Individual Differences in Working Memory Capacity Predict Sleep-Dependent Memory Consolidation

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BRIEF REPORT

Individual Differences in Working Memory Capacity Predict Sleep-Dependent Memory Consolidation

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Decades of research have established that "online" cognitive processes, which operate during conscious encoding and retrieval of information, contribute substantially to individual differences in memory. Furthermore, it is widely accepted that "offline" processes during sleep also contribute to memory performance. However, the question of whether individual differences in these two types of processes are related to one another remains unanswered. We investigated whether working memory capacity (WMC), a factor believed to contribute substantially to individual differences in online processing, was related to sleep-dependent declarative memory consolidation. Consistent with previous studies, memory for word pairs reliably improved after a period of sleep, whereas performance did not improve after an equal interval of wakefulness. More important, there was a significant, positive correlation between WMC and increase in memory performance after sleep but not after a period of wakefulness. The correlation between WMC and performance during initial test was not significant, suggesting that the relationship is specific to change in memory due to sleep. This suggests a fundamental underlying ability that may distinguish individuals with high memory capacity.

Keywords: memory, sleep, individual differences, working memory capacity

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It has been known for several decades that conscious, or *online*, cognitive processes, such as elaborative rehearsal during encoding, promote durable storage of information in long-term memory and contribute substantially to individual differences in learning (e.g., Craik & Lockhart, 1972). However, it has been known for almost as long that unconscious, or *offline*, processes that operate during sleep also play an important role in learning. It was initially proposed that the benefit afforded by sleep was a passive mechanism of protection from interference (cf. Jenkins & Dallenbach, 1924), but current theories typically posit an active consolidation process, in which information acquired during the day is processed during subsequent sleep. Consistent with this view, several studies have shown that information is reactivated on a cellular level during sleep (Dave & Margoliash, 2000; Ji & Wilson, 2007; Louie & Wilson, 2001; Wilson & Mc-Naughton, 1994). That is, neurons that fire during task activity fire in a similar manner during sleep, and this reactivation may be an underlying mechanism of consolidation.

Research has further established that a period of sleep can consolidate declarative memory (Fenn, Gallo, Margoliash, Roediger, & Nusbaum, 2009; Gais, Molle, Helms, & Born, 2002; Plihal & Born, 1997, 1999), procedural learning (Brawn, Fenn, Nusbaum, & Mar-

goliash, 2010; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002), and perceptual learning (Fenn, Nusbaum, & Margoliash, 2003; Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994; see Diekelmann & Born, 2010; McGaugh, 2000, for reviews) in humans. As a specific example, recall of paired associates improves after sleep but does not improve after an equal interval of wakefulness (Plihal & Born, 1997, 1999). Sleep has also been found to increase resistance to interference in declarative memory (Ellenbogen, Hulbert, Jiang, & Stickgold, 2009), suggesting that offline processing may strengthen memory representations.

Thus, evidence suggests that learning is influenced by both online and offline processes. However, whether offline processing contributes to individual differences in memory has been all but neglected in the literature, as has the question of whether online and offline processes are related to one another. With this in mind, we conducted the first large-scale study of individual differences in sleep-dependent consolidation. The purpose of this study was to investigate whether individual differences in a measure of sleep-related consolidation assumed to reflect offline, or unconscious, memory processing would correlate with individual differences in a measure assumed to reflect online, or conscious, processing.

Our specific question was whether individual differences in the change in memory performance after sleep would correlate with a measure of working memory capacity (WMC). WMC refers to the ability to maintain and manipulate information during online processing (Engle, 2002) and has been shown to predict success in many cognitive tasks, including reading comprehension, decision making, problem solving, and vocabulary learning (Engle & Kane, 2004). Furthermore, WMC correlates strongly with performance

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on standardized tests of cognitive ability such as the SAT and ACT (Turner & Engle, 1989), and with performance on tests thought to provide relatively pure measures of general intelligence (Engle, Tuholski, Laughlin, & Conway, 1999). Based on this evidence, WMC is regarded as a fundamental component of the human cognitive system, and it has even been suggested that it is the major source of individual differences in human intelligence (e.g., Engle & Kane, 2004; Kyllonen, 1996).

There is strong evidence to suggest that WMC reflects the ability to control attention during online task performance (Engle, 2002). However, it has recently been proposed that WMC also reflects long-term memory (LTM) processes. Specifically, Unsworth and Engle (2007) proposed that individual differences in WMC arise from processes involved in maintaining information over a short period, as well as processes involved in LTM search and retrieval. Consistent with this view, a recent study showed that measures of LTM and short-term memory (STM) in list recall each accounted for significant and unique variance in WMC (Unsworth, Spillers, & Brewer, 2010). We predicted that if WMC is related to LTM memory processes, then it may also be related to memory storage, specifically, consolidation during sleep.

Method

Participants

The participants were 348 right-handed native English speakers who reported no history of sleep or memory disorders. Ninety-three participants were excluded from all analyses because they reported napping during a waking retention interval. Naps of even very short duration can improve performance in this task (Lahl, Wispel, Willigens, & Pietrowsky, 2008). The remaining 255 participants (149 women, 106 men) had a mean age of 19.4 ± 2.0 (mean ± SD) years. Participants were undergraduate students at Michigan State University and were given course credit for participation.

Design

Participants completed two experimental sessions, separated by a 12-hr retention interval and were assigned to one of two experimental conditions. For one group (wake condition), the first session occurred at 9:00, and the second session occurred at 21:00 after a waking day. For the other group (sleep condition), the first session began at 21:00 and the second session was at 9:00 the following morning after a regular sleep phase. The first session included a study phase and cued recall test, and the second session included a second cued recall test followed by the operation span (OSPAN) task. Participants also reported their sleep patterns for 1 week prior to the study.

Stimuli

The stimulus set used to assess declarative memory consolidation consisted of 48 pairs of semantically related nouns. Participants studied all 48 word pairs, but eight pairs did not appear on either of the tests (four that appeared at the beginning and four that appeared at the end of the study phase) to control for primacy and recency effects on memory performance. Word pairs were adapted from Gais and Born (2004) and were matched for frequency, imagery, and concreteness (Francis & Kucera, 1982; see the Appendix for complete stimulus list).

Procedure

During the training phase, each word pair was presented in a random order for 4,000 ms, with a 1,500-ms intertrial interval. After the training phase, participants were given a cued recall test on 40 word pairs. The first word of the pair was presented on the computer screen, and participants were asked to type the second word. No time limit was imposed on their responses. After each response, participants received two forms of feedback. They were first told whether their response was correct or incorrect and were then shown the correct word pair, regardless of response. Words were presented randomly during the test. Participants were trained to a criterion of 60% correct to roughly equate recall performance on Test 1. If criterion was not met on the first test, the entire cued recall test was repeated, including feedback, until criterion was achieved. As in previous studies in which this paradigm has been used (cf. Plihal & Born, 1997, 1999), feedback was given during the final recall test in Session 1.

During the second session, participants were first given a cued recall test on the 40 word pairs. As in the first test, they were given the first word in the pair and were asked to type the second word. No time limit was imposed on responses. On this test, however, participants did not receive feedback on any of the trials. After the recall test, participants completed the OSPAN task (Unsworth, Heitz, Schrock, & Engle, 2005) to assess WMC. Each trial consisted of an equation, followed by a letter. The participants' task was to verify whether an answer provided for the equation was correct or incorrect, and then to remember the letter. After between three and six trials, a recall screen appeared on which participants were shown 12 letters and instructed to click on those that had been presented.

Results

Consistent with previous claims that consolidation during sleep improves declarative memory performance, the group that was tested after sleep showed a significant improvement in recall performance over the retention interval while the wake group did not. As can be seen in Figure 1, the wake group showed very little improvement in recall from the final test at the end of training (mean ± SEM in Test 1: 29.9 ± 0.37, correctly recalled items) to the test given after the 12-hr retention interval (Test 2: 30.6 ± 0.47), whereas the sleep group showed large improvement from Test 1 (30 ± 0.4) to Test 2 (34.4 ± 0.37). Using a repeated-measures ANOVA with recall test (Test 1, Test 2) as a within-subject factor and condition (sleep, wake) as a between-subjects factor, we found a significant main effect of condition, $F_{1, 223} = 14.26$, $p < .001$, and recall test, $F_{1, 223} = 111.7$, $p < .01$, and a significant interaction between the factors, $F_{1, 223} = 61.8$, $p < .001$. Planned comparisons showed that the sleep group reliably improved from Test 1 to Test 2, $t(110) = 14.7$, $p < .001$, $d = 1.97$, but that the change in performance in the wake group failed to reach significance, $t(113) = 1.7$, $p = .08$, $d = 0.23$, although there was a trend for performance to improve. These results cannot be attributed to baseline differences in performance because performance did not differ at the end of the first session between the two groups, $t(223) = 0.15$, $p = .89$. This suggests that memory for the paired associates was strengthened more after sleep than after an equal interval of wakefulness.

Next, we performed analyses to investigate whether individual differences in OSPAN were related to individual differences in
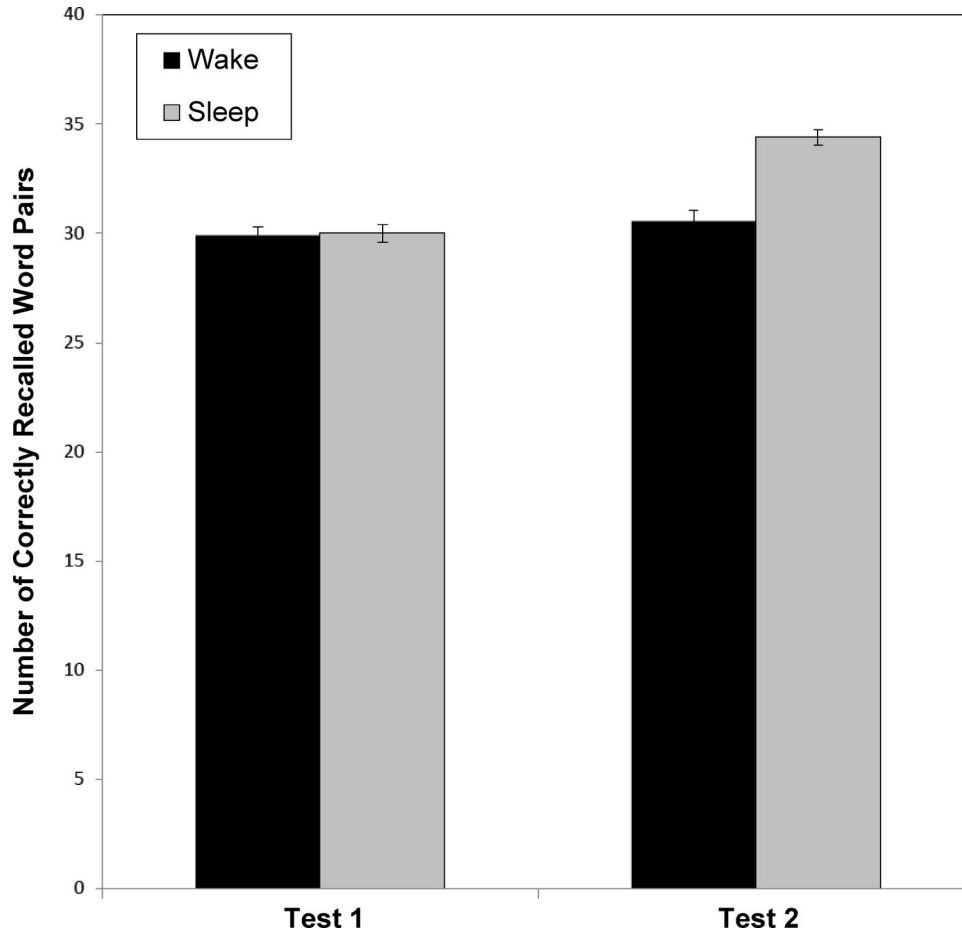
Figure 1. Number of word pairs correctly recalled (out of 40) for wake and sleep conditions at Test 1 and Test 2.

consolidation, which we operationalized as change in performance across sleep or waking (i.e., the number of correctly recalled word pairs at Test 2 minus the number recalled at Test 1). There was a large amount of variability in performance change. In fact, expressed as a percentage of final memory performance in Test 1, amount of change ranged from a loss of 42% to a gain of 37% in the wake group and from a loss of 3% to a gain of 44% in the sleep group. Furthermore, there was a positive correlation between OSPAN and performance change in the sleep condition ($r = .23$, $p = .02$), suggesting that participants high in WMC tended to show greater improvement in recall after sleep than did those low in WMC (Figure 2b). This correlation was not significant in the Wake condition ($r = -.11$, *ns*; Figure 2a). The difference in the correlations across conditions was significant, $z = 2.44$, $p = .02$. Finally, there was not a significant correlation between OSPAN and final performance on Test 1 ($r = -.07$) in the sleep group. As previously mentioned, participants were trained to criterion in this session. We therefore expected that performance would be roughly equated across different levels of WMC and did not expect to find a correlation between WMC and performance on this test. This pattern of results indicates that WMC did not predict memory performance during the first session; it only predicted the change in memory over time.

To further test for differential relations between OSPAN and change in memory performance across conditions, we conducted a regression analysis with performance change as the dependent variable. Following a standard approach for testing for an interaction between a continuous variable and a categorical variable (cf. Cohen, Cohen, West, & Aiken, 2003), we regressed performance change onto OSPAN (mean-centered) and condition (dummy-coded) and then onto the OSPAN × Condition interaction. A significant increment in variance accounted for in the second step would indicate an OSPAN × Condition interaction. As can be seen in Table 1, there was a large effect of condition on performance change, $R^2 = .226$, $\beta = .42$, $t(201) = 6.51$, $p < .001$, reflecting the large difference in performance change across conditions illustrated in Figure 1. The effect of OSPAN was not significant, $R^2 = .001$, $\beta = .04$, $t(201) = 0.63$, $p = .53$. However, as shown in Figure 3, and consistent with the pattern of correlations in Figure 2, the OSPAN × Condition interaction was significant, $R^2 = .020$, $\beta = .15$, $t(201) = 2.34$, $p = .02$. OSPAN positively predicted performance change in the Sleep condition, but not in the Wake condition.

To ensure that our results were not affected by diurnal or circadian effects on performance, we tested performance during the initial training session and the test session for both groups. There were no significant differences between the sleep and wake
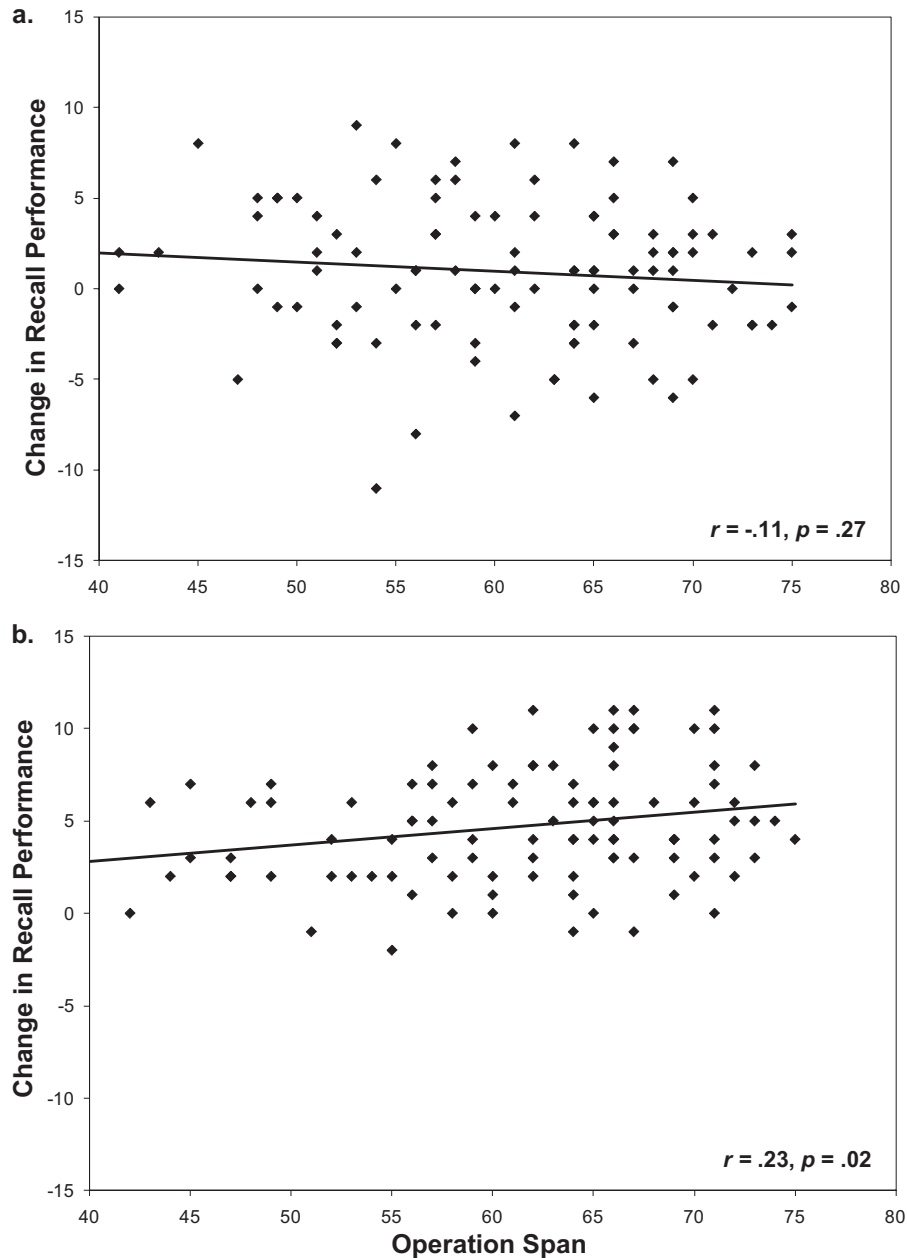
Figure 2. Correlation between operation span score and change in recall performance between Test 1 and Test 2 for (a) the wake condition and (b) the sleep condition.

groups in final recall performance, $t(223) = 0.15$, $p = .89$, or the average number of runs to reach criterion, $t(223) = 0.79$, $p = 0.43$, in the first session. The groups also did not show significant differences in OSPAN scores in the second session, $t(223) = 0.12$, $p = .91$. Taken together, these results suggest that time of day at test cannot explain our findings.

Last, we wanted to ensure that our results could not be explained by individual differences in amount of sleep. It is possible that high-WMC individuals simply slept more than low-WMC individuals, and with this in mind, we tested for a correlation between OSPAN score and self-reported amount of sleep on the night of the

study and self-reported average sleep for the week prior to the study. Correlations between OSPAN and sleep on the night of the study ($r = -.02$) and average amount of sleep ($r = -.15$) were both negative, although neither was significant. Furthermore, there was no evidence for a correlation between amount of sleep on the night of the study and the change in recall performance from Test 1 to Test 2 ($r = -.01$) in the sleep group. This is not surprising as short naps have shown consolidation effects in this task (Lahl et al., 2008).

To summarize, we found that a measure of WMC, which can be assumed to reflect online memory processing, positively predicted

Table 1

Regression Model for Performance Change

Variable	R^2	β	*t*	*p*
Step 1				
Condition	.226	.42	6.51	<.001
Operation span	.001	.04	0.63	.53
Step 2				
Condition × Operation Span	.020	.15	2.34	.02

Note. Degrees of freedom: Step 1 = (2, 202); Step 2 = (3, 201).

increases in declarative memory performance after sleep. Importantly, we also found that WMC did not predict performance during the initial training session; it only predicted the change in performance across sleep. This finding suggests that individual differences in WMC not only relate to online processing of information and conscious memory acquisition but also relate to offline processing during sleep and nonconscious memory processing.

Discussion

Consistent with results of previous studies (cf. Plihal & Born, 1997, 1999), we found evidence for sleep-dependent consolidation in paired-associates learning. There was a significant increase in memory performance across a period of sleep but not across a period of wakefulness. We assume that improvement over baseline in the sleep condition reflects consolidation of the feedback given in the final test of Session 1. More important, a measure of WMC

predicted performance change for participants in the sleep condition but not for those in the wake condition. We speculate that WMC-related differences at encoding may affect subsequent offline processing. In particular, although there was no correlation between WMC and memory performance during training, high-WMC individuals may have created stronger associations between words at encoding. There is some evidence to suggest that stronger associative connections during waking show greater reactivation during sleep. One study investigating hippocampal replay in rats found that cells that fired together more often during spatial exploration were more likely to fire together during subsequent sleep (O'Neill, Senior, Allen, Huxter, & Csicsvari, 2008). Furthermore, one recent study has found that sleep preferentially consolidates memories that are associated with stronger hippocampal activation at encoding (Rauchs et al., 2011). It is possible that high-WMC individuals create stronger associative traces during initial acquisition. These traces might then be more likely to be reactivated during sleep, resulting in a greater increase in memory after sleep.

It is also possible that people with different levels of WMC differ in the quality of their sleep. Although there was no evidence from the current study that longer sleep duration was related to stronger consolidation, there is evidence from other studies to suggest that certain sleep features are associated with declarative memory consolidation. Several recent studies have shown that improvement in declarative memory is correlated with Stage 2 sleep spindles (Clemens, Fabo, & Halasz, 2005; Genzel, Dresler, Wehrle, Grozinger, & Steiger, 2009) and that declarative memory
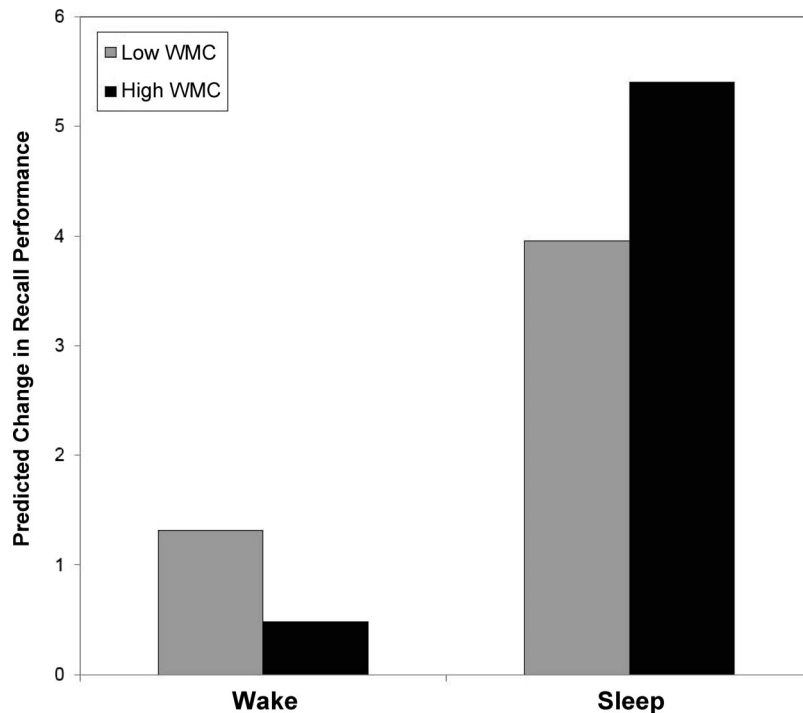

Figure 3. Illustration of Condition × Operation Span interaction (i.e., predicted change in recall from Test 1 to Test 2 for low- versus high-operation span in wake versus sleep conditions). WMC = working-memory capacity.

acquisition prior to sleep results in an increase in spindle density (Schabus et al., 2004; Schabus et al., 2008). Furthermore, recent work with rats has shown that memory reactivation during sleep is correlated with spindle activity (Johnson, Euston, Tatsuno, & McNaughton, 2010). This is important to the current study because related work has shown that individuals high in general intelligence show increased spindle activity during sleep, regardless of prior learning (Bódizs et al., 2005; Schabus et al., 2006). As previously mentioned, WMC is highly correlated with general intelligence (e.g., Kane et al., 2004). Therefore, it is possible that individuals high in WMC simply have higher baseline spindle activity during sleep and in turn derive greater benefit from sleep.

Although we speculate that the correlation between WMC and sleep-dependent consolidation reflects a direct relationship between these variables, we cannot rule out, on the basis of the present study, the possibility that this correlation reflects other factors. For example, it is possible that this correlation is due to long-term memory ability. Long-term memory contributes to WMC (Unsworth & Engle, 2007), and sleep improves long-term declarative memory (cf. Plihal & Born, 1997, 1999). Therefore, it seems possible that LTM ability, reflecting hippocampal functioning, accounts for the correlation between WMC and consolidation. An important goal in future research would be to measure a broader range of factors to better understand the relationship between WMC and sleep-dependent consolidation.

In conclusion, this is the first study to demonstrate that individual differences in WMC relate to changes in memory performance after sleep. More research is required to clarify the nature of this relationship, but a provocative possibility is that individual differences in offline processing translate into individual differences in working memory performance. For example, consolidation processes may facilitate acquisition of verbal knowledge, and in turn, verbal knowledge (vocabulary) may be beneficial in performing WMC tasks like operation span that involve remembering words. Future research aimed at addressing this sort of possibility will significantly advance scientific understanding of mechanisms underlying both online and offline memory processing.

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Appendix

Stimuli Used in This Experiment

The first four and final four word pairs (bold typeface) were presented during training but did not appear on any of the recall tests. Word pairs were presented randomly during study and test (with the exception of the initial and final four pairs).

LINEN–FEATHER
VOWEL–CURRY
HAMMER–ORANGE
WAGON–BUTTER
SCHOOL–TEST
TOWER–BELL
JOURNEY–MAP
FAMILY–MARRIAGE
MOTHER–CHILD
WALL–PAINT
KITCHEN–POT
GROUP–PERSON
FIRE–SMOKE
INSECT–ANT
CAMP–TRAIL
KNIGHT–BISHOP
VALLEY–HILL
FOREST–TIMBER
GLACIER–SNOW
TOAST–EGG
TEAM–CREW
BOOK–STORY
RAIN–FLOOD
GALE–WIND

BUILDING–HALL
ANIMAL–FOX
SEA–TIDE
PLANT–LEAF
BAR–DRINK
MOUNTAIN–BOULDER
CRADLE–DOLL
PLAY–DRAMA
BIRD–ROBIN
GRAIN–OATS
ROAD—CAR
BLACKSMITH–METAL
TAIL–CAT
THREAD–NEEDLE
ILLNESS–DOCTOR
POND–FROG
CIRCUS–BALLOON
RIVER–CANOE
GUN–BULLET
COAST–BEACH
LILY–CHIMNEY
SHERIFF–COP
ODOR–CLIMATE
COFFEE–TEA