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Timely sleep facilitates declarative memory consolidation in infants

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Abstract

Human infants devote the majority of their time to sleeping. However, very little is known about the role of sleep in early memory processing. Here we test 6- and 12-mo-old infants' declarative memory for novel actions after a 4-h [Experiment (Exp.) 1] and 24-h delay (Exp. 2). Infants in a nap condition took an extended nap (≥30 min) within 4 h after learning, whereas infants in a no-nap condition did not. A comparison with age-matched control groups revealed that after both delays, only infants who had napped after learning remembered the target actions at the test. Additionally, after the 24-h delay, memory performance of infants in the nap condition was significantly higher than that of infants in the no-nap condition. This is the first experimental evidence to our knowledge for an enhancing role of sleep in the consolidation of declarative memories in the first year of life.

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Abstract: Human infants devote the majority of their time to sleeping. Yet, very little is known about the role of sleep in early memory processing. Here we test 6- and 12-month-old infants' declarative memory for novel actions after a 4-hour (Exp. 1) and 24-hour delay (Exp. 2). Infants in a nap condition took an extended nap (> 29 min.) within 4 hours after learning whereas infants in a no-nap condition did not. A comparison to age-matched control groups revealed that after both delays, only infants who had napped after learning remembered the target actions at the test. Additionally, after the 24-hour delay, memory performance of infants in the nap condition was significantly higher than that of infants in the no-nap condition. This is the first experimental evidence for an enhancing role of sleep in the consolidation of declarative memories in the first year of life.

Significance statement: The potential benefits of infant sleep for memory processing are largely unexplored. Here we show evidence that having an extended nap (> 29 minutes) within 4 hours of learning helps 6- and 12-month-old infants to retain their memories for new behaviors across a 4- and 24-hour delay. This suggests that infants rely on frequent naps for the formation of long-term memories.

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Introduction

At a time in life when growth and development occur at an unparalleled rate, human infants spend the majority of their time asleep. The notion that "sleeping like a baby" is important for the developing organism might therefore sound like a truism. In fact, strikingly little is known about specific functions of sleep in the first year of life. In adult populations, sleep has enormous benefits for cognitive functioning, particularly for memory (1). Memories can be different in nature, depending on the underlying learning experiences. Commonly, declarative memories (i.e., memory for facts and events) are distinguished from nondeclarative memories (i.e., memory for habits and skills (2)). In adults, sleep has versatile effects on both memory systems (3). In addition to facilitating memory consolidation and thus helping adults to retain memories over time (4), "sleeping on it" enhances, for example, the obtainment of new insights into previously encountered problems (5) and the flexible connection of existing stores of knowledge (6). Thus, sleep has effects on the quality and the quantity of adult memories. Recently, research has shown that, unlike in adults, sleep seems especially valuable for declarative, rather than nondeclarative, memory consolidation in preschool- and school-aged children (7–11). Relatedly, children outclass adults in converting implicit to explicit knowledge (12). While there might be an overall beneficial effect of sleep for learning and memory throughout the life-span, the effects on specific memory processes thus appear to differ markedly depending on the developmental status of an individual.

Almost all studies on the association between sleep and cognitive development in infancy have been correlational in nature, making it impossible to infer causal relationships (e.g., (13, 14). To date, only two experimental investigations have considered the role of sleep for infant memory, and both have examined this within the context of language processing (15, 16). In these studies, taking an extended nap within 4 hours after having been exposed to

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auditory word-strings of an artificial language appeared to facilitate 15-month-old infants'
ability to extract the grammatical structure of that language. Thus, sleep seemed to change the
way infants processed novel information after learning i.e., the quality of infants' memories.
The beneficial effect of sleep occurred both after a 4-hour (15) and a 24-hour (16) retention
interval. Critically, however, it is not clear which form of memory underlies these effects
(17). Knowing which type of memory is measured when assessing effects of sleep on memory
in a certain developmental phase is vital. Otherwise, no general conclusion about the relation
between sleep and memory can be drawn beyond the specific task that was used in a study. A
further, completely unexplored, question refers to the effect of sleep on the quantity of
infants' memories. During their natural sleep-wake cycle, do infants remember more new
information if they sleep soon after learning it than if they stay awake after learning? Lastly,
the developmental origins of sleep-dependent memory are unknown. Does sleep already
contribute to memory consolidation in the first year of life?

Here we test in two experiments whether sleeping after learning facilitates 6- and 12-
month-old infants' declarative memory consolidation, using a well-established deferred
imitation paradigm (18–21). Deferred imitation procedures assess memory by presenting the
infant with a model who demonstrates a series of actions with objects, and measuring the
infant's ability to reproduce these actions after a delay (i.e., at test). Deferred imitation is a
widely recognized measure of nonverbal declarative memory (22–25). In Experiment 1, we
assessed memory after a 4-hour delay during which infants in a nap condition slept for at least
30 minutes uninterruptedly. A 4-hr delay was chosen as this interval has been successfully
used in previous studies (15, 16) and because the longest awake period for 6-month-old
infants is typically just over 4 hours (26). This delay ensured that infants in the nap conditions
were allowed sufficient time for their naps, even if they did not fall asleep immediately after
learning. Infants in the no-nap condition could realistically be expected to stay awake during
the interval, but were included if they napped for no more than 29 minutes during the

retention interval. In Experiment 2, we assessed memory after a 24-hour delay. Again, only infants in a nap condition slept for at least 30 minutes within 4 hours of learning. All infants had an extended period of sleep (i.e., during the night) before the test. In both experiments, memory for the target actions was inferred if infants in the experimental conditions produced a significantly higher number of target actions at test than infants in age-matched baseline control conditions who had not seen any demonstrations of the target actions prior to the test (see Fig. 1 for design and procedure). We hypothesized for both experiments that, if sleep facilitates memory consolidation, only those infants who slept after learning would exhibit retention of the target actions at the test.

Results

Experiment 1. In the nap condition, the infants slept an average of 106 min ($SEM = 6$) during the 4-hr delay. On average, infants fell asleep 47 min after the actigraph had been attached after the demonstration session (first visit) ($SEM = 4$). Their first sleep epoch lasted for 81 min on average ($SEM = 7$). Twenty-one infants in the no-nap condition slept briefly (i.e., < 30 min of uninterrupted sleep) during the retention interval, for an average of 16 min ($SEM = 2$). Their first sleep epoch started on average after 128 min ($SEM = 9$) and lasted for 16 min ($SEM = 2$). Due to individual differences in naturally scheduled nap times, the time of the test session for infants in the nap and no-nap condition ranged from 12:00 p.m. to 7:15 p.m., with a mean test time of 3:07 p.m. Mean test-time for the nap condition was 3:06 p.m. and mean test-time for the no-nap condition was 3:08 p. m. Across the nap and no-nap conditions, there was no significant relationship between time of test and the number of target actions imitated at the test, $r = 0.086$, $P = 0.451$.

To assess whether infants in the nap and no-nap conditions exhibited retention for the target actions, we conducted a 2 (Age: 6 months, 12 months) x 3 (Condition: nap, no-nap, baseline) ANOVA. There was a significant effect of condition, $F(2,114) = 6.770$, $P = 0.002$,

$n_p^2 = 0.106$ (nap condition: $M = 0.98$, $SD = 1.29$; no-nap condition: $M = 0.55$, $SD = 0.99$;

baseline condition: $M = 0.15$, $SD = 0.58$; see Tables S1, S2 for more detailed information on

imitation scores). Bonferroni post-hoc tests revealed that only infants in the nap condition

remembered the target actions at the test. These infants produced a significantly higher

number of target actions than infants in the baseline condition, $M_{diff} = 0.83$, $P = 0.001$, $d =$

0.83. In contrast, infants in the no-nap condition did not produce significantly more target

actions than infants in the baseline condition, $M_{diff} = 0.40$, $P = 0.231$, $d = 0.49$ (cf. Fig. 2, left

side). These infants, thus, did not remember the target actions. There was no difference in the

number of target actions produced between the nap and no-nap conditions, $M_{diff} = 0.43$, $P =$

0.182, $d = 0.37$. There were no age-related differences in imitation scores, $F(1,114) = 0.671$,

$P = 0.414$, $n_p^2 = 0.006$. Also, there was no interaction effect between age and condition,

$F(2,114) = 0.323$, $P = 0.725$, $n_p^2 = 0.006$. To control for potential effects of alertness or

tiredness on the spontaneous production of target actions, half of the infants in the baseline

control condition napped and the other half of infants did not nap before participating in the

test session. There were no differences in spontaneous production of the target actions

between infants who had napped and those who had not napped prior to the test session, $t(38)$

$= 0.541$, $P = 0.592$. Infants in the nap and no-nap condition were engaged with the task to a

similar degree at test (i.e., touched the puppet for a comparable length of time, $t(68.338) =$

0.230, $P = 0.818$). Furthermore, the latency to carry out the first target action (i.e., remove the

mitten) during test did not differ between infants in the nap and no-nap condition (nap

condition: $M = 35$ sec, $SD = 28$; no-nap condition: $M = 37$ sec, $SD = 31$), $t(24) = 0.238$, $P =$

0.814). Thus, it is unlikely that the differences in imitation scores could be attributed to

infants in the no-nap condition simply being tired at test. However, this possibility cannot be

ruled out entirely as infants in the no-nap group had been awake for an average of 165 min

($SEM = 16$) before test whereas infants in the nap condition had only been awake for an

average of 59 minutes ($SEM = 6$) before test, $t(50.338) = 6.114$, $P = .000$.

To explore potential relations between sleep variables and imitation scores within conditions, we correlated latency to first sleep, length of first sleep epoch, and total time spent asleep with infants' imitation scores. In the nap condition, none of these correlations were significant (latency: $r = -0.093$, $P = 0.566$; length first epoch: $r = 0.040$, $P = 0.804$; overall sleep: $r = 0.046$, $P = 0.778$). In the no-nap condition, none of these correlations were significant either. Only those infants who had slept during the retention interval were considered when correlating imitation scores with latency to first sleep and length of first sleep epoch with imitation scores (latency: $r = -0.209$, $P = 0.363$; length first epoch: $r = -0.266$, $P = 0.244$). All infants in the no-nap group were considered for the correlation between total time spent asleep and imitation scores, $r = -0.078$, $P = 0.631$.

As an inevitable consequence of embedding the demonstration and test sessions into infants' natural sleeping pattern (such that infants in the nap condition were scheduled to have a nap shortly after learning whereas infants in the no-nap condition were scheduled to stay awake), infants in the nap and no-nap conditions differed with respect to sleeping before learning as well as after learning. We evaluated the potential influence of prior sleep on the encoding of target actions in infants in the baseline condition (half of whom had slept within the 4 hrs preceding the session). These infants first received a test session which was identical to the test session conducted with infants in the nap and no-nap conditions. Immediately afterwards, they received demonstrations of the target actions. After the demonstrations, they were given an immediate test session where they had the opportunity to imitate the target actions. This immediate test was conducted to assess learning of the target actions. A 2 (Age group: 6 months, 12 months) x 2 (Group: Prior nap, No prior nap) x 2 (Phase: Test, Immediate imitation) ANOVA revealed a significant effect of Phase, $F(1, 30) = 10.673$, $P < 0.003$, $n_{\mathrm{p}}^{2} = 0.262$, indicating that the number of performed target actions increased significantly from test to immediate imitation. There were no other significant effects, biggest

$F(1, 30) = 1.107$, $P = 0.301$, $n_\text{p}^2 = 0.036$. Thus, infants learned the target actions equally well regardless of whether they had napped within 4 hrs before learning or not. This analysis confirmed that initial encoding of the target actions did not vary as a function of prior sleep in 6- and 12-month-olds and that, indeed, sleeping after rather than before learning determined memory performance at test.

Experiment 2. It is not possible to answer questions about the timing of sleep required for memory consolidation with the results from Experiment 1. It might be the case that sleep needs to start soon after learning. Alternatively, sleeping at any time, including periods that occur much later (e.g., at night) might be sufficient. We tested these alternatives in Experiment 2 where a 24-hour delay occurred between learning and test so that all infants had an extended period of sleep during the night prior to the test. Furthermore, by allowing recovery sleep, the potential problem of tiredness during test for infants in the no-nap condition could be reduced.

In the nap condition, the infants slept an average of 90 min ($SEM = 6$) within 4 hours after learning. On average, infants fell asleep 40 min after the actigraph had been attached ($SEM = 5$). Their first sleep epoch lasted for 69 min on average ($SEM = 7$). Twenty-three infants in the no-nap condition slept briefly (i.e., < 30 min of uninterrupted sleep) within 4 hours after learning, for an average of 15 min ($SEM = 1$). Their first sleep epoch started on average after 111 min ($SEM = 12$) and lasted for 14 min ($SEM = 2$). Time of the test session for infants in the nap and no-nap conditions ranged from 8:00 a.m. to 4.00 p.m. with a mean test time of 11.40 a.m. Mean test time for infants in the nap condition was 10.55 a.m. and mean test time for infants in the no-nap condition was 12.25 p.m. There was no significant relationship between time of test and the number of target actions imitated at the test, $r = -0.102$, $P = 0.424$. Infants in the nap and no-nap condition did not differ in their patterns of

night-time sleep (i.e., total sleep duration, total time awake at night, number of awakenings), $\Lambda = 0.926$, $F(3,60) = 1.597$, $P = 0.199$.

Consistent with Experiment 1, only infants in the nap condition remembered the target actions at the test, $F(2, 90) = 7.680$, $P = 0.001$, $n_p^2 = 0.146$ (nap condition: $M = 0.97$, $SD = 1.2$; no-nap condition: $M = 0.38$, $SD = 0.75$; baseline condition: $M = 0.13$, $SD = 0.55$), $M_{diff} = 0.84$, $P = .001$, $d = 0.9$. Infants in the no-nap condition did not exhibit retention of the target actions, $M_{diff} = 0.25$, $P = 0.784$, $d = 0.38$. Furthermore, infants in the nap condition performed a significantly higher number of target actions than infants in the no-nap condition, $M_{diff} = 0.59$, $P = 0.026$, $d = 0.59$ (Fig. 2, right side). There was no effect of age on imitation scores, $F(1,90) = 0.013$, $P = 0.908$, $n_p^2 = 0.000$. Also, there was no interaction effect between age and condition, $F(2,90) = 0.972$, $P = 0.382$, $n_p^2 = 0.021$. Infants in the nap and no-nap condition touched the puppet for a similar length of time during test, $t(62) = -0.569$, $P = 0.571$. Furthermore, the latency to carry out the first target action during test did not differ between infants in the nap and no-nap condition (nap condition: $M = 37$ sec, $SD = 28$; no-nap condition: $M = 36$ sec, $SD = 41$, $t(8.962) = 0.063$, $P = 0.951$. Infants in the no-nap group had been awake for an average of 48 min ($SEM = 10$) before the test. Infants in the nap condition had been awake for an average of 114 minutes ($SEM = 15$) before test, $t(56.180) = -3.661$, $P = 0.001$. Given that in this experiment infants in the no-nap condition had been awake for a significantly shorter time than infants in the nap condition, it is unlikely that the difference in imitation scores between the nap and no-nap group was due to infants in the no-nap group being tired at test.

To explore potential relations between sleep variables and imitation scores within conditions, we correlated latency to first sleep, length of first sleep epoch, and total time spent asleep within 4 hours after learning with infants' imitation scores. In the nap condition, the length of infants' first sleep epoch and the overall amount of sleep were negatively related to

infants' imitation scores (length first epoch: $r = -0.452$, $P = 0.009$; overall sleep: $r = -0.355$, $P = 0.046$). Latency to first sleep epoch was not significantly related to the imitation scores, $r = -0.079$, $P = 0.669$. In the no-nap condition, none of these correlations were significant. Only those infants who had slept during the 4 hours following learning interval were considered when correlating imitation scores with latency to first sleep and length of first sleep epoch with imitation scores (latency: $r = 0.206$, $P = 0.347$; length first epoch: $r = 0.029$, $P = 0.896$; overall sleep: $r = 0.170$, $P = 0.352$).

Lastly, we compared the imitation scores of the nap and no-nap conditions across experiments. There were no significant differences between the nap condition in Exp. 1 and Exp. 2, $t(70) = 0.021$, $P = 0.983$. There was no significant difference between the no-nap condition in Exp. 1 and Exp. 2, $t(69.861) = 0.855$, $P = 0.396$.

Discussion

The findings from Experiments 1 and 2 provide converging evidence for a causal role of sleep in declarative memory consolidation in the first year of life. Those infants who took an extended nap within 4 hours after learning exhibited retention of the target actions, and performance was almost identical after the 4- (Exp. 1) and 24-hr (Exp. 2) delay. Imitation scores of infants in the nap conditions were consistent with previous research involving 6- and 12-month-olds using the puppet task where infants reproduced 1 to 1.5 target actions after a 24-hr delay (18, 27). A lack of age-related differences in performance is common when testing these two age groups with this task (18, 27). Although infants in the nap condition in Experiment 2 spent a significant amount of time awake between learning and test, their retention of the target actions did not suffer in comparison to Experiment 1. This indicates that sleeping soon after learning safeguarded the memory traces against interference from subsequent incoming information during awake periods. Thus, sleep does not merely protect

newly formed memories by shielding an organism from other stimuli but orchestrates an active process of memory trace strengthening early in ontogeny.

Those infants who did not take a longer nap within 4 hours after learning failed to exhibit retention at the test. Hence, for sleep to benefit memory consolidation, infants needed to nap relatively soon after learning the novel information. This could be explained by the two-stage model of memory consolidation, according to which two separate stores work hand-in-hand to create long-lasting and stable memory traces (28, 29). One store, the hippocampus, allows fast learning and acts as an intermediate buffer which retains information for a limited time. The other store, the neocortex, learns at a slower rate and serves as a long-term store. New information is thought to be encoded in parallel in the hippocampus and neocortical networks. Consolidation during sleep is achieved by the repeated reactivation of recently acquired memory traces in the hippocampus which triggers parallel reactivation in the neocortical networks. This results in a continual redistribution and strengthening of representations in the neocortex. Possibly, the storage capacity of the hippocampus is still relatively limited in the developing brain (11), thus consolidation during sleep has to occur often in infancy .

Relatedly, younger infants, such as the age-groups in the present experiments, appear to weigh all aspects of a learning situation equally. Older infants prioritize central elements of a learning situation (e.g., the stimuli) over less important aspects (e.g., the room in which the learning takes place) (30). Infants who have not learned yet to filter out irrelevant information and who display exuberant learning (31) might burden their intermediate store with "unnecessary" information. As a presumable consequence, the store fills up relatively fast and information encoded at the beginning of a longer awake period gets discharged to free up space for more recent information before it can be consolidated during sleep.

There is some evidence to suggest that a small interval between learning and sleep may also be particularly beneficial for declarative memory consolidation in adults (32, 33). The

timing of sleep after learning might thus be an issue important throughout the life-span. It needs to be considered, however, that staying awake after learning subjects a newly acquired memory to interference or even forgetting, before sleep sets in. To conclusively determine which delays between learning and sleep onset are particularly beneficial for sleep-dependent memory consolidation in both infants and adults, it will be necessary to assess forgetting during the awake interval before sleep onset (34). One question in this context is whether there is a linear relationship between post-learning sleep delay and sleep-dependent memory consolidation i.e., the sooner sleep starts the better for memory consolidation. Alternatively, there might be time windows during which sleep needs to start but the exact time of sleep onset within these windows is irrelevant. The lack of a significant correlation between sleep delay and memory performance in the present experiments tentatively speaks for the latter idea, at least for infants.

Another open question refers to potential influences of circadian rhythm on sleep-dependent memory performance. In adult populations, napping at different times during the day (e.g., morning vs. afternoon (35) appears to be equally effective for memory consolidation (34)). In the present study, the lack of a significant correlation between time of day and imitation scores does not support the idea of sleep being differently effective for memory consolidation in infants during different times of the day. However, future studies could more rigorously test for circadian influences on sleep-dependent memory consolidation for example, by testing the effect of naps taken during different times of day in infants who regularly nap multiple times per day.

A logical next step for future studies will be to examine the mechanisms that underlie the facilitative role of sleep for memory consolidation in infants. In the present study, the correlations between length of sleep after learning and imitation scores were inconsistent across conditions and experiments. This could indicate that in addition to quantity, sleep

quality plays an important role in declarative memory consolidation in infants. In human adults, slow-wave-sleep is causally related to declarative memory consolidation (36). Whether this is the case in human infants as well will need to be determined by recording sleep physiology. In the first year of life, infants often enter sleep through REM sleep (37). Thus, very short naps might not suffice for memory consolidation because of a lack of, or a very small amount of, slow-wave sleep. In the present study, the crucial difference between the nap and no-nap condition might thus have been the opportunity for infants to spend sufficient time in slow wave sleep.

Materials and methods

Participants. The final sample of Exp. 1 consisted of sixty 6-month-old (M_{age} = *188* days, *SD* = *6*) and sixty 12-month-old (M_{age} = 172 days, *SD* = 6) healthy, full-term infants (60 females) who were recruited from local birth registers. Thirty-four additional infants were tested but not included in the final sample. Infants were primarily excluded because their sleeping behavior was inconsistent with their group assignment (n = 18). Consistent with previous research (15, 16), a nap was defined as 30 min or more of uninterrupted sleep in the 4-hr interval between demonstration and test session. Additional infants were excluded due to technical failure (n = 5), experimenter error (n = 7), failure to touch the puppet during test session (n = 1), fussiness (n = 2), and maternal interference (n = 1). Of the 40 infants in the baseline control condition, six infants were excluded from analysis of effects of prior sleep on learning due to fussiness (n = 2), experimenter error (n = 2), technical error (n = 1), and refusal to remain seated (n = 1).

The final sample of Exp. 2 consisted of forty-eight 6-month-old (M_{age} = 185 days, *SD* = 7) and forty-eight 12-month-old (M_{age} = 367 days, *SD* = 7) healthy, full-term infants (48 females) who were recruited from local birth registers. Twenty-two additional infants were tested but not included in the final sample. Infants were excluded because their sleeping

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behavior was inconsistent with their group assignment ($n = 9$) due to technical failure ($n = 5$), experimenter error ($n = 1$), maternal interference ($n = 4$), missing sleep log ($n =1$), refusal to remain seated during test ($n = 1$), parent present at test different from parent present at demonstration ($n = 1$).

Apparatus and Stimuli. Four different hand puppets were used (counterbalanced across groups and gender) which were specifically made for research purposes and not commercially available. The puppet stimuli have been successfully used in a number of deferred imitation studies with 6- and 12- month-old infants (18, 20, 27). There were two puppets resembling a mouse and two resembling a rabbit, one of each being grey and one pink. Each puppet was made of soft fur and about 30cm high. A removable felt mitten matching the color of the puppet was placed over each puppet's right hand. A jingle bell was secured to the inside of the mitten.

To record sleep/wake patterns, Micro Motionlogger® Actiwatches (Ambulatory Monitoring inc.) were used. Actigraphy is a valid and accurate method for assessing sleep-wake patterns in infants (38, 39). Actiwatches record activity and use an algorithm specifically developed for this purpose to establish whether the infant is awake or asleep for each minute an actiwatch is worn. Parents were additionally asked to keep a log of their infant's sleep which started with the infant's wake up time on the morning of the first visit and ended at the beginning of the experimenter's second visit. Since actigraphy is exclusively based on recording activity, the log also included information about the times when the parents removed the actiwatch and periods during which the infants experienced externally produced motion (e.g., being carried) which can result in inaccurate actiwatch data. For periods that parents reported their infant to have experienced externally produced motion or to have removed the actiwatch, the sleep log entries were used to calculate sleep duration. If only portions of a nap fell within periods of movement, we combined sleep log and actigraphy

data. For example, if a nap started in a period of external movement and continued after movement had terminated we used the log to establish the start time and actigraphy data to determine the end of a nap. We exclusively used the actigraphy data to calculate sleep duration outside of periods of external movement and removal of the actiwatch. Across both experiments, we recorded 160 naps during the 4 hr window of sleep in the nap and no-nap conditions. The logs were used in 43 cases (27%) i.e., at least one time point (beginning or end) of a nap was determined with the help of the log.

Design and Procedure. This research was approved by the Department of Psychology ethics review board at Ruhr-Universität Bochum. Informed parental consent was obtained prior to participation. In each experiment, infants were randomly assigned to a nap, no-nap, or baseline condition, with an equal number of females and males in each condition. Each infant was visited in their home twice. In Experiment 1, there were $n = 40$ infants in each of the three conditions (twenty 6- and twenty 12-month-olds) and there was a 4-hour delay between visits. In Experiment 2, there were $n = 32$ infants in each of the three conditions (sixteen 6- and sixteen 12-month-olds) and there was a 24-hour delay between visits. To identify a suitable time for the experimenter's visits in relation to each infant's natural sleep/wake cycle, caregivers were consulted. Infants in the nap condition participated in the demonstration session (first visit) shortly *before* they were naturally scheduled to have a nap and thus took a nap within 4 hours of the first visit. Infants in the no-nap condition participated in the demonstration session shortly *after* they had had a naturally scheduled nap and, therefore, did not take a nap within 4 hours of the first visit. Parents were instructed to abstain from keeping their infants awake for the study. Infants in the baseline control condition did not participate in the demonstration session during the first visit. However, like the infants in the other conditions, they were visited twice and received the actiwatch at the end of the first visit. Their spontaneous production of any of the target actions was assessed at test.

In Experiment 1, to test for potential effects of alertness or tiredness on spontaneous production of the target actions and on learning, half of the infants in the baseline control condition napped and the other half of infants did not nap before participating in the test session. As the spontaneous production of the target actions was not affected by sleep in Experiment 1, prior sleep was not manipulated in the baseline condition in Experiment 2.

Demonstration session (first visit). For the demonstration, the infant sat on their caregiver's knee and was held firmly by the hips. The experimenter knelt in front of the infant and demonstrated three target actions with the puppet, out of the infant's reach. First, the experimenter removed the mitten from the puppet's hand. Second, she shook the mitten three times, sounding the bell inside. Third, she replaced the mitten. Previous research has shown that 6-month-old infants require twice the number of demonstrations as 12-month-old infants to exhibit retention after a delay (18). Therefore, the 6-month-old infants received a total of six demonstrations of the target actions and the 12-month-old infants received a total of three demonstrations. The stimulus and the target actions were not verbally described or labeled. After the demonstrations, the puppet was immediately placed out of the infant's view.

Test session (second visit). The test session was identical for all groups. The bell inside the mitten was removed before the test session to avoid prompting memory retrieval. The infant sat on their caregiver's knee and the experimenter held the puppet within reach of the infant. Each infant was given 90 seconds to imitate the target actions after first touching the puppet. Production of the target actions was not verbally or physically prompted. All sessions were video-recorded.

Scoring: In both experiments, each infant could perform a maximum of three target actions (remove mitten, shake mitten, (attempt to) replace mitten). To score on "remove mitten," infants had to remove the mitten so that it was entirely detached from the puppet's hand. To score on "shake mitten," infants had to hold the mitten in either of their hands and

shake the mitten in a motion retracing itself. Simply moving the mitten in one direction did not count. To score on "(attempt to) replace mitten," infants had to hold the mitten in either of their hands and touch the puppet's right hand with the mitten. Infants also scored if they attempted to cover up the puppet's right hand with the mitten by placing the opening of the mitten on the puppet's right hand. The presence or absence of each of the three target actions was scored from the videotaped test session using the software INTERACT (Version 9, Mangold International GmbH, Arnstorf, Germany) which allows frame by frame analysis of video records. A second independent rater who was blind to the infants' group assignment coded 50% of the videos in each Experiment. In Experiment 1, inter-rater reliability was $\kappa =$ .98. In Experiment 2, inter-rater reliability was $\kappa = .95$.

Acknowledgements

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Figure Legends

Fig. 1: Schematic overview of design and procedure of Exp. 1 and 2. DI = Deferred imitation. The demonstration and test sessions were embedded into infants' naturally occurring sleeping patterns.

Fig. 2. Mean imitation scores in Exp. 1 (left side) and Exp. 2 (right side) as a function of condition. Error bars represent *SE* of *M*. * $P < 0.05$, ** $P < 0.01$

| Condition	First visit	Sleep within 4hrs after learning	Second visit
Nap (Exp. 1 & 2)	Demonstration DI Start actigraphy	≥ 30 min. of uninterrupted sleep →	Stop actigraphy Test DI
No-nap (Exp. 1 & 2)	Demonstration DI Start actigraphy	< 30 min of uninterrupted sleep →	Stop actigraphy Test DI
Baseline (Exp. 1)	Start actigraphy	50% of infants: ≥ 30 min of sleep 50% of infants: < 30 min of sleep →	Stop actigraphy Test DI Demonstration DI Immediate Imitation
Baseline (Exp. 2)	Start actigraphy	No manipulation of sleep →	Stop actigraphy Test DI
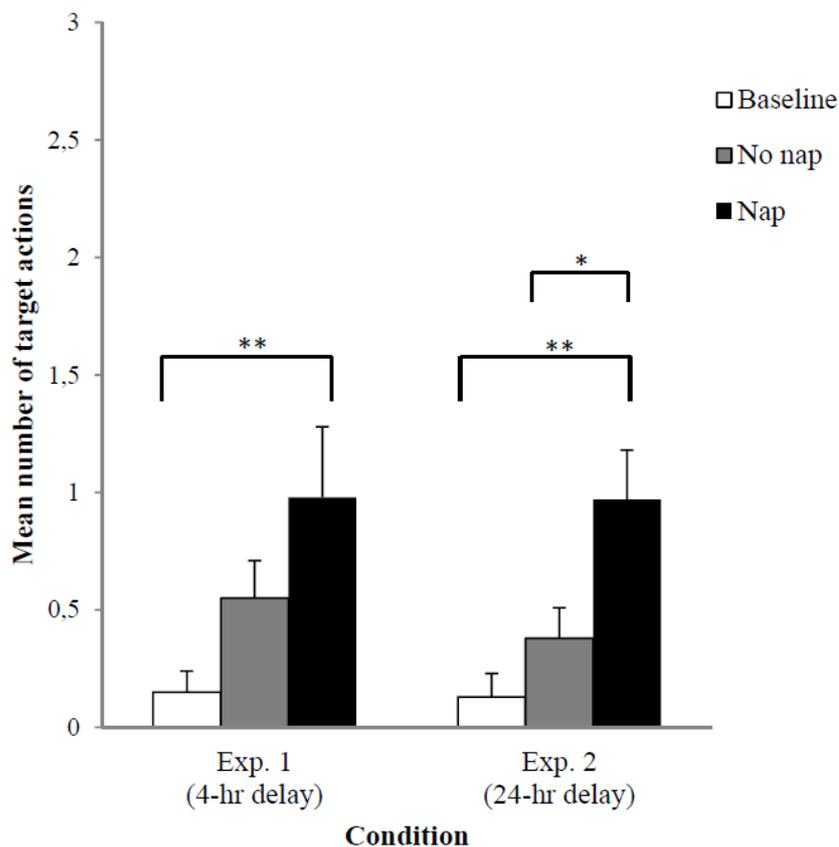
Table S1

Percentage of infants in the baseline, nap and no-nap condition who performed each of the

three target actions (remove, shake, replace) at test in Exp. 1 and 2.

Experiment	Condition	Remove	Shake	Replace
1 (4-hr delay)	Baseline	7.5	2.5	5
	Nap	40	27.5	30
	No-nap	25	10	20
2 (24-hr delay)	Baseline	6.25	3.13	3.13
	Nap	43.75	28.13	25
	No-nap	21.88	3.13	12.5

Table S2

Mean imitation scores (*SD*) and number of participants per condition and age-group for each experiment.

| | | Experiment 1 | | | | | | Experiment 2 | | | | | |
| | | Nap | | No-nap | | Baseline | | Nap | | No-nap | | Baseline | |
		n	*M (SD)*	*n*	*M (SD)*	*n*	*M (SD)*	*n*	*M (SD)*	*n*	*M (SD)*	*n*	*M (SD)*
	6 months	20	1 (1.34)	20	0.4 (0.82)	20	0.05 (0.22)	16	1.06 (1.34)	16	0.19 (0.54)	16	0.19 (0.75)
Age group	12 months	20	0.95 (1.28)	20	0.7 (1.13)	20	0.25 (0.79)	16	0.88 (1.01)	16	0.56 (0.89)	16	0.06 (0.25)