predictors. A significant regression was found, once again, for Normalized Error RT of Forward composite items ($F(3,14) = 8.11$, $p = 0.0022$; $p = 0.0178$ after correcting for 8 multiple comparisons) with $R^2 = 0.6348$. Normalized Error RTs were equal to 1.2208 – 0.0068 (N1/N2) – 0.0095 (SWS) + 0.0093 (REM), with SWS contributing significantly to the model ($p = 0.0078$). The more SWS subjects had, the faster was their erroneous response in identifying Forward composite items as “Old” (Figure 3, inset). This effect remained highly significant in a follow-up analysis, computing the Pearson correlation between Normalized Error RTs of Forward composite items and the percent of time spent in SWS out of total sleep time ($r(17) = -0.647$, $p < 0.004$; Figure 3, main). No other effects were significant in the multiple regression analyses.

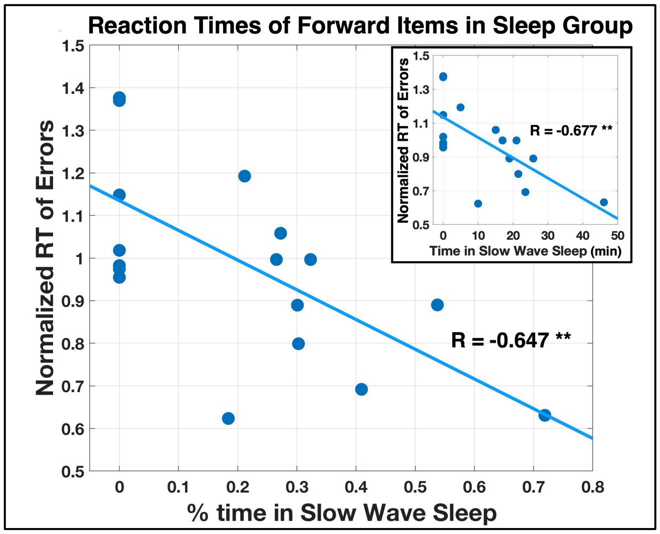

Figure 3: Normalized reaction times of error responses for Forward composite items as a function of minutes spent in slow wave sleep (inset) and percent of time spent in slow wave sleep out of total sleep time (main), for subjects in the sleep group. ** $p<0.008$.

Discussion

We found that subjects who take a nap following exposure to components of a composite word are more likely to falsely recognize being presented with that composite word compared to subjects who did not nap. Moreover, the more time subjects spent in SWS during the nap, the quicker it took them to make that error, likely indicating a higher confidence in their response (Wiedemann & Kahana, 2016). These effects, however, were apparent only if subjects were exposed to the component words one after the other, and only if they were presented in the order that matches their appearance in the composite word, but not if they were presented in the reverse order.

Our findings are consistent with the prediction of a recent “temporal scaffolding” model of memory consolidation during SWS, which emphasizes the role of time compression in memory replay (Lerner et al., 2017a). Specifically, the model predicts that compressed replay of a recently encoded sequential experience may lead to elements within this experience to bind together and create a unified memory that no longer preserves the original sequential nature of the experience. Given that memory replay during SWS is predominantly in the forward direction (Diba & Buzsaki, 2007), the model predicts that such unified memories would be created if the sequence presentation order matches that of the unified memory, but not otherwise. Consistent with the model, we only found a difference between the Sleep and Wake groups in the Forward composite condition, but not when component words were presented in the backward direction. Moreover, consistent with the model’s emphasis on replay of stored sequences, there was no difference between the groups when the component words were separated to different trials during the exposure session, a condition that yielded only few false memories on average (Figure 2). Finally, and also consistent with the model, there was no difference between the groups in a baseline condition consisting of totally novel words, which, as expected, also yielded few false memories on average.

One important contrast with the model’s predictions was the finding that, for Backward composite items, both the Sleep and the Wake group had increased levels of false memories (compared, for example, to the Novel words condition). This unexpected effect suggests that backward items tend to be combined together irrespective of sleep. This finding might be accounted for if taking under consideration the fact that memory replay could also occur during waking. Rodent studies suggest that compressed replay in the hippocampus is elicited at wake as well, often during resting periods following completion of a task, and, unlike sleep, it tends to include backward replay of recently encoded memory sequences and not just forward replay (Diba & Buzsaki, 2007). While the function of wake replay is still debated, some suggest it could contribute to memory consolidation in the same manner as sleep replay does (Rasch & Born, 2013). Since both Sleep and Wake subjects in our task had a period of rest following the completion of the task (before they went to bed or saw a movie, respectively), such backward replay could potentially have been elicited and contribute to the formation of false composite memories for the Backward items (i.e., replaying the sequence of events pet->car backwards could result in the activation of “carpet” in its regular order). Another possibility is that composite memories of both Forward and Backward items were already formed during the initial experience simply because of their close temporal proximity (and aided by the fact they were always presented in the same color), but sleep was essential in maintaining the Forward composite memories. Further research is needed to explore these possibilities.

Several previous studies have suggested that false memories could arise following sleep. Specifically, using the Deese-Roediger-McDermott (DRM) paradigm (e.g., Payne et al., 2009), it was shown that sleep following exposure to a group of words with a related theme (e.g., *Pillow*, *Bed*, *Night*) could lead to the formation of a false memory for the theme word (*Sleep*). However, these effects are not always found (e.g., Fenn, Gallo, Margoliash, Roediger, & Nusbaum, 2009) and they seem to decrease rather than increase with time spent in SWS (Pardilla-Delgado & Payne, 2017; Payne et al., 2009). In other words, the mechanism contributing to the effect seen in the DRM paradigm is likely different than the one presented here, and relates to deep semantic processing of the stored stimuli rather than the time-compression property of replay during SWS (Pardilla-Delgado & Payne, 2017). A more related effect to the one presented here is the demonstration that sleep in humans preferentially facilitates memory of sequences when they are presented during test in the original forward direction compared to backwards, a finding that was interpreted as resulting from memory replay during sleep (Drosopoulos et al., 2007). Our findings add to that previous demonstration by introducing the element of time compression in the process, and by showing it specifically relates to SWS.

Conclusion

In the current study, we demonstrated that an afternoon nap could lead to the formation of false composite memories made of events that were previously presented sequentially. The importance of these results is twofold. First, our novel behavioral paradigm potentially allows for tapping replay compression mechanisms during sleep, opening the door for various future investigations of this phenomenon in humans. Second, our findings provide evidence for the functional role of time compression in memory replay, suggesting it contributes to the association of disparate yet proximal events and showing that in addition to the regular facilitation seen in the majority of studies, this mechanism could also lead to impairments in memory.

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