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### Title

Context matters: changes in memory over a period of sleep are driven by encoding context.

### Permalink

<https://escholarship.org/uc/item/2hc5n14r>

### Journal

Learning & Memory, 30(2)

### ISSN

1072-0502

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### Publication Date

2023-02-01

### DOI

10.1101/lm.053634.122

Peer reviewed

1 **Context matters: Changes in memory over a period of sleep are driven by encoding context**

2

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## Abstract

17 During sleep, recently acquired episodic memories (i.e., autobiographical memories for specific  
18 events) are strengthened and transformed, a process termed consolidation. These memories are  
19 contextual in nature, with details of specific features interwoven with more general properties  
20 such as the time and place of the event. In this study, we hypothesized that the context in which a  
21 memory is embedded would guide the process of consolidation during sleep. To test this idea, we  
22 employed a spatial memory task and considered changes in memory over a 10-hour period  
23 including either sleep or wake. In both conditions, participants ( $N = 62$ ) formed stories that  
24 contextually bound four objects together, and then encoded the on-screen spatial position of all  
25 objects. Results showed that the changes in memory over the sleep period were correlated among  
26 contextually linked objects, whereas no such effect was identified for the wake group. These  
27 results demonstrate that context-binding plays an important role in memory consolidation during  
28 sleep.

29

30 **Keywords:** Sleep, memory consolidation, context

31

## 32 **Introduction**

33 After initial encoding, memories are further processed and strengthened, a process  
34 termed memory consolidation. Consolidation occurs during both wake and sleep,  
35 with some debate over each state's unique contribution (e.g., Wamsley and  
36 Summer, 2020; Wang et al., 2021). The physiological characteristics of sleep, and  
37 specifically non-rapid-eye-movement sleep (NREM), together with the relative  
38 paucity of perceptual input that may interfere with processing, are thought to  
39 provide an optimal environment for memory consolidation (Diekelmann and Born,  
40 2010; Paller et al., 2021).

41 Most research on consolidation has considered sleep's role in the evolution of  
42 memory for relatively impoverished, isolated stimuli, as is common in memory  
43 research. However, real-life memories are rarely isolated, but rather are linked with  
44 other memories that were encoded in the same context. Retrieving a specific detail  
45 about an event, for example, can produce a plethora of associations and an  
46 experience of reliving the full event, a phenomenon termed "mental time travel"  
47 (Tulving, 1983). Recollection of a specific detail effortlessly and involuntarily  
48 involves the retrieval of other contextually bound details about the same event  
49 (e.g., Wheeler and Gabbert, 2017). This memory interrelatedness is fundamental to  
50 our understanding of memory in daily living, but little is known about its impact on  
51 consolidation in general or on consolidation during sleep in particular.

52 In this study, we explored whether memories that are contextually bound to one  
53 another, and therefore likely to be retrieved together, are also likely to be  
54 reactivated together during sleep. The term "context" is notoriously difficult to  
55 define, yet most memory researchers agree that it includes spatiotemporal features  
56 or other aspects of a remembered event accompanying its defining components  
57 (Smith, 1994; Stark et al., 2018; Dulas et al., 2021). Free recall studies that  
58 considered the temporal context in which memories were encoded have shown that  
59 memories encoded in temporal proximity are more likely to be retrieved together  
60 (i.e., the contiguity effect; Kahana, 1996). Retrieval in free recall tasks is also  
61 guided by the semantic relatedness between different words, an effect termed  
62 semantic clustering (Shuell, 1969; Polyn et al., 2009).

63 Accordingly, we sought to determine whether contexts driven by temporal or  
64 semantic links between memories guide consolidation during sleep as in wake. The  
65 experiment contrasted sleep and wake using a between-subjects design.  
66 Participants used their personal electronic devices at home to create and record  
67 unique stories linking arbitrary objects with cohesive narratives. Then, they were  
68 required to encode the on-screen positions of each object. After a 10-hour delay  
69 that either did or did not include nocturnal sleep, they were tested on object  
70 positions. We hypothesized that the context in which a memory resided would  
71 explain variance in consolidation-related memory changes. Put differently, our  
72 prediction was that objects that were linked to the same narrative would have  
73 correlated memory trajectories over sleep.

74

## 75 **Results**

76 Participants were randomly assigned to Wake and Sleep groups ( $n=31$  each; Figure  
77 1a). The groups followed the same protocol, which included engaging in two  
78 experimental sessions, with the second session starting approximately 10 hours  
79 after the first. The Wake group trained in the morning and were then tested in the  
80 evening, whereas the Sleep group trained in the evening and were tested in the  
81 morning. Training consisted of a story building stage (Figure 1b) and a position  
82 learning stage (Figure 1c). In the story building stage, participants encoded  
83 contextually bound sets, which included an image of a location linked with four  
84 images of objects. In the position learning stage, they learned the on-screen  
85 positions of the objects. Learning was organized into six blocks, each including  
86 objects from two contextually bound sets which were learned in temporal proximity.  
87 Participants were tested on object positions twice - once shortly after learning and  
88 once after the delay period (Figure 1d).

89 The Wake and Sleep groups did not differ in terms of age [ $t(60) = 0.08, p = 0.93$ ],  
90 Morningness-Eveningness scores [ $t(60) = 1.47, p = 0.15$ ], or the length of the delay  
91 between the first and second sessions [ $t(60) = 0.33, p = 0.74$ ]. The Stanford  
92 Sleepiness Scale assessed before the beginning of the first session showed higher  
93 sleepiness for the Sleep group relative to the Wake group (2.29 vs 3.48,  
94 respectively;  $t(60) = 4.29, p < 0.001$ ). To consider whether differences in fatigue or  
95 time of day (i.e., circadian effects) might have impacted learning or memory  
96 performance on the first session, we compared positioning error rates for the first  
97 session's test between groups and found no significant differences [ $F(1, 2815) =$   
98  $1.06, p = 0.30$ ; Sleep group =  $15.42\% \pm 1.3$ , Wake group =  $17.27\% \pm 1.3$ ; Model  
99 #1 in Table 1].

### 100 **Memories recalled at intermediate confidence levels benefited more from** 101 **sleep than wake**

102 In their tests of spatial recall, participants were required to indicate their confidence  
103 level in each trial (Figure 2a). As expected, error rates were lower as confidence  
104 levels increased across both sessions and groups [ $F(2, 5713) = 445.16, p < 0.001$ ;  
105 Guess =  $26.04\% \pm 0.9$ , Think =  $17.32\% \pm 0.8$ , Know =  $10.68\% \pm 0.8$ ; Model #2 in  
106 Table 1, Figure 2b; see Supplementary Figure 1 for breakdown by group and  
107 session]. To test whether sleep improved memory in this task, we used a model to  
108 predict memory on the second session based on pre-delay error rates and group  
109 (Wake vs Sleep; Model #3 in Table 1). In this analysis, a main effect of group would  
110 indicate a uniform effect of sleep/wake, and an interaction between pre-delay errors  
111 and sleep would indicate that the effect of sleep/wake depended on the initial  
112 strength of the memory. Our results indicated that neither effect was significant  
113 [ $F(1,2757) = 2.2, p = 0.14$  for the main effect of group;  $F(1,2757) = 0.2, p = 0.66$   
114 for the interaction].

115 In an exploratory analysis, we next incorporated confidence levels into the analysis  
116 to test whether the effect of sleep on memory for object positions interacts with  
117 confidence levels. We therefore used a model to predict memory on the second  
118 session based on three factors: memory on the first session, confidence levels

119 collected on the first session, and group (Wake vs Sleep; Model #4 in Table 1). As  
120 expected, both memory on the first session and confidence levels, as well as this  
121 interaction, were positively correlated with memory on the second session (all  $p$   
122 values  $< 0.001$ ). Interestingly, two significant interactions suggested that  
123 confidence levels drove memory benefits: the interaction between group and  
124 confidence level [ $F(2, 2749) = 6.65, p < 0.01$ ]; and the interaction between group,  
125 confidence level, and memory on the first session [ $F(2, 2749) = 3.5, p < 0.05$ ]. The  
126 effect of group and the interaction between group and memory on the first session  
127 were not significant ( $p > 0.26$ ).

128 To resolve the interactions, we conducted analyses separately for each confidence  
129 level, as collected during the first session's test (Model #5 in Table 1; Figure 2c). All  
130 three models found that memory on the first session significantly predicted memory  
131 on the second session (all  $p$  values  $< 0.001$ ). However, only the objects rated with  
132 the "think" confidence level showed a significant effect of sleep, indicating overall  
133 greater memory benefits of sleep relative to wake [ $F(1,966) = 14.9, p < 0.001$ ;  
134 Figure 2c, center]. In addition, these objects also showed an interaction between  
135 group and memory on the first session, indicating a differential effect of sleep on  
136 memory for objects based on their initial memory strength [ $F(1,966) = 8.26, p <$   
137  $0.01$ ]. In other words, results indicated that sleep improved memory for  
138 intermediate confidence objects, with greater improvement selectively for objects  
139 with good pre-sleep accuracy. No significant effects emerged for the objects rated  
140 with the "guess" confidence level (all  $p$ -values  $> 0.42$ ) or the "know" confidence  
141 level (all  $p$ -values  $> 0.10$ ).

142

### 143 **Variability in memory benefits over sleep is explained by shared context**

144 To investigate the role of context in the consolidation of memories, we considered  
145 the change in memory over the delay between the first and second sessions (i.e.,  
146 the memory trajectories). Our analytic approach was to leverage the variability in  
147 trajectories to evaluate the impact of shared contexts. If the context binding  
148 memories together plays some active role during the delay period, we expected  
149 contexts to explain some of the variability in trajectories. More specifically, we  
150 hypothesized that context would drive consolidation during sleep. Therefore, we  
151 hypothesized that memory trajectories for objects linked within the same  
152 contextually bound sets (i.e., interlinked within the same story) would be more  
153 correlated than chance if that delay included sleep. We did not have an *a-priori*  
154 hypothesis regarding the impact of a wake delay of similar duration, but if sleep has  
155 a privileged role in memory consolidation, then trajectories would be less correlated  
156 after wake relative to sleep.

157 To test this hypothesis, we considered all objects that were not designated as  
158 "guesses" in our analysis. For each participant, we calculated the intraclass  
159 correlation coefficient, a measure of overall agreement between different values  
160 within a group. This measure, ICC, reflects how clustered together contextually  
161 bound memory trajectories are. For each participant, we used a permutation test to  
162 generate a null distribution of ICC values by shuffling the labels in 10,000 different

163 permutations. We then calculated a Z-score for the participant's "true" ICC value  
164 based on this distribution (Figure 3a). Our results showed that the Z-scores obtained  
165 for the Sleep group were higher than zero, indicating that they had higher-than-  
166 chance ICCs [ $t(30) = 2.97, p < 0.01$ ]. The Wake group did not show a similar effect  
167 [ $t(30) = -0.3, p = 0.62$ ]. Finally, we compared the "true" ICCs for the Sleep and  
168 Wake group and found no significant difference between the two [ $t(60) = 1.29, p =$   
169  $0.10$ ; Figure 3b]. Taken together, these results suggest that memories that share a  
170 semantic context are consolidated together during sleep.

171 To explore whether a similar effect can be observed for temporal context (i.e., with  
172 the temporal proximity between memories at encoding driving consolidation  
173 benefits), we leveraged the structure of our task. Each block during the position  
174 learning stage included two contextually bound sets which were learned within  
175 temporal proximity of one another (Figure 1c). We therefore hypothesized that  
176 memory trajectories for objects within one set would be correlated with the  
177 trajectories of the set learned within the same block in the Sleep group. Like before,  
178 we did not have an *a-priori* hypothesis regarding the Wake group, except that  
179 context would have a lesser impact on delay-related changes on that group relative  
180 to the Sleep group.

181 The analytic approach employed to test this hypothesis was similar to the one used  
182 to test within-set intraclass correlations. The average memory trajectories were  
183 calculated per set and then submitted to an ICC test to consider within-block  
184 correlations for each participant. These results were used to calculate Z-scores  
185 based on a distribution constructed using a permutation test. Unlike for semantic  
186 contexts, our results did not support our hypotheses. Both in the Sleep group and in  
187 the Wake group, true ICC values were not significantly different from those obtained  
188 in the permutation test [ $t(30) = 0.10, p = 0.46$ ;  $t(30) = 0.49, p = 0.69$ , respectively;  
189 Figure 3c]. Additionally, ICC values were not significantly higher for the Sleep versus  
190 the Wake group [ $t(60) = -0.53, p = 0.70$ ; Figure 3d]. Taken together, our results did  
191 not support the hypothesis that temporal context plays a role in consolidation  
192 during sleep.

193

## 194 **Discussion**

195 In this study, we investigated whether the encoding contexts of memories impact  
196 the manner in which they are consolidated over a 10-hour delay. Objects bound  
197 together by unique encoding contexts were tested before and after a delay that  
198 either did or did not include nocturnal sleep. Results showed that sleep improved  
199 retrieval only for memories rated with an intermediate level of confidence. Our  
200 analyses considered two different types of contexts - semantic contexts (i.e.,  
201 memories shared meaningful narrative connections with one another) and temporal  
202 contexts (i.e., memories were encoded within the same time interval). We found  
203 that some of the variability in memory changes over the delay were explained by  
204 semantic context only if the delay included sleep. Conversely, we found that  
205 temporal context did not significantly explain memory-change variance over wake  
206 or sleep.

207 These results complement other findings from our group demonstrating that  
208 manipulating consolidation using external cues during sleep impacts contextually  
209 bound memories (Schechtman et al., 2022). Whereas that study utilized methods to  
210 bias reactivation selectively towards certain memories in a nap setting, the current  
211 study did not involve a causal manipulation, instead focusing on the consequences  
212 of nocturnal sleep with spontaneous, endogenous memory reactivation. In addition,  
213 this study included a wake control that allowed us to probe the specific interaction  
214 between context and sleep. Encouragingly, the two studies together converge on  
215 the conclusion that context guides memory processing during sleep. Moreover, a  
216 central limitation of the current study – that it reveals changes in correlation  
217 patterns but falls short of demonstrating causality – is overcome by the other study  
218 from our group. Likewise, a central limitation of the study of Schechtman et al.  
219 (2022)—that it involves cued rather than spontaneous reactivation and may  
220 therefore not reflect the cognitive benefits of non-manipulated sleep—is overcome  
221 by the present study.

222 Our results, showing a benefit of sleep only for memories rated with an intermediate  
223 level of confidence (“think” vs “guess”/“know”), diverge from previous findings  
224 exploring the relationship between memory strength and consolidation. Previous  
225 studies suggested that sleep is especially beneficial for weakly encoded memories  
226 (e.g., Drosopoulos et al., 2007; Diekelmann et al., 2010). If this were the case in our  
227 study, one would expect the greatest sleep benefits for object locations recalled  
228 with the lowest confidence. A general difficulty in considering the question of  
229 memory strength across experiments is that differences between tasks and  
230 cognitive demands make comparisons extremely challenging. It could be, for  
231 example, that memories in the intermediate confidence zone in our study would  
232 have been rated as weakly encoded in the context of another study. Are “weakly  
233 encoded” memories defined in a relative way (i.e., the weakest memories for a  
234 given task) or in an absolute way (i.e., based on some task-independent metric,  
235 such as exposure time or depth of processing)? This question has not been  
236 thoroughly investigated. Finally, it is worth mentioning that others have  
237 hypothesized that sleep preferentially benefits memory in the intermediate range  
238 (Stickgold, 2009, Figure 4), as in our study.

239 As with many studies comparing sleep with wake, our study has several notable  
240 limitations. First, our design does not allow us to disentangle the beneficial effects  
241 of sleep from the detrimental effects of wake interference. The changes over a  
242 delay period involving sleep may have nothing to do with sleep itself, except for it  
243 being a period of time that is less cognitively demanding and prone to interference  
244 relative to a similar period of time spent awake. Second, the circadian differences  
245 between the two groups (i.e., the time of day of the first and second session) may  
246 have contributed to the differences between them. Although we have tried to rule  
247 this explanation out by analyzing the effects of time of day on performance, this  
248 factor may still have had some contribution to the observed results. Finally, our null  
249 results with regard to the effects of temporal context on consolidation should be  
250 interpreted cautiously. Despite the present findings, the idea that temporal  
251 encoding factors influence consolidation should not be ruled out. Our design



252 intentionally emphasized semantic context in its task demands, whereas temporal  
253 contexts were encoded incidentally. The structure of our experimental blocks may  
254 have also hampered the operationalization of temporal context by adding many  
255 strong event boundaries within blocks (e.g., breaks between trials). More research  
256 should be conducted to address the role of temporal context on consolidation  
257 during sleep.

258 Experimentally comparing sleep and wake is especially daunting when context is  
259 involved. Context reinstatement has been shown to drive retrieval during wake  
260 (Abernethy, 1940; Godden and Baddeley, 1975), raising the possibility that the  
261 observed within-set clustering stems from retrieval-related effects rather than  
262 sleep-related effects. However, we did not observe a significant effect of context on  
263 retrieval in the Wake group, suggesting that context reinstatement during retrieval  
264 was not a major driving force in our results. The most parsimonious conclusion,  
265 therefore, is that context had a sleep-specific effect on memory. Notwithstanding,  
266 the lack of a significant difference between intraclass correlations in the Sleep and  
267 Wake group qualifies this claim, and additional studies are required to address  
268 alternative interpretations.

269 Our results demonstrate that memories are not consolidated independently of one  
270 another during sleep – the associative links that comprise the context in which  
271 memories were encoded played a key role in the overnight consolidation process.  
272 As research studies in cognitive neuroscience increasingly include more naturalistic  
273 designs, there should be a growing emphasis on incorporating more of the  
274 complexity of memory interrelationships along with richer environments. The  
275 present results constitute another step towards clarifying how memory processes  
276 must be understood in the context of their overarching contexts – during both wake  
277 and sleep.\_

278

279

## 280 **Materials and Methods**

### 281 **Participants**

282 Participants were recruited from Northwestern University's academic community,  
283 and included paid participants and participants who completed the experiment for  
284 course credit. Participants had to have an Android phone and be in the United  
285 States while conducting the experiment. In total, 77 participants were recruited (45  
286 men, 31 women, and one genderqueer person; average age = 23.29 years  $\pm$  0.53,  
287 standard error). Fifteen participants were not included in the final analyses: six  
288 participants withdrew before completing the experiment; six participants  
289 encountered technical issues; two participants in the Wake group (see below)  
290 napped during the day; and one participant completed the final test after more than  
291 12 hours. The final sample included 62 participants (42 men, 20 women; average  
292 age = 23.02  $\pm$  0.57 years). These participants were divided into the Wake and  
293 Sleep groups ( $n = 31$  each; the Wake group included 20 men and 11 women,  
294 average age = 22.97  $\pm$  0.8 years; the Sleep group included 22 men and 9 women,  
295 average age = 23.06  $\pm$  0.81 years). All participants consented to participate in the  
296 study. The study protocol was approved by the Northwestern University Institutional  
297 Review Board.

298 Participants were randomly assigned to be in either the Wake group or the Sleep  
299 group. Both groups underwent the same protocol with the exception of the time of  
300 day of the two experimental sessions (Figure 1a).

### 301 **Materials**

302 Participants used their personal Android phones to complete the experiment. A  
303 custom application, named "StoryTask," was designed using MIT App Inventor  
304 (Patton et al., 2019). Participants installed the application on their phones and used  
305 it to record their audio and touch-screen responses and to present visual and  
306 auditory stimuli and instructions. Participants held their phones vertically  
307 throughout the task.

308 Visual stimuli consisted of 48 images of objects and 12 images of places. Object  
309 images were square and portrayed either inanimate objects (e.g., a telephone) or  
310 animals (e.g., a cat) on a white background. Most images were taken from the BOSS  
311 corpus (Brodeur et al., 2010; Brodeur et al., 2014), and some were taken from  
312 copyright-free online image databases (e.g., <http://www.pixabay.com>).

313 At the core of the experiment was a spatial positioning task, during which  
314 participants had to memorize the on-screen positions of images. To standardize the  
315 task across devices with different dimensions and resolutions, images were  
316 presented within a confined rectangular area of the screen (i.e., the active area).  
317 The area was defined as the maximal vertical rectangle that fit within each  
318 participant's screen so that its height will be exactly double its width. The size of  
319 the side of each square object image was 20% of the area's width (i.e., each image  
320 occupied 2% of the active area).

321 Place images portrayed distinct places (e.g., a movie theater; a desert) and were  
322 shown horizontally, with a 1:2 proportion between their height and length,  
323 respectively. Images were taken from copyright-free online image databases (e.g.,  
324 <http://www.pixabay.com>).

325 Place images were each associated with a set of four arbitrarily chosen objects to  
326 create contextually bound sets. Object images were each assigned a random  
327 position within the active area. These positions were chosen to be distant from the  
328 middle of the screen and any other object's location (Euclidean distance > 10% of  
329 screen width) and were chosen to be at least 10% of the screen's width from any of  
330 the active area's four sides.

### 331 **Procedure**

332 Participants were told that the first session would take approximately 90 minutes  
333 and the second approximately 20 minutes. They were asked to complete the  
334 second session 10 hours after starting the first. Participants in the Wake group were  
335 asked to complete the first session in the morning and to avoid napping during the  
336 day. Participants in the Sleep group were asked to complete the first session in the  
337 evening.

338

339 After consenting to participate in the study, participants filled out a set of  
340 questionnaires, including the Stanford Sleepiness Scale (Hoddes et al., 1973) and  
341 the reduced version of the Morningness-Eveningness Questionnaire (Adan and  
342 Almirall, 1991; Loureiro and Garcia-Marques, 2015). Then, they were instructed to  
343 download and install the application.

344 The instructions for the first stage of the task were presented in a video embedded  
345 in the application (<https://youtu.be/964KR0y7GbU>). For this stage (Story building,  
346 Figure 1b), participants had to invent a story occurring in the locale depicted in the  
347 scene image and involving each of four objects shown. In total, they created 12  
348 stories, each recorded using their device's microphone. After each story,  
349 participants were required to answer three questions for each object: (1) Was the  
350 object in motion (not static) during the story? (2) Did the object produce a sound as  
351 part of the story? (3) Did the object appear throughout the whole story, start to  
352 end? The responses to these questions were conveyed using button presses (Figure  
353 1b, right).

354 After creating and recording all stories, participants began the second stage of the  
355 experiment (Position Learning, Figure 1c). For this task, participants completed six  
356 training blocks, each including eight objects that were part of two contextually  
357 bound sets. The instructions for this stage were presented in a video embedded in  
358 the application (<https://youtu.be/ekC1eUnIsC4>). Before each block, participants  
359 were allowed to listen to the two stories they recorded earlier (Figure 1c, left). Then,  
360 they were shown each object in its assigned on-screen position. Next, they  
361 underwent a continuous, multi-trial learning task to encode each object's position.  
362 Each positioning trial began with a presentation of the object image along with its

363 associated location (e.g., balloon, desert; Figure 1c, center) and one of the three  
364 questions presented previously. The participant had to answer that question  
365 correctly (i.e., as indicated during the story-building stage) to continue to the next  
366 part of the trial and had 7 seconds to respond by pressing “yes” or “no.” In the next  
367 part, participants attempted to recall each object’s on-screen position within a 7-  
368 second response interval. Recall was deemed correct if the position indicated by the  
369 participant was within a short distance of the true position (less than 20% of the  
370 active area’s width). As feedback, the object appeared in the true position. The next  
371 trial then ensued. Each block consisted of repeated loops of trials with the drop-out  
372 method. Objects were considered learned if they were correctly positioned in two  
373 consecutive trials, and learned objects were dropped from the following loop. A  
374 block ended when this learning criterion was achieved for all objects.

375 After learning, participants had to take a break for at least 5 minutes before starting  
376 the next stage (Test, Figure 1d). Here, participants tried to place each object in its  
377 true position. Objects were presented in a pseudorandom order and no feedback  
378 was provided. In each trial, participants had 7 seconds to position the object. After  
379 each trial, participants indicated their confidence level on a 3-level Likert scale (“I  
380 guessed,” “I think I remember,” “I’m sure I remember”). After positioning all 48  
381 objects, participants were tested on recognizing object-location associations. For  
382 each object, four images of locations were presented, including the location  
383 previously presented with the object. Participants attempted to indicate which  
384 location was linked with each object. This test concluded the first session.

385 The application was designed so that participants would be unable to start the  
386 second session until at least 6 hours after completing the first session. In the  
387 second session, participants first filled out another questionnaire, and then began a  
388 test that was identical to that of the first session (including the object-scene  
389 association test). After completing the second session, participants were instructed  
390 to email their data to the experimenter, erase the data from their device, and  
391 uninstall the application.

## 392 **Statistical analyses**

393 Data were analyzed using Matlab 2018b (MathWorks Inc, Natick, MA). Intraclass  
394 correlations with missing values were calculated using the irrNA (version 0.2.2)  
395 package in R (version 4.1.2).

396 To account for differences in screen sizes, the sizes of all visual stimuli were  
397 proportional to the participant’s screen size and spatial accuracy was estimated  
398 using units normalized to the screen size. Memory performance was assessed by  
399 fitting mixed linear models. Memory for individual objects was considered in these  
400 analyses, accounting for random intercept effects for different participants. An  
401 ANOVA was used to report the statistical significance of the components of the  
402 model, and dummy variables were used for comparisons between conditions. Table  
403 1 includes the models used in this analysis. Some analyses were conducted on a  
404 subset of objects based on the ordinal confidence levels (e.g., limited to the  
405 “guessed” trials). In these cases, all objects rated with those confidence levels on  
406 the first session’s test were considered.

407 Our main hypothesis was that variability in memory trajectories would be explained  
408 by shared contexts. To test this hypothesis, we used intraclass correlation (Koo and  
409 Li, 2016). This metric, ICC, is symmetrical (i.e., whereas *inter*-class correlations  
410 predict Y from X, *intra*-class correlations predict how clustered together different  
411 values of X are) and can be used to calculate the correlation between more than  
412 two values. We used the (1, k) form of ICC (Shrout and Fleiss, 1979; Koo and Li,  
413 2016). For object positions that were not rated by participants as guessed, we  
414 calculated the change in positioning error over the delay. We then calculated the  
415 ICCs for each participant to consider two sub-hypotheses: (1) to test whether  
416 semantic clustering explained the variability in the changes in memory over the  
417 delay period, we considered ICC for objects linked within the same contextually  
418 bound set; (2) to test whether temporal context explains the variability in the  
419 changes in memory over the delay period, we calculated the mean change for each  
420 contextually bound set (i.e., four objects) and then used an ICC analysis to test  
421 whether those are correlated within block (i.e., whether performance for two sets  
422 linked within the same training block were correlated). The ICCs obtained through  
423 these analyses were compared with the ICC results obtained through permutation  
424 tests with mixed labels ( $n = 10,000$ ) for each participant. The permuted distribution  
425 was used to calculate a Z-score for the true results for each participant, and these  
426 Z-scores were then submitted to a one-tailed one-sample t-test against the value 0  
427 across participants. In addition, we used a one-tailed two-sample t-test to test  
428 whether the true ICC for the Sleep group was higher than that of the Wake group.  
429 Analyses that did not include object-level measures of performance were conducted  
430 using two-tailed two-sample t-tests.

431

432 **Acknowledgments:** This work was supported by NIH grant R00-MH122663 and by  
433 NSF grants BCS-1921678 and BCS-2048681.

434 **Author contribution:** All authors contributed to the design of this study and  
435 helped revise the manuscript. E.S and J.H collected the data. E.S conducted the  
436 analyses and wrote the initial draft of the manuscript.

437 **Competing interests:** The authors declare no competing financial interests.

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#	Model specification
1	<b>PreError ~ WakeOrSleep + (1 PptNum)</b>
2	<b>SpatialError ~ Confidence + (1 PptNum)</b>
3	<b>PostError ~ WakeOrSleep * PreError + (1 PptNum)</b>
4	<b>PostError ~ WakeOrSleep * PreError * Confidence + (1 PptNum)</b>
5	<b>PostError ~ WakeOrSleep * PreError + (1 PptNum)</b> Calculated separately for each confidence level

**Table 1: Mixed linear models used in analyses.** SpatialError - spatial error in a test; PreError - spatial error in the first experimental session; PostError - spatial error in the second experimental session; WakeOrSleep - categorical group indicator; PptNum - categorical participant indicator; Confidence - ordinal confidence level. In all models with more than one factor or covariate, the interaction terms were considered as well.



512 **Figure 1: Experimental design.** (a) Participants were randomly assigned to either  
513 the Wake or Sleep group. (b) In the first session, both groups developed and  
514 recorded 12 stories linking a location (e.g., a desert) with four objects. After  
515 recording the stories, they responded to three yes/no questions about their stories  
516 for each object (the right panel shows one example question). (c) Next, participants  
517 engaged in a position learning task. Each object was assigned a random on-screen  
518 position. Each block included objects from two contextually bound sets. First,  
519 participants were offered a chance to listen to the two stories. After initiating the  
520 block, participants were asked in each trial to respond to an object-specific question  
521 (middle panel). If they were correct, they attempted to place the object in its correct  
522 position. The block continued until all objects were learned to criterion. Feedback  
523 was provided in all trials. (d) At the end of the first session, participants were tested  
524 on their spatial memory. In each trial, participants also indicated their confidence  
525 level. An identical test was conducted in the second session.

526

527 **Figure 2: Memories recalled at moderate confidence levels benefited from**  
528 **sleep.** (a) Distribution of confidence as rated by participants. (b) Average error  
529 rates for each confidence level. Error bars represent standard errors of the mean for  
530 all objects. (c) The effects of sleep on memory for objects rated with different  
531 confidence levels. Panels show the error rates for the first and second sessions on  
532 the X and Y axes, respectively (log-log scale). Each dot represents a single object,  
533 pooled across participants. The lines show the linear correlation between first and  
534 second session errors (note that lines seem curved due to the log-log axes). For  
535 objects with intermediate confidence level, the sleep group showed significantly  
536 lower post-sleep errors. \* -  $p < 0.05$ .

537

538 **Figure 3: Variability in memory benefits over sleep is explained by shared**  
539 **semantic context.** (a) We hypothesized that binds between objects linked within  
540 the same contextually bound sets would drive changes in memory performance  
541 over sleep. If this were the case, memory trajectories (i.e., changes in memory  
542 between the first and second session) would be correlated within sets for the sleep  
543 group. Intraclass correlation coefficients (ICC) were calculated to estimate within-set  
544 correlations and converted to Z-scores for each participant in the Sleep (left) and  
545 Wake (right) groups. Insets show the distribution of the non-normalized ICC values  
546 for both groups. (b) Direct comparison between the correlation coefficients for the  
547 Sleep and Wake groups. (c) We hypothesized that the temporal context binding  
548 together sets that were learned within the same blocks would drive changes in  
549 memory performance over sleep. If this were the case, average memory trajectories  
550 within sets would be correlated within blocks for the sleep group. Intraclass  
551 correlation analyses to consider the effect of temporal context on memory.  
552 Designations follow those introduced in panel b. (d) Direct comparison between the  
553 correlation coefficients for the Sleep and Wake groups. Error bars signify standard  
554 errors of the mean across participants in all panels. \* -  $p < 0.05$ ; n.s -  $p > 0.05$ .