

April 2021

Slow Wave Sleep in Naps Supports Episodic Memories in Early Childhood

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<https://doi.org/10.7275/20272468> https://scholarworks.umass.edu/masters_theses_2/1017

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SLOW WAVE SLEEP IN NAPS SUPPORTS EPISODIC MEMORIES IN EARLY
CHILDHOOD

A Thesis Presented

by

SANNA M. LOKHANDWALA

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
Of the requirements for the degree of

MASTER OF SCIENCE

February 2021

Psychology

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ABSTRACT

SLOW WAVE SLEEP IN NAPS SUPPORTS EPISODIC MEMORIES IN EARLY CHILDHOOD

FEBRUARY 2021

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Naps have been shown to benefit declarative memories in early childhood. This benefit has been associated with sleep spindles during the nap. However, whether young children's naps and their accompanying physiology benefit other forms of declarative learning is unknown. Using a novel storybook task, we found performance was better following a nap compared to performance following an equivalent interval spent awake. Moreover, performance was better the following day if a nap followed learning. Further, change in post-nap performance was positively associated to the amount of time spent in slow wave sleep. This suggests that slow wave sleep in naps may support episodic memory consolidation in early childhood. Taken in conjunction with prior work, these results suggest that multiple features of brain physiology during naps may contribute to declarative memory processing in early childhood.

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CHAPTER 1

INTRODUCTION

Memories are much more like paintings than photographs. Memories do not just “capture” a moment or idea only to be stored away. Instead, like the combination of strokes, colors, and techniques needed to create an artistic experience, new information is actively combined with our preexisting knowledge, and this active integration allows us to learn from and adapt to experiences in a unique way. In this regard, memories form the developmental foundation of our ability to learn. Early childhood, particularly the preschool years (3-5 years), is a critical time for memory development, as this is a period during which humans are particularly receptive to learning (Phillips & Shonkoff, 2000).

The preschool years

To capitalize on the developmental plasticity present in early childhood, intervention and education initiatives have begun to incorporate cognitive, social, and emotional curricula into their frameworks (Bierman et al., 2008; U.S. Department of Health and Human Services, 2010). In doing so, preschool education may have both immediate and lasting implications for cognitive, social, and academic abilities, particularly for disadvantaged children. While children from low-income families are at risk for academic underachievement (Arnold & Doctoroff, 2003; Jordan et al., 2006), studies have shown that early childhood education programs relay both immediate and long-term gains (Bitler, Hoynes, & Domina, 2014; Schweinhart, Barnes, & Weikart, 1993; Campbell & Ramey, 1995; Reynolds et al., 2000). For example, attendance in Head Starts, which are federal child development programs targeting low-income families and children at risk for academic underachievement (Jenkins, Farkas, Duncan,

Burchinal, & Vandell, 2016), has been shown to lead to significant gains in cognitive skills, specifically in receptive vocabulary, early mathematics, and early literacy (Bitler, Hoynes, & Domina, 2014).

The intensive intervention work from the hallmark Abecedarian Project highlights the long-term benefits of participating in such education initiatives. This longitudinal prospective study examined the benefits of early education intervention and found that children who were a part of the preschool treatment group (i.e., child centered care with a curriculum emphasizing adaptive behavior, cognition, and language skill development) scored significantly higher on intellectual and academic measures in young adulthood (Campbell, Ramey, Pungello, Sparling, & Miller-Johnson, 2002). These short- and long-term gains in cognitive and academic abilities described above imply that it is critical to take advantage of children's ability to learn during the preschool years.

Early memory development

Not only are these years an important time for learning (Woolfolk & Perry, 2013), but they are also an important time for brain development, as the brain reaches approximately 90% of its adult size by the age of 5 (Dekaban & Sadowsky, 1978). In particular, the hippocampus develops during this period, illustrating a nonlinear increase in hippocampal volume well into adolescence, followed by smaller age-related changes thereafter (Uematsu et al., 2012; øtsby et al., 2009; Krogsrud et al., 2014). The hippocampus is a structure that is critical for learning and memory formation (Squire, 2009). It is responsible for the acquisition, organization, and storage of *declarative* memories – memories for facts and events, and those memories we can consciously recall (Squire & Zola-Morgan, 1991).

Declarative memory encompasses both semantic memory (i.e., memory for facts) and episodic memory (i.e., memories for specific experiences), and is arguably the form of memory most focused on in formal education and everyday settings. Declarative memory consolidation, the off-line strengthening and stabilization of memories, involves the hippocampus (Eichenbaum, 2000). Newly encoded memory traces are temporarily stored in the hippocampus and are gradually transferred to more long-lasting representations in the neocortex (Buzsáki, 1989). Growing evidence suggests that sleep facilitates the transfer of these memories from the hippocampus to the cortex, a process termed sleep-dependent memory consolidation (Born et al., 2012; Maquet, 2001).

Sleep supports memory

Historically, sleep has been considered a period of dormancy that is essential for the rest, healing, and growth of all organisms (Berger & Phillips, 1995; Oswald 1980). Growing work indicates that sleep's benefits extend beyond physical restoration to include cognition (Spencer, 2013; Walker & Stickgold 2004; see Dieklmann, Wilhelm, & Born, 2009, for a review). For instance, when learning a list of semantically unrelated word pairs, adults who learned the list in the evening and recalled them 12 hrs later (i.e., after a period of sleep), performed significantly better when compared to adults who learned the list in the morning and recalled them 12 hrs later (i.e., after an interval spent awake; Wilson, Baran, Pace-Schott, Ivry, & Spencer, 2012). This suggests that sleep may be critical to memory consolidation.

Unlike adult sleep which is composed of primarily one sleep bout (overnight sleep), sleep in early childhood is particularly unique. Preschool-aged children are at an age during which their sleep transitions from a biphasic sleep pattern – characterized by

two daily sleep bouts, nap and overnight sleep – to a monophasic schedule – characterized by a single overnight sleep bout (Iglowstein, Jenni, Molinari, & Largo, 2003).

A growing number of studies in children have indicated a beneficial influence of sleep, including the nap opportunity, on learning and memory in multiple domains (Desrochers, Kurdziel, & Spencer, 2016; Backhaus, Hoeckesfeld, Born, Hohagen, & Junghanns, 2008; Berger, Miller, Seifer, Cares, & LeBourgeois, 2012, William & Horst, 2014). For example, when preschool aged children (3-5 yrs) were trained on a visuo-spatial learning task (similar to the game “Memory”), children retained what they learned when they napped after learning, but forgot many of the learned items when they spent an equivalent interval awake (Kurdziel, Duclos, & Spencer, 2013). Such studies illustrate that memories in both adults and children are benefited by sleep.

Mechanisms underlying sleep-dependent memory consolidation

While numerous behavioral studies support sleep’s benefit on memory consolidation, recent studies have begun to address the physiological mechanisms underlying this process. Notably, studies including sleep physiology indicate that slow wave sleep (SWS) and sleep spindles (bursts of brain activity, 9-16 Hz, that occur most commonly in non-REM (nREM) stage 2 sleep) are associated with memory consolidation (Baran, Mantua, & Spencer, 2016; Steriade & Amzica, 1998; Wilhelm, Diekelmann, & Born, 2008). The association observed between SWS and memory performance is in line with the active system consolidation hypothesis, which specifies that during SWS, newly encoded memories are repeatedly reactivated in the hippocampus, supporting the transfer of information from the hippocampus to the neocortex (Born & Wilhelm, 2012; see

Rasch & Born, 2013 for review). In one study, post sleep performance was related to increased activation in the anterior and posterior part of the left hippocampus. Such activity has been shown in adults when memories are cued during SWS (Rasch, Büchel, Gais, & Born, 2007).

In another study, adults learned to associate spoken words with pictures of scenes or objects prior to a nap. During nREM sleep, a subset of these spoken words were replayed. Not only was memory superior for these replayed associations but for associations learned before sleep, the words produced greater spindle activity (Cairney, Guttesen, El Marj, & Staresina, 2018). Taken together, these studies suggest that properties of sleep actively play a role in memory consolidation.

While declarative memory has been associated with SWS and spindles in adults, few studies have considered the relevant sleep features which support memory consolidation in early childhood. However, in a study of declarative memory (a visuospatial learning task), we found that sleep spindle density predicted memory consolidation during naps in preschool-age children (Kurdziel et al., 2013). Mechanistically, sleep spindles and hippocampal ripples (high frequency field oscillations; 100-300 Hz) are embedded in slow waves, and these oscillations interact in a fine-tuned manner to allow the transfer of newly encoded memories (e.g., declarative memories) from the hippocampus to the neocortex (Rasch & Born, 2013; Schabus et al., 2006).

Current study

The purpose of the present study was twofold. First, we sought to determine whether the benefit of naps on visuospatial learning in early childhood, as demonstrated in Kurdziel et al., 2013, would generalize to other declarative memory tasks. Specifically, we used a task which required learning the episodic sequence of events in a storybook to probe episodic memory. This task is both age-appropriate and has ecological validity. Williams and Horst (2014) used a similar task with word learning from the storybook as their outcome variable. They found that napping shortly after learning may be important for word learning compared to staying awake. However, this study used a between-subjects design, in which children who were habitual nappers were assigned to the nap condition and non-habitual nappers were assigned the wake condition. We (Kurdziel et al., 2013) and others (Lam, Mahone, Mason, & Scharf, 2011; Watamura, Donzella, Kertes, & Gunnar, 2004) have hypothesized that children who nap may fundamentally differ from those who no longer nap, with superior brain development and cognitive skills for non-nappers even when controlling for age. For this reason, we used a within-subject design to compare learning of event sequences from age-appropriate storybooks. We hypothesized that naps would benefit learning on this task. However, a reasonable alternative hypothesis that we considered is that naps may have a unique role in visuospatial learning given that this task taps the spatial-detecting place cells of the hippocampus, where neural replay during sleep has been found (Ji & Wilson, 2007; Skaggs & McNaughton, 1996).

Our second objective was to determine whether nREM2 sleep spindles play a general role in declarative memory consolidation in early childhood. Based on Kurdziel and colleagues (2013), we hypothesized that consolidation of episodic storybook learning

would likewise be related to sleep spindle density in early childhood naps. However, studies in adults suggest the specific sleep mechanism may be task dependent and that SWS may instead facilitate episodic learning (Baran et al., 2016; Gais & Born, 2004 for review; Marshall & Born, 2007; Tucker et al., 2006). In one study, participants had less forgetting of the episodic components of a declarative task (temporal context) following sleep and this was suggested to be attributed to SWS (Rauchs et al., 2004). Thus, we considered the role of both sleep spindles and SWS in episodic memory consolidation in preschool children.

CHAPTER 2

METHOD

Participants

Participants were 22 children 36-71 months of age (7 females; $M = 51.23$ months, $SD = 8.95$). Children were recruited through the university's Infant and Child Database and through advertising on parent-directed social media groups. Children were eligible if they had normal or corrected-to-normal vision, no history of diagnosed sleep disorders, if they were not using any sleep-affecting or psychotropic medications, had no learning or developmental disabilities, had not recently travelled outside of the local time zone, and were deemed likely to nap in the laboratory. Five participants were excluded due to scheduling conflicts ($n=2$), inability to comply with study procedures ($n=2$), and technical difficulties ($n=1$). Additionally, when assessing children's memory performance across the nap and wake condition, performance of one participant was deemed an extreme multivariate outlier (defined as 3 SDs above the average Cook's distance) and was subsequently excluded from all analyses.

Procedure

All procedures were approved by the University of Massachusetts Amherst Institutional Review Board. Approximately four days prior to the first experimental condition, caregivers provided informed consent for their child's participation. Child assent was obtained at each experimental stage. At this time, parents were also given a study packet that included questionnaires and instructions on how to use/care for the Actiwatch. Children were fitted with the Actiwatch. The experimental sessions took place in the sleep lab. Using a within-subjects design, participants were randomly assigned to

begin with either a nap or wake condition. The alternate condition took place approximately one week later.

For each session, children and their caregivers were scheduled to arrive at the sleep lab approximately 1 hour before the child's typical nap time (typically around 12:00 p.m.). Once comfortable, the child completed the practice phase of the storybook task. In this phase, the child was read the practice book. The experimenter read one page at a time, engaging the child with the story (e.g., "Look at Maddie's birthday cake!"). Next, the child was presented with the picture cards for that story. The child was then asked to place the cards in order as they occurred in the story. Feedback on correct sequencing was provided in this phase.

In the encoding phase, immediately following the practice phase, the experimenter read two stories to the child. The experimenter sat adjacent to the child and read one page at a time. Short breaks between the two stories were permitted if the child required them (e.g., going to the bathroom). In the subsequent immediate recall phase (Figure 1B), children were presented with picture cards from the stories and asked to put them in the correct order (one story at a time). No feedback was provided.

Following immediate recall, in the nap condition the child was fitted with a PSG cap and given a 2-hr nap opportunity in which sleep was promoted (e.g., via back rubs and lullabies). In the wake condition, the child was also fitted with the PSG cap to ensure wakefulness while they engaged in quiet activities (e.g., puzzles, drawing). Thirty minutes following the nap/wake condition (approximately 3:00 p.m.), children completed the delayed recall phase. The child was again presented with the picture cards and asked

to arrange them in order of the storybook without feedback. Subsequently, the caregiver and child left the lab and continued with their day.

In both conditions, the caregiver and child returned to the lab the following day, approximately the same time the stories were read the previous day, for the 24-hr recall phase. The child was given the story cards once more and asked to put them in the correct order. No feedback was provided.

Following each recall phase, the child self-reported their sleepiness (Maldonado, Bentley, & Mitchell, 2004) and mood (Stern, Arruda, Hooper, Wolfner, & Morey, 1997) using pictorial Likert scales. Experimenters separately rated sleepiness and mood of the child using the same scales.

Measures

Storybook Task. Episodic memory was investigated with a story-based task similar to that of Williams and Horst, 2014 and the NIH Toolbox Picture Sequence Memory Test (Bauer et al., 2013). Stimuli consisted of one 5-page practice book (*Birthday Party*) and four 10-page experimental books (*Trip to the Zoo*, *Going Camping*, *Making Cookies*, *Playing in the Park*), all designed in-house. Books were printed on 18 cm x 11 cm pages. Each book described an age-appropriate event or activity (e.g., going camping). The first page of each story consisted of a goal sentence complemented by an illustration. The subsequent 9 pages depicted a series of events described with a short sentence (Figure 1A). Two books followed a generally logical sequence (e.g., baking cookies) and two books followed generally an arbitrary ordered events (e.g., playing in the park) and provided greater difficulty. Encoding consisted of reading two experimental

books, one with a logical sequence and one with an arbitrary sequence, with books counterbalanced across nap and wake conditions. To assess memory, ten picture cards (five for the practice book), capturing the various activities from the story, were created for each book.

Polysomnography (PSG). PSG was acquired during naps using customized 32-channel PSG electrode caps (EasyCaps; Brain Products GmbH, Germany). The EEG montage included 24 cortical electrodes (Fz, F3, F4, F7, F8, FCz, FC1, FC2, FC5, FC6, C3, C4, CP1, CP2, CP5, CP6, Pz, P3, P4, P7, P8, POz, O1, and O2), two EOG electrodes, and two EMG electrodes. EEG data were recorded relative to ground at FPz and referenced to Cz and the contralateral mastoids (A1 and A2). The EMG leads were referenced to each other.

Actigraphy. Children also wore actigraphy watches (Actiwatch Spectrum, Philips Respironics, Bend, OR) on the non-dominant wrist continuously for 16 days (fitted approximately 3-4 days prior to the child's first session). The Actiwatch sampled activity at 32 Hz, with a sensitivity of <.01 g and activity was stored in 15-s epochs. Caregivers were instructed to press an event marker to mark the beginning and end of sleep bouts.

Questionnaires. To assess children's general sleep habits, a primary caregiver completed the Child Sleep Habits Questionnaire (CSHQ; Owens, Spirito, & McGuinn, 2000). Primary caregivers also filled out a daily sleep diary for the child, noting sleep onset and offset. An in-house health and demographics questionnaire completed by parents was used to characterize the participant population.

Data Analysis

Storybook Task. Of interest was the change in memory from immediate recall to delayed and 24-hr recall across the two conditions. Memory performance was measured as the sum of adjacent pairs of events remembered correctly divided by the maximum score. Each correct adjacent pairing received a score of 1, with a maximum score of 9 per storybook (e.g., a sequence of 1-3-4-6-5-7-8-2-9-10 would receive a score of 3 as 3-4, 7-8, and 9-10 are correct adjacent pairs). Scores were combined for the two storybooks in each condition for a maximum score of 18. Two-tailed paired-samples *t*-tests were used to compare differences in performance across immediate, delayed, and 24-hr recall. *P*-values below $\alpha = .05$ were considered statistically significant. Analyses were uncorrected for multiple comparisons.

To assess changes in memory following the nap and wake conditions, immediate recall accuracy was subtracted from delayed recall accuracy to create a delayed difference score (i.e., change in accuracy%; $(\text{delayed recall} - \text{immediate recall}) * 100$). The difference score was calculated for both the nap and wake conditions to further control for baseline differences. Likewise, we calculated a 24-hr difference score while controlling for immediate recall accuracy (24-hour difference score; $(\text{24-hr recall} - \text{immediate recall}) * 100$). Two-tailed paired-samples *t*-tests were used to compare between the nap and wake conditions and their difference scores. Pearson's correlations were used to determine relationships between memory performance and sleep physiology.

Polysomnography. Sleep stages were identified according to the American Academy of Sleep Medicine standards (AASM, 2017). Sleep staging was verified by a second trained experimenter. Sleep spindles (and their peak amplitude and frequency) were detected at C3 using an established algorithm (Ferrarelli et al., 2007) and further visually inspected

for spindles specifically in nREM2. The EEG signal was sampled at 500 Hz, and band pass-filtered between 10 and 16 Hz (Chebychev filter order 6 with passband corner frequencies of 11 Hz and 15 Hz and stopband corner frequencies of 10 Hz and 16 Hz). The algorithm then detected spindles based on an upper threshold of 6 and lower threshold of 2 (as detailed in McClain et al., 2016). Spectral analysis was performed in MATLAB using EEGLAB (Delorme & Makeig, 2004), ERPLAB (Lopez-Calderon & Luck, 2014), and custom in-house functions (available upon request; see Jones, Fitzroy, & Spencer, 2019). Spectral analysis was derived from C3 based on previous literature (see Cremone, Kurdziel, Fraticelli-Torres, McDermott, & Spencer, 2017). Slow wave activity was characterized as activity during SWS in the delta range, specifically between 0.5 and 4 Hz.

Actigraphy. Actigraphy data was scored with Actiware software (Philips Respironics) following standard protocols (Acebo et al., 2005). Specifically, participants with less than three days of data were excluded from analysis ($n = 9$) based on previous work using similar criteria (Penpraze et al., 2006). Thirteen children's sleep bouts were scored with reference to event markers and sleep diaries (10 of these children had nap data and were used in subsequent analysis). Sleep onset was determined as the first 3 minutes of uninterrupted sleep and sleep offset was determined by the last 5 minutes of continuous sleep (Acebo et al., 2005). Sleep duration was defined as the total minutes of sleep from sleep onset and sleep offset.

CHAPTER 3

RESULTS

Memory Performance

Children were able to learn the task as demonstrated by >45% accuracy for immediate recall in both the nap and wake conditions. Immediate recall did not differ across conditions ($t(21) = -.201, p = .843$; Table 1). Further, there were no significant differences between the storybooks with a logical vs. arbitrary order of events at baseline ($t(21) = 1.232, p = .232$). Moreover, immediate recall was not predicted by age ($r = .133, p = .554$) nor gender ($t(20) = .163, p = .872$).

Delayed recall accuracy was significantly greater in the nap condition compared to the wake condition ($t(21) = 3.272, p = .004$; Table 1). To control for baseline memory performance, we compared the delayed difference scores across conditions. Accuracy was again better in the nap condition compared to the wake condition ($t(21) = 3.050, p = .006$; Figure 2A), indicating a benefit of the nap on this form of episodic learning.

We considered whether better memory following the nap reflected impairments in the wake condition as opposed to benefits of the nap condition. In other words, children's behavior following nap deprivation (inattentive, emotionally dysregulated) may have impaired performance. There were no differences in child- or experimenter-reported mood following the nap and wake intervals ($ps > .248$). However, child-rated sleepiness was greater following an interval spent awake ($t(21) = -2.143, p = .044$) and experimenter-rated sleepiness of the child was marginally significant ($t(21) = -1.993, p = .059$).

Considering this, we examined whether sleepiness accounted for differences in performance following nap and wake intervals. Both child- and experimenter-rated sleepiness was associated with performance following wake ($ps = .008$), but this was not the case following the nap ($ps > .776$). If sleepiness accounted for acute differences, it would be expected that these differences would dissipate the next day, following unrestricted overnight sleep. Children continued to perform significantly better when they had napped following learning the prior day compared to when they had not napped (24-hr recall accuracy: $t(21) = 3.947$, $p = .001$; Table 1). This next-day nap benefit remained when controlling for immediate baseline performance (24-hr difference score: $t(21) = 3.716$, $p = .001$; Figure 2B). This suggests that the benefit of the nap compared to the wake condition could not be attributed to short-term behavioral differences across the conditions.

Relations Between Memory and Nap Physiology

Actigraphy was used to assess habitual sleep (Table 2). Children napped, on average, 3.28 days/week. Parent reports of children napping (from the CSHQ) was a bit higher, reporting on average, 4.72 days/week. This difference reflects that more children had CSHQ data than actigraphy data.

Average actigraphy recorded nap length was 89.85 min (SD = 28.53 min). Average length of PSG-recorded naps in the laboratory was 94.18 min (SD = 13.22 min). Naps included little ($n = 3$, 1-10 min) to no ($n = 19$) REM sleep. Consistent with prior work, naps were largely comprised of nREM stage 2 sleep and SWS (Cremone et al., 2017; Kurdziel et al., 2013; Table 2).

We tested the hypothesis that the sleep spindle-dependent declarative memory benefit observed in our prior work (Kurdziel et al., 2013) would generalize to the present task. However, spindle density in nREM stage 2 was not associated with change in recall accuracy over the nap ($r = -.145$, $p = .520$; Figure 3A). Further, spindle density in SWS was also not associated with change in recall accuracy post-nap ($r = -.178$, $p = .428$). Next, we tested the alternative hypothesis that SWS supported nap-dependent changes in memory. Here we found a positive significant correlation between time spent in SWS and change in accuracy following the nap ($r = .572$, $p = .005$; Figure 3B).

CHAPTER 4

DISCUSSION

Our previous work (Kurdziel et al., 2013) suggests that declarative memory consolidation over a nap is a function of sleep spindles. Here, we investigated whether this spindle-dependent nap benefit is generalizable to other declarative memory tasks or, rather, is task specific. Our data indicate that episodic memory is benefited following a nap. Furthermore, this nap-dependent benefit extends to the next day, as children performed better approximately 24 hours after learning when they had napped the day before compared to when they had stayed awake during the nap interval. Our findings thus suggest that napping the day prior has lasting effects on memory retention for young children, and that overnight sleep cannot undo the adverse consequences of nap deprivation on memory consolidation.

Further, in examining nap physiology, we showed that time spent in SWS during the nap may underlie nap-dependent changes in performance for episodic memory. This is in contrast to our previous work which found a relationship between nap-dependent consolidation of visuo-spatial learning and sleep spindle density. However, our results are in line with work in young adults in which declarative memory retention correlates positively with the amount of SWS contained in the sleep bout (Barrett & Ekstrand, 1972; Diekelmann, Biggel, Rasch, & Born, 2012). This may suggest SWS during a nap (more proximally following learning), allows for an increased opportunity for memory consolidation. We consider two alternatives. One, this association between SWS and memory performance in contrast to Kurdziel's results may indicate that the physiological mechanism is task dependent. That is, tasks that involve remembering spatial context

may be more reliant on sleep spindles while tasks that involve episodic sequences may be more reliant on SWS. Alternatively, it is possible that findings implicating sleep spindle and the present result implicating SWS may actually be pointing to the same mechanism. Specifically, sleep spindles are embedded in slow waves and it may be this embedded mechanism which supports the consolidation of various forms of declarative memories. It is unclear why different relations emerge for the two studies however studies in adults likewise point to the ripple-spindle-slow oscillation mechanism even though rarely does more than one association reach significance. This is an important area for future research.

Interestingly, there is not much forgetting over wake (Table 1), rather learning appears protected over wake and enhanced by sleep. This is likely an artifact related to the fact that children are being tested on identical recall probes. That is, children are asked to put the same stories together at three different time points. Thus, it is difficult to rule out a practice effect. However, if this was merely a practice effect, we would expect there to be a steady increase at each time point irrespective of napping or being nap deprived. This underlines the adverse consequence of missing out on the midday nap on memory consolidation.

Prior work found children who nap regularly experienced the greatest loss in learning when deprived of the nap compared to non-habitual nappers (Kurdziel et al., 2013). This finding has been thought to reflect differences in brain maturation, with non-habitual nappers having more mature memory networks and thus a decreased need for frequent consolidation. Considering that enrollment for the present study required that children are likely to nap in the laboratory (frequently enough they are likely to nap in the

lab), we did not have a sufficient number of non-habitual nappers (0-1 nap/week) enrolled in the study to consider the role of nap habituality in our findings. Parent-reported and actigraphy-estimated nap habituality suggest that the majority of children were also not habitual nappers (> 5 naps/week). Thus, the current sample does not allow for disentangling whether change in performance following nap/wake is independent of napping status.

Another limitation of the study is the absence of overnight physiology. Without the overnight component, it is difficult to disentangle whether a midday nap affects overnight physiology. For example, it may be that when a child is kept awake during the nap opportunity, they may be getting more deep sleep (SWS) overnight. Thus, it cannot be discerned whether greater 24-hr SWS leads to better performance across the two sleep bouts. However, this is unlikely as it cannot explain our finding that greater SWS during children's naps predicted better memory performance immediately following the nap.

Finally, it is important to note that the present task, like the visuo-spatial task, may not be fully representative of all declarative memory tasks and some task-specificity may still exist. While we characterize the sequential ordering of a storybook as emblematic of episodic memory, it may be beneficial to consider a more traditional episodic memory task such as a free recall task (i.e., a list of to-be-remembered items) where the order in which items are remembered is unimportant. Such a task may allow for memories to be “internally cued” by a particular cognitive process (e.g., episodic cognition) versus “externally cued” by evidence in the environment (e.g., picture cards from a story; Tulving, 1985).

Together, these data suggest that naps support early education goals for preschool age children. However, preschool classrooms are increasingly curbing the nap opportunity to make room for curriculum demands. Given evidence that sleep dependent consolidation is important for children's learning, such classroom practices may be hindering children's ability to effectively learn. Findings from the current study not only suggest sleep close to learning is beneficial to episodic learning but that SWS present in these naps may facilitate the consolidation of such memories. Thus, preserving the nap opportunity should be a valued part of the preschool curriculum.

Table 1. Memory Performance and Child Behavior Ratings During In-Lab Visit (standard deviations in parentheses)

	Nap condition	Wake condition	p-value
Immediate Recall (%)	46.23(21.18)	47.18(25.19)	.843
Delayed Recall (%)	59.68(23.34)	42.41(22.43)	.004
24-hr Recall (%)	65.41(22.73)	46.64(23.02)	.001
Sleepiness			
- Child rated	1.40(1.05)	2.09(1.48)	.044
- Experimenter rated	1.50(0.91)	2.14(1.46)	.059
Mood			
- Child rated	1.68(.95)	1.95(1.40)	.248
- Experimenter rated	1.82(.96)	1.82(1.33)	>.99

Table 2. Descriptive Variables for Actigraphy and Polysomnography-Recorded Naps (standard deviation in parentheses)

	Actigraphy (n=10)	Polysomnography (n=22)
Naps/week	3.28 (1.78)	--
Nap length (min)	89.85 (28.53)	94.18 (13.22)
Time in bed (min)	97.22 (31.84)	121.55 (8.63)
Sleep onset latency (min)	4.0 (4.8)	14.93 (8.75)
Non-REM stage 1 (%)	--	8.59 (5.76)
Non-REM stage 2 (%)	--	35.22 (11.92)
SWS (%)[†]	--	55.82 (14.17)
REM (%)[†]	--	0.37 (1.17)
Spindle density (spindles per minute of non-REM stage 2 sleep)	--	0.72 (.38)
Spindle counts (nREM2)	--	23.27 (11.78) Range: 1-44 spindles
Spindle frequency (Hz)	--	12.91 (.32)
Spindle amplitude (μV)	--	27.99 (8.02)

[†]Note SWS = slow wave sleep; REM = rapid eye movement

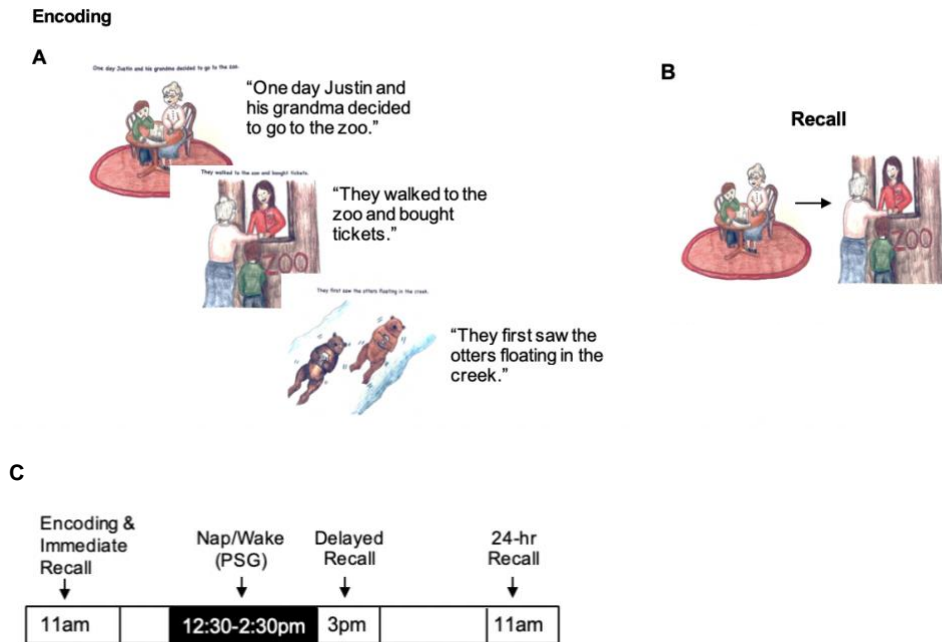


Figure 1. (A) Preschool children were read four 10-page experimental books. The first page of each book began with a goal sentence with the subsequent nine pages illustrating actions or events. (B) During all three recall time points, children were handed picture cards of the story and asked to put the story back in order. (C) During the midday nap opportunity, children were fitted with a PSG cap and were either nap or wake promoted (the alternate condition taking place approximately one week later), with delayed recall following 30-min later. Children were given the picture cards and asked to put the story back in order again. They did this once more the following day during 24-hr recall.

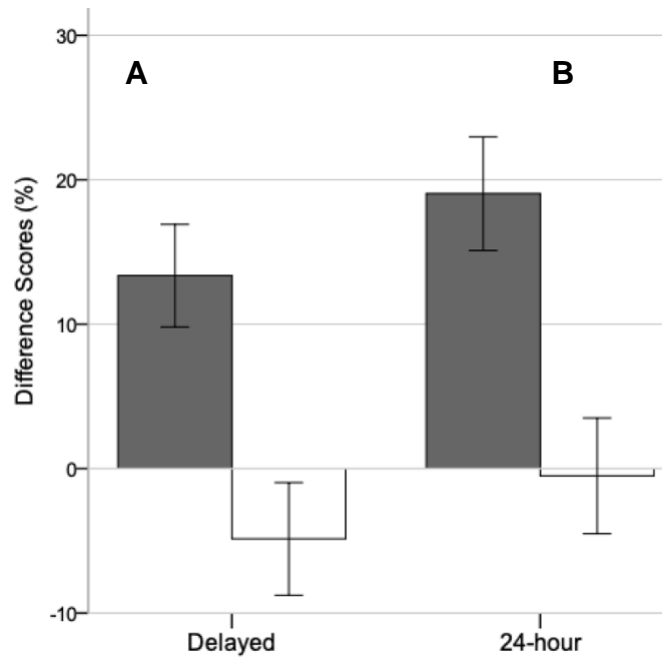


Figure 2. (A) Change in accuracy (delayed – immediate) was significantly greater following the nap condition (gray bars) relative to the wake condition (white bars; “Delayed”). (B) This nap benefit persisted to the next morning (“24-hour”). Error bars represent ± 1 SE.

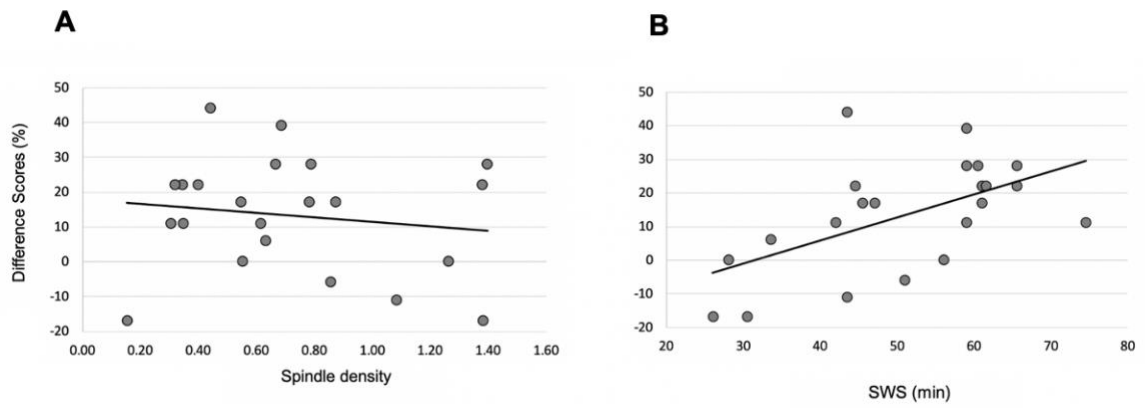


Figure 3. (A) Associations between change in recall accuracy (delay-immediate) and sleep spindle density (number of spindles per minute of non-REM stage 2; $r = -.145$) and (B) time spent in SWS ($r = .551$).

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