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Naps promote flexible memory retrieval in 12-month-old infants

Carolin Konrad[1], Sabine Seehagen[1][3], Silvia Schneider[1], & Jane S. Herbert[2]

[1] Ruhr-Universität Bochum, Bochum, Germany

[2] University of Sheffield, Sheffield, UK

[3] Current Affiliation: University of Waikato, Hamilton, New Zealand

Corresponding author:

Carolin Konrad

Ruhr-Universität Bochum

Department of Psychology

Massenbergstr. 9-13

44787 Bochum

Germany

Phone: + 49 (0)234 32 23128

Fax: + 49 (0)234 32 14435

Email: carolin.konrad@rub.de, sabine@waikato.ac.nz, silvia.schneider@rub.de,

J.S.Herbert@sheffield.ac.uk

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Flexibility in applying existing knowledge to similar cues is a corner stone of memory development in infants. Here, we examine the effect of sleep on the flexibility of memory retrieval using a deferred imitation paradigm. Forty-eight 12-month-old infants were randomly assigned to either a nap or a no-nap demonstration condition (scheduled around their natural daytime sleep schedule) or to a baseline control condition. In the demonstration conditions, infants watched an experimenter perform three target actions on a hand puppet. Immediately afterwards, infants were allowed to practice the target actions three times. In a test session 4-hours later, infants were given the opportunity to reproduce the actions with a novel hand puppet differing in color from the puppet used during the demonstration session. Only infants in the nap-condition performed significantly more target actions than infants in the baseline control condition. Furthermore, they were faster to carry out the first target action than infants in the no-nap condition. We conclude that sleep had a facilitative effect on infants' flexibility of memory retrieval.

Key words: memory, sleep, infancy, imitation, flexibility of retrieval

“Sleep on it” is a commonsense suggestion in situations where we try to resolve a complex problem or make an important decision. In adults, a large number of studies have shown that sleep is indeed beneficial for cognitive functioning, particularly for memory (for reviews, see Diekelmann & Born, 2010; Rasch & Born, 2013). Sleep not only facilitates the retention of recently learned information (Gais & Born, 2004) but can also produce qualitative changes in memory representations (Stickgold & Walker, 2013). For example, sleep helps adults to gain new insight into a hidden abstract rule of a previously encountered mathematical problem (Wagner, Gais, Haider, Verleger, & Born, 2004) and to connect recently encoded memories with existing stores of knowledge (Dumay & Gaskell, 2007; Ellenbogen, Hu, Payne, Titone, & Walker, 2007). Sleep can thus help adults to use their memories in a more flexible way.

Although sparsely studied, there is some evidence that sleep might also affect the speed of memory retrieval. In Wagner et al.’s (2004) study, while there was an overall effect of sleep on insight, not all participants responded this way. These “non-responders” profited from sleep in a different way: they were faster in solving the mathematical tasks with the rote procedure compared to participants who stayed awake. Thus, while sleep improved the probability of gaining insight, it did not deterministically help all participants to discover the hidden rule. Furthermore, in a study using a navigation task in a virtual maze, adults who took a brief nap after learning found their way through the maze faster and with fewer steps than adults who stayed awake for an equivalent amount of time (Wamsley, Tucker, Payne, & Stickgold, 2010).

In comparison to the adult literature, our understanding of sleep’s role for facilitating memory processing early in life is less complete. In a seminal study on memory reactivation in 3-month-olds, Fagen and Rovee-Collier (1983) determined that retention ratios on the mobile conjugate reinforcement paradigm increased as a function of time since reactivation, but also as a function of sleep duration during their 8 hour retention interval. In discussing their results, the authors raised important questions about the nature of the retrieval process and the overall quality (richness) of the memory representation across time. Despite broad interest over the intervening decades in the relationship between infant sleep and early memory abilities, only three studies have considered the potential benefits of sleep on early memory flexibility. These studies, all in the domain of language processing, suggest that sleep can change the quality of infant memories (Friedrich, Wilhelm, Born, & Friederici, 2015; Gomez, Bootzin, & Nadel, 2006; Hupbach, Gomez, Bootzin, & Nadel, 2009). In the studies by Gomez et al. (2006) and Hupbach et al. (2009), 15-month-old infants were familiarized to auditory word-strings of an artificial language that all followed the same grammatical rule in which the first word predicted the third one (e.g., 'pel' predicted 'jic'). Infants' reaction to the word-string dependencies they were familiarized with and to word-strings they were not familiar with (now 'pel' predicted 'rud') was tested in a head-turn preference paradigm after a retention interval. Infants who took an extended nap within 4 hours after familiarization showed a consistent preference for the type of word-strings that they heard during the very first trial of the test phase (familiar or unfamiliar word-strings): If the first word string they heard was familiar, they preferred the familiar dependencies in the following trials. If the first word string they heard was unfamiliar, they preferred the unfamiliar dependencies in the following trials. This behavior was observed both 4 and 24 hours later and was interpreted as the application of an abstract rule to the first word-string during the test phase (i.e., the dependency of the first and third word). Infants who did not nap within 4 hours of learning attended for significantly longer to the exact word-strings they had been familiarized with after a 4-hr delay, indicating retention (Gomez et al., 2006). They did not show retention after a 24-hour interval (Hupbach et al., 2009). At no time did infants in the no-nap condition appear to extract the grammatical rule of the artificial language. The authors concluded that a nap after learning facilitated abstraction in infants' language learning.

Recently, Friedrich et al. (2015) showed that sleep also serves semantic generalization in 9- to 16-month-old infants. In that study, event-related potentials revealed that only those infants who took a nap during a 1- to 2-hour retention interval were able to apply recently learned words for objects to new members of the same object category. Thus, sleep seems to facilitate the abstraction and generalization of infants' existing memories, at least in the domain of language processing. Whether similar effects of sleep are observable in infants' overt behavior is currently unknown.

In the present study we examined the effect of sleep on the flexibility of memory retrieval by 12-month-olds using the deferred imitation paradigm. This paradigm also provided us with the opportunity to assess whether sleep increases the speed of retrieval during infancy.

During the first years of life, there are marked developmental changes at all stages of memory processing: encoding, storage, and retrieval (for a review, see Hayne, 2004). In terms of encoding, studies with different methods such as visual recognition memory (VRM) (Hunter & Ames, 1988), mobile conjugate reinforcement paradigm (Davis & Rovee-Collier, 1983; Greco, Rovee-Collier, Hayne, Griesler, & Earley, 1986; Hill, Borovsky, & Rovee-Collier, 1988), and deferred imitation tasks (Barr, Dowden, & Hayne, 1996; Hayne, Boniface, & Barr, 2000) have consistently shown that infants encode new information faster with increasing age. In terms of storage, the duration of infants' memories gradually increases during the first years of life, a pattern which is again found across different paradigms (Hartshorn et al., 1998; Herbert & Hayne, 2000; Morgan & Hayne, 2011). In terms of retrieval, VRM, mobile conjugate reinforcement, and deferred imitation studies consistently find that with age, infants become increasingly more flexible at applying previously acquired knowledge to novel situations (for review, see Hayne, 2004). Being able to retrieve memories in the presence of cues that are slightly different from those encountered at encoding helps avoid unnecessary re-learning when potentially useful knowledge is already stored in memory (Jones & Herbert, 2006). At a young age, infants' memories are characterized by a high degree of specificity. For example, at 6 months of age even small changes in the learning context between encoding and retrieval (e.g., change of the room or immediate surroundings) can disrupt memory retrieval (Hayne, Boniface, & Barr, 2000; Learmonth, Lamberth, & Rovee-Collier, 2004; Robinson & Pascalis, 2004). With increasing age, changes in the context are better tolerated, but changes in aspects more closely associated with a learning task, such as changes in the stimuli (e.g., changes in color and form) or in the identity of a teacher (Learmonth, Lamberth, & Rovee-Collier, 2005) can still disrupt memory retrieval during the second year of life (Hayne et al., 2000; Hayne, Greco, Earley, Griesler, & Rovee-Collier, 1986; Hayne, MacDonald, & Barr, 1997; Herbert & Hayne, 2000). In sum, with increasing age infants encode information faster, remember for longer, and are able to cope with increasing dissimilarities between the learning and the retrieval context/stimuli.

Here, we use a deferred imitation procedure to test the effect of naps on the flexibility of memory retrieval. In a typical deferred imitation procedure, a model demonstrates novel actions to an infant during a demonstration session and the infant's ability to reproduce these target actions is assessed after a delay (e.g., Barr et al., 1996; Meltzoff, 1985). Memory for the target actions is inferred if infants in the demonstration condition(s) perform significantly more target actions at test than infants in a baseline control condition who have not seen any demonstrations of the target actions. Infants' ability to flexibly retrieve their memories is typically assessed by changing some attributes of the context and/or the stimuli between the demonstration and test session (e.g., using stimuli that are different in color or shape at test).

In addition to age, several factors occurring within and outside the testing situation have been shown to facilitate memory flexibility in deferred imitation tasks. Within the testing situation, providing infants with a distinct demonstration and test context (Jones & Herbert, 2008), using verbal cues to describe the event during the demonstration and test session (Herbert, 2011; Herbert & Hayne, 2000), and allowing infants to practice the target actions after the demonstration session (e.g., Hayne, Barr, & Herbert, 2003; Learmonth et al., 2005) enhances memory flexibility. Practice, for example, is thought to facilitate the accessibility of the memory for the target action by affording an enriched encoding opportunity for the infant (Hayne et al., 2003). This enriched encoding includes additional information about characteristics of the stimuli (e.g., texture, weight) and the target actions. Thus, the representation infants can form during a practice session involves more modalities than during a demonstration session where the infant only watches the target actions.

A few studies have also investigated experiences occurring outside of the deferred imitation testing situation that facilitate the flexibility of memory retrieval. Although these experiences cannot be manipulated within an experimental setting, infants who are growing up in a bilingual environment (Brito & Barr, 2012, 2014), or who have started to independently explore the world through the onset of crawling (Herbert, Gross, & Hayne, 2007) show enhanced memory flexibility. In the present study we consider whether sleep, a variable that can be manipulated and that improves adults' ability to resolve complex problems, might also enhance the flexibility of memory retrieval in infants.

There is initial evidence within the deferred imitation literature of a relationship between sleep and two aspects of memory processing, namely, encoding and storage. In terms of encoding, Konrad, Herbert, Schneider, and Seehagen (2016) recently found that the sleep quality during the prior night was related to 6-month-old, but not 12-month-old, infants' immediate imitation of a sequence of target actions demonstrated on a puppet (remove, shake, and replace the puppet's mitten; Barr et al., 1996). Using the same puppet task, Seehagen, Konrad, Herbert and Schneider (2015) found that sleep strengthens the memory for specific target actions in 6-

and 12-month-old infants. In that study, only those infants who took an extended nap within 4 hours after the demonstration exhibited retention of the target actions after a 4- or 24-hour delay. Thus, deferred imitation studies have revealed facilitative effects of overnight sleep and daytime naps on the encoding and storage of information during the first year of life. It remains unclear whether sleep has a similar facilitative impact on infants' memory retrieval in the deferred imitation task.

In the puppet imitation task, infants become progressively able to retrieve their memory across a change of the stimulus' color between encoding and retrieval when they are aged between 12- and 18-months (Hayne et al., 1997). Therefore, in the present study we examined the effect of daytime sleep on the flexible retrieval of memory across a stimulus change at 12-months of age. We hypothesized that only those infants who napped after the demonstration would exhibit flexible memory retrieval when tested with a puppet different in color, while infants who did not nap would not flexibly retrieve their memory. Our second question was whether facilitated accessibility would become evident in the speed of memory retrieval as well. In deferred imitation task this can be measured by the latency to perform the first target action during the test session. We predicted that, on average, infants who napped after the demonstration would retrieve their memories faster than infants who did not nap (Wagner et al., 2004).

Method

Participants

The final sample consisted of forty-eight 12-month-old (M_{age} = 365 days, *SD* = 8 days) healthy, full-term infants (50 % female) who were recruited from local birth registers. Eight additional infants were tested but not included in the final sample due to: sleep during the retention interval in the no-nap condition (*n* = 2), no sleep during the retention interval in the nap condition (*n* = 2), technical failure (*n* = 1), experimenter error (*n* = 1), failure to touch the puppet during practice trials (*n* = 1), and developmental delay (*n* = 1). Since previous studies showed that advances in locomotor abilities and being bilingual can facilitate flexible memory retrieval (Brito & Barr, 2012, 2014; Herbert et al., 2007), we assessed whether infants were already able to walk and whether they were growing up in a bilingual environment. Five infants in each experimental condition (nap and no-nap) were able to walk alone at the time of test (at least 1 meter without using hands for support). Two infants in the no-nap condition were bilingual.

Apparatus

Stimuli. Four different hand puppets were used in the present study, two resembling a mouse and two resembling a rabbit, one of each being gray and one pink (counterbalanced within and across conditions). The puppets were made out of soft fur and were about 30 cm high. They were specifically made for research purposes and not commercially available. 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. The puppet stimuli have been widely used in deferred imitation studies with 12-month-old infants (e.g., Barr et al., 1996; Hayne et al., 1997; Jones & Herbert, 2008; Konrad et al., 2016; Seehagen et al., 2015).

Sleep records. Infants' sleep/wake behavior was assessed using Mircro Motionlogger® Actiwatches (Ambulatory Monitoring inc.) which are similar in appearance to a wristwatch and record the frequency of movement. The validated Sadeh actigraph scoring algorithm (Sadeh, Sharkey, & Carskadon, 1994) was used to estimate for each minute whether the infant was awake or asleep. Actigraphy is a valid and accurate method for assessing sleep-wake patterns in infants (e.g., Müller, Hemmi, Wilhelm, Barr, & Schneider, 2011; Sadeh, Acebo, Seifer, Aytur, & Carskadon, 1995). Parents were additionally asked to keep a log of their infant's sleep for the duration of the retention interval and to indicate the sleep times before learning. Parents noted periods during which they removed the actiwatch (e.g., while changing diapers) and periods during which the infant was moved externally (e.g., being pushed in a pram or stroller) as such instances can lead to artifacts in the actigraph 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. The sleep log was also used to calculate the duration over which the infant had been awake before learning. Otherwise we used the actigraphy data to calculate sleep duration in the nap condition and to confirm the absence of sleep in the no-nap condition.

Design and Procedure

Infants were randomly assigned to one of the experimental conditions (nap or no-nap) or a baseline control condition (each *n* = 16, 50 % females per condition) as they became available. Infants in the experimental conditions were visited in their home twice, with a 4-hour delay between visits. The delay was chosen in accordance with previous studies investigating sleep-dependent memory processing in infants (Gomez et al., 2006; Hupbach et al., 2009; Seehagen et al., 2015). During the first visit (demonstration and practice session), a female experimenter demonstrated the three target actions with one puppet to the infant and then allowed the infant to practice the target actions. During the second visit (test session), the infants were presented with a novel puppet that had the same form but differed in color from the puppet they had seen during the first visit (e.g., grey mouse at the demonstration and practice session and pink mouse at the test session).

A practice procedure was used during the demonstration session due to the results of pilot testing with *N* = 19 twelve-month-old infants (*n* = 18 in a nap condition, *n* = 1 in a no-nap condition). The pilot testing was conducted preceding the main study because there is no published data available involving infants tested with a color change in the puppet after a 4 hour retention interval. We conducted pilot testing primarily with infants in the nap condition since this group were expected to show a higher degree of flexibility of memory retrieval and we sought to ensure that the task was not too difficult for this age-group per se. Pilot testing showed that all infants failed to exhibit retention of the target action 4 hours later without a practice session (all infants had an imitation score of 0). A practice procedure was thus implemented to provide infants with a richer encoding opportunity.

Infants in the nap condition were first visited shortly *before* they were naturally scheduled to have a nap within the following 4 hours. Infants in the no-nap condition were first visited *after* they had had a naturally scheduled nap and were, therefore, not expected to take a nap within the following 4 hours. To ensure that infants in the no-nap condition were not sleep deprived at test, parents were instructed not to deliberately try to keep their infant awake. If an infant in the no-nap condition fell asleep, they were excluded from the study. Previous research has shown that the timing of prior daytime naps does not influence the initial learning of target actions in the puppet task (Seehagen et al., 2015). In the demonstration conditions, the actiwatch was attached to each infant's left ankle at the end of the first visit and removed at the beginning of the second visit.

Infants in the baseline control condition did not participate in a demonstration session. They only participated in a test session where they were allowed to interact with one of the puppets to assess their spontaneous production of any of the target actions. Their sleeping behavior prior to the baseline session was not varied as a previous study showed that sleep versus wakefulness in the preceding 4 hours does not affect infants' baseline performance in the puppet task (Seehagen et al., 2015).

Demonstration and practice session. During the demonstration and practice session, the infant sat on their parent's lap and was held firmly by the hips. The experimenter knelt in front of the infant and demonstrated three target actions with one puppet, out of the infant's reach: (1) removing the mitten from the puppet's hand, (2) shaking the mitten three times, making the bell ring, and (3) replacing the mitten. This sequence of actions was repeated two more times and lasted a total of approximately 30 s. The experimenter did not describe or label the puppet or the target actions. Immediately after the demonstrations, the puppet was held within reach of the infant and he or she had the opportunity to practice the target actions three times. To ensure that all infants in the demonstration groups had similar experiences with stimuli, a three-step protocol was followed during the practice phase. If the infant did not remove the mitten during a practice trial, the experimenter first pointed to the mitten. If the infant then did not remove the mitten, the experimenter removed the mitten half way off the puppet's hand. If the infant still did not remove the mitten, the experimenter removed the mitten and gave it to the infant. This procedure was the same during all three practice trials and ensured that all infants saw the mitten being removed three times during the practice trials and that each infant had a similar physical experience with the mitten. The practice session lasted a total of approximately 2 min. The puppet was then removed from the infant's sight.

Test session. Before the test session, the bell inside the mitten was removed to avoid prompting memory retrieval (e.g., Barr, Vieira, & Rovee-Collier, 2001; Hayne et al., 1997). The infant sat on their parent's lap and the experimenter held the novel puppet within reach of the infant. Each infant was given 90 s to interact with the puppet from the time they first touched the puppet. The experimenter did not verbally or physically prompt the production of the target actions.

Coding

All sessions were video-recorded from the right hand side of the experimenter. The videotaped practice and test sessions were scored for the presence of any target actions using the software INTERACT (Version 9, Mangold International GmbH, Arnstorf, Germany). For the practice session, an infant received a practice score between 0 and 9. In each practice trial, infants received a score from 0 to 1 for the removal of the mitten (1 point for removal without any help of the experimenter; 0.66 points for removal after the experimenter had pointed to the mitten; 0.33 points for removal after the experimenter had removed the mitten half way; and 0 points for no removal, that is if the experimenter gave the mitten to the infant). One point each for shaking and replacing the mitten was added to this score per practice trial. For one infant in the nap-group, there was a technical failure for the video recording of the practice session who thus had to be excluded from the practice session analyses.

For the test session, the latency to first touch the puppet (from when the puppet was within reach until the infant first touched it) and to remove the mitten (from the first touch of the puppet until the mitten was completely removed from the puppet's hand) and the number of target actions produced were coded. Each infant received an imitation score from 0 to 3: One point was given for the removal of the mitten, one point for shaking (a motion retracting itself), one point for replacing or attempt to replace the mitten on the right hand of the puppet. The order in which the target actions were carried out was not relevant for allocating points. A second independent coder who was blind to the hypotheses of the study and the infants' group assignment coded 50% of the test session videos. Inter-rater reliability for the target actions was very good, kappa = .94. Inter-rater reliabilities using intraclass correlation coefficients for the latency to first touch the puppet and the latency to remove the mitten were very good, $r = .97$, and perfect $r = 1$.

Results

Sleep Parameters

In the nap condition, infants slept for an average of 86 minutes (*SD* = 44 min; range = 42 min to 176 min) in total and took an average of 1.25 (*SD* = 0.58) naps during the retention interval. The first nap lasted for an average of 76 minutes (*SD* = 41 min). The delay between the end of the practice session and the first nap was 73 minutes (*SD* = 45 min) on average. The actigraph data were used to determine sleep duration for all but two naps, which occurred during external movement. Due to individual differences in sleeping patterns, the time of day the test session was conducted in the experimental conditions ranged from 12:00 to 17:00. Mean test time in the nap condition was 14:13, in the no-nap condition 16:11, and in the baseline control condition 10:43. Time of test differed significantly between all conditions, $F(2, 45) = 25.51$, $p < .001$, $\eta_p^2 = .541$. However, mean imitation scores in the experimental conditions were not related to test time, $r = -.023$, $p = .901$. The average time an infant was awake for before the demonstration and practice session was 140 minutes (*SD* = 84 min) in the nap condition and 57 minutes (*SD* = 53 min) in the no-nap-condition. Infants were not woken up from sleep for the demonstration/practice session. Infants in the nap condition had been awake for 69 minutes (*SD* = 46 min) before the test session, while infants in the no-nap condition had been awake for 276 minutes (*SD* = 50 min) before the test session. Duration of wakefulness before the test session was not related to imitation scores in the nap ($r = .28$, $p = .295$) or in the no-nap condition ($r = .09$, $p = .745$).

Mean imitation scores in the nap group did not significantly correlate with sleep duration of the first nap ($r = -.44$, $p = .064$), total sleep duration ($r = -.15$, $p = .582$), or delay between demonstration session and onset of the first nap ($r = -.25$, $p = .353$). There was a significant positive correlation between the number of naps and the mean imitation score, $r = .56$, $p = .025$. Speed of memory retrieval (i.e., latency to remove the mitten) did not correlate with any of the sleep parameters, biggest $r = -.31$, $p = .39$.

--- Insert Table 1 about here ---

Practice Session

In each experimental condition, eleven infants did not remove the mitten during the first practice trial without help, meaning that the three-step protocol for removal was used. For the second trial, seven infants in each condition needed the three-step protocol. In the third practice trial, for five infants in the no-nap and eleven infants in the nap condition the protocol was used. There was no significant difference in the practice scores (see Table 1) between infants in the nap and the no-nap conditions, $t(29) = 1.11$, $p = .277$, $d = 0.38$, indicating that infants in both experimental conditions learned the target actions equally well. Furthermore, there were no significant correlations between the practice score and the number of target actions performed at test session in the nap ($r = .39$, $p = .129$) or no-nap condition ($r = .15$, $p = .587$). Thus, variations in the practice scores did not explain imitation scores at test. There was no difference in latency to first touch the puppet during the test session (see Table 1) between conditions, $F(2, 45) = 0.18$, $p = .84$, $\eta_p^2 = .008$, suggesting that infants in all conditions were equally motivated to interact with the puppet.

Main Analyses

Flexibility of memory retrieval. Infants in the nap condition had a mean imitation score of 1.31 (SD = 1.40), infants in the no-nap condition had a mean imitation score of 0.69 (SD = 0.87), and infants in the baseline control conditions a mean imitation score of 0.38 (SD = 0.81) (see Figure 1). To assess whether there were differences in imitation scores between conditions, a one-way ANOVA was conducted. There was a significant main effect of condition, $F(2, 45) = 3.24$, $p = .048$, $\eta_p^2 = .126$. Bonferroni post-hoc tests indicated that there was no significant difference in imitation scores between infants in the nap and no-nap condition, $M_{diff} = .63$, $p = .308$, $d = .55$. However, in deferred imitation studies, memory is inferred if the imitation score in the demonstration conditions exceeds the score of infants in the baseline control condition (see Meltzoff, 1985; Hayne, 2004). Bonferroni post-hoc test revealed that only infants in the nap condition exhibited memory flexibility, performing significantly more target actions at test than infants in the baseline control condition, $M_{\text{diff}} = .94$, $p = .048$, $d = .85$. In contrast, infants in the no-nap condition did not perform a significantly more target actions than infants in the baseline control condition, $M_{diff} = .31$, $p = 1.0$, $d = .38$.

To ensure that these results were not merely reflecting some infants failing to encode the target actions during the demonstration and practice session, we conducted further analyses with only those infants in the nap and no-nap condition who showed some evidence of encoding. For this purpose, we next considered only the data from those infants who had a practice score bigger than 0. Applying this criterion, infants in the nap condition ($n = 13$) had a mean imitation score of 1.54 ($SD = 1.45$), infants in the no-nap condition ($n = 15$) had a mean imitation score of 0.73 ($SD = 0.88$). A one-way ANOVA revealed that there was a significant main effect of condition, $F(2, 41) = 4.45$, $p = .018$, $\eta_p^2 = .178$. Bonferroni post-hoc test revealed that only infants in the nap condition performed a significantly more target actions at test than infants in the baseline control condition, $M_{\text{diff}} = -1.16$, $p = .016$, $d = 1.05$. In contrast, infants in the no-nap condition did not perform significantly more target actions than infants in the baseline control condition, $M_{diff} = -.36$, $p = 1.0$, $d = .45$. There was no significant difference in imitation scores between infants in the nap and no-nap condition, $M_{diff} = .81$, $p = .154$, $d = .70$.

Speed of memory retrieval. To examine whether sleep affected the speed of memory retrieval in the demonstration conditions, a one-tailed Mann-Whitney-U test was conducted for the latency to produce the first target action during the test session. Table 1 displays number of infants who removed the mitten during the test session and the mean latency of the action. Although a similar number of infants in both conditions successfully removed the mitten ($n = 9$ in the nap condition, $n = 7$ in the no-nap condition), infants in the nap condition (*Mdn* = 1.96) did so faster than infants in the no-nap condition (*Mdn* = 22.63), $U = 13$, $z = -1.96$, $p = .025$, $r = -0.49$, indicating a facilitative effect of sleep on the speed of memory retrieval. This difference remains significant even when only including those infants who had a practice score above 0, $U = 8$, $z = -2.32$, $p = .011$, $r = -0.55$.

--- Insert Figure 1 about here ---

Discussion

The present study suggests that post-learning naps promote flexibility of memory retrieval in infants. Only infants who took a nap during the retention interval performed more target actions at test than infants in the baseline control condition, revealing that they were able to generalize their knowledge from one stimulus to another that differed in color. In contrast, infants who did not nap failed to perform significantly more target actions at test than infants in the baseline control condition. These results are in line with the findings of Gomez et al. (2006) and Hupbach et al. (2009), and Friedrich et al. (2015) who found an effect of napping on abstraction and generalization of word meanings in infants. The effect is unlikely to be due to differences in the initial learning of the target actions between the nap and the no-nap condition. Seehagen et al. (2015) found that 6- and 12-month-old infants who either had or had not taken a longer nap within 4-hours preceding participation in an imitation task learned novel actions equally well. In addition, in the present study there were no differences in the amount of practice of the target actions after the demonstrations between nap and no-nap condition, and the results were unchanged even after excluding those infants who had a practice score of 0. The nap and the no-nap condition did not differ significantly in imitation scores.

In deferred imitation procedures, memory is inferred if, at test, infants in the experimental condition(s) perform significantly more target actions than infants in the baseline control condition (cf. Hayne, 2004). Following this approach, the results of the present study suggest that infants in the nap condition successfully retrieved their memory about the puppet and its affordances which enabled them to imitate the target actions. In contrast, infants in the no-nap condition failed to retrieve the memory for the puppet and its affordances which prevented them from imitating the target actions. It seems difficult to account for this pattern of results without acknowledging that sleep had an effect on flexibility of memory retrieval in our sample. Nevertheless, the results would be even more compelling if there was a statistical difference in the mean number of imitated target actions between the nap and no-nap condition. Interestingly, in a prior study on sleep-dependent memory consolidation using the same puppet task (Seehagen et al., 2015) such a difference was only found when infants were tested after a 24-hr but not after a 4-hr delay. After the 4hr delay, there was a very similar pattern of results as in the present study. That is, infants in the nap condition exhibited memory for the target actions, as indicated by a significant difference between their mean imitation scores and that of infants in the baseline control condition. In contrast, infants in the no-nap control condition did not exhibit memory for the target actions namely, they did not perform more target actions at test than infants in the baseline control condition. Hence we suggest that in the paradigm used in the present study, a significant difference in imitation scores between the nap and no-nap condition might also emerge after a 24-hr delay. In other words, the magnitude of sleep effects on the flexibility of memory retrieval will potentially increase over longer retention intervals. This prediction would be in line with the observations of Fagen and Rovee-Collier (1983) regarding the relationship between time and sleep duration on infant memory.

There are at least two explanations for how infants' memory for the target actions could have been processed during sleep, which are not mutually exclusive. According to the active consolidation hypothesis, memory for the target actions could become integrated into a network of related representations through a process of active replay of memories during sleep (Diekelmann & Born, 2010). During sleep, the still labile memories that were recently encoded in hippocampal and cortical networks are strengthened and formed into more stable representations (Feld & Diekelmann, 2015; Frankland & Bontempi, 2005). Specifically, the memories are thought to become integrated into cortical networks of existing related knowledge through the reactivation in the hippocampal-neocortical network (Frankland & Bontempi, 2005). In the present study, after consolidation during sleep, the memories for the target actions could have been more easily accessible because infants were now able to use a wider range of retrieval cues through the original memory's new connections with related concepts (e.g., other types of puppets, previous memories of shaking objects; Eichenbaum, Otto, & Cohen, 1994). Presumably, this facilitated accessibility is also reflected in the speed of memory retrieval in our study. From this perspective, sleep might have increased the speed of recall for infants in the nap condition by making the memory more easily accessible.

A second explanation for the present results could be that sleep does not uniformly consolidate all recently encoded information, as stated in the selective memory consolidation hypothesis (Stickgold & Walker, 2013). From this perspective, only those memories that are relevant for the organism should be kept to allow optimal functioning. It is thus important to distinguish between relevant and irrelevant memories and to only transfer relevant information into long-term memory (Stickgold & Walker, 2013). From this view, infants who napped may have selectively consolidated the memory of the target actions during sleep. To identify and retain the relevant memories in the demonstration and practice phase of the present study, the infant needed to select the most important information from the various inputs occurring during encoding, such as the exact color and features of the hand puppet, the room the task took place in, the experimenter conducting the demonstrations, the target actions. Presumably, only the infants who napped within the retention interval were able to achieve this differentiation and thus to retain the most relevant information, which is how to perform the target actions. The representation of the target actions was presumably strengthened during sleep so that retrieval could occur at a faster rate in the nap condition. From this perspective, infants who did not nap might not have been able to retrieve the relevant memory because it was bound to other memories (e.g., color and texture of the puppet) which were irrelevant for this test and could not serve as retrieval cues. This explanation is speculative at this point and the mechanisms that are involved in selective memory consolidation still remain unclear (Stickgold & Walker, 2013).

Whether memory storage (as in Seehagen et al., 2015) and flexibility of memory retrieval are facilitated by different processes during sleep, and whether one process is more facilitated by sleep than the other, remains to be determined. Nonetheless, comparing the mean imitation scores of the nap and the no-nap condition of the present study with the mean imitation scores of the respective conditions from Seehagen et al. (2015), it seems that the effect of sleep is more pronounced for the more challenging generalization task, resulting in numerically larger differences between the nap and no-nap conditions.

It should be noted that the present results could be alternatively explained by (partly) attributing them to a negative effect of fatigue instead of positive effect of sleep. It is possible that tiredness in infants in the no-nap condition at the time of test contributed to the differences in the speed of memory retrieval. In line with that explanation, it is possible that tiredness did not affect the infants' general motivation to interact with the puppet (as visible in the non-significant difference between the latency to touch the puppet), but specifically impaired higher level cognitive processes (i.e., to retrieve the memory of the observed target actions and to apply the memory to the new puppet). Studies with school-aged children and adults revealed that sleep restriction affected particularly complex high-level cognitive tasks, while performance on low-level cognitive tasks was not impaired (Biggs et al., 2010; Gomez et al., 2011; Randazzo, Muehlbach, Schweitzer, & Walsh, 1998). On the other hand, as 12-month-old infants typically take a mean of 1.53 naps per day (Sadeh, Mindell, Luedtke, & Wiegand, 2009), it is in their normal rhythm to stay awake for 4 hours (Jacklin, Snow, Gahart, & Maccoby, 1980; Weissbluth, 1995). Thus, the effects found in the present study are rooted in infants' normal routine and thus have relevance for understanding their everyday cognitive functioning. To rule out all possible effects of tiredness in the no-nap condition at test and to examine how stable the sleep-dependent effect is, further studies could be conducted with a 24-hour delay where all infants have recovery sleep between learning and test.

There was a significant positive relation between the number of naps during the retention interval and imitation scores, suggesting that infants rely on frequent napping for memory consolidation. Findings from other studies regarding relations between sleep parameters and memory performance have been somewhat inconsistent. Seehagen et al. (2015) found negative correlations between the length of the first sleep as well as overall sleep duration and imitation scores in the nap condition in Experiment 2, while there were no such associations in Experiment 1. In contrast, the study by Fagen and Rovee-Collier (1983) reported a positive relation between the amount of sleep during the retention interval and memory retrieval in 3-month-old infants, using the mobile conjugate reinforcement paradigm. Lukowski and Milojevich (2013) also found a positive association between the usual nap duration and generalization across cues in 15-month-old infants using a correlational design. Together, these findings illustrate that naps are crucial for the developing memory in infants, but more research is needed to answer the question which frequency and duration of naps is most beneficial for different memory processes in infants.

Obtaining insights into the factors influencing memory and cognitive development in infants is important for understanding later developmental outcomes. Despite relatively detailed knowledge about the benefit of sleep for cognitive functioning in adult populations, the origins of this relationship remain largely unclear. One reason for this lack of research, especially in the emerging field of experimental sleep research with infants, is that investigators are faced with several methodological challenges (Lukowski & Bell, 2015). For example, when planning a study, the infant's frequent daytime napping and their rapid development of sleep consolidation in the first year of life have to be kept in mind. Taking into consideration the infant's individual sleep-wake rhythm and the large variance in sleep durations and frequencies creates major challenges in experimental designs and limits the choice of, for example, the length of retention intervals and the maximum time an infant stays awake. Furthermore, sleep deprivation studies are difficult with infants for ethical and practical reasons. As Lukowski and Bell (2015, p.186) put it: "Creativity and ingenuity are necessary to identify ways in which daytime naps and nighttime sleep might be modified so as to examine effects on daytime behavior". The way in which cognition is measured in these studies is also crucial in order to determine the mechanisms underlying any difference between sleep and non-sleep conditions. By utilizing the deferred imitation procedure, a versatile and ecologically valid method for assessing memory in infants and the impact of early experiences on cognition is available (Barr & Hayne, 2003; Rovee-Collier, Hayne, & Colombo, 2001; Heimann & Meltzoff, 1996; for a review, see Hayne, 2004). Capitalizing on infants' natural tendency to copy other people's actions, the present study shows that a well-timed daytime sleep can promote flexible memory retrieval even during infancy. This effect of sleep was not only reflected in the mean number of actions retrieved compared to the baseline control condition, but also in the speed of memory retrieval.

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Tables

Table 1

Condition	Practice score *M* (*SD*)	Latency to first touch during test session in s *M* (*SD*)	Latency to remove mitten during test session in s *M* (*SD*)
Nap	3.3 (2.4)	3.1 (2.9)	8.4 (14.7)
n	16	16	9
No-nap	4.2 (2.3)	3.9 (4.8)	31.8 (27.4)
n	15	16	7
Baseline	-	3.8 (4.9)	45.7 (22.6)
n		16	3

Figures

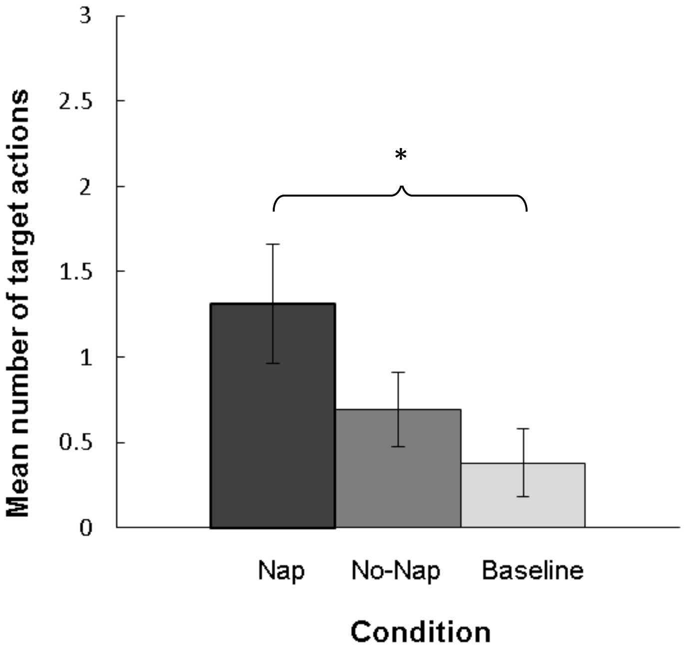

Figure 1.

Captions

Table 1

Means and Standard Deviations for Interaction Behavior as a Function of Experimental Condition.

Figure 1. Mean Number of Target Actions for each Condition. Error Bars represent SE of M.

* $P < 0.05$