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Abstract

Research with adults has shown that a person’s internal context, or state, influences how memory functions. This factor is rarely considered in research on infant memory, in part because of the practical and ethical difficulties of manipulating these variables in infants. In this article, we argue that models of infant memory will remain limited in scope and accuracy if the internal context of participants is not considered. As a case in point, we present emerging literature on sleep-dependent memory. Our review shows that for infants, timely sleep after a learning experience helps them retain and further process new memories. Studies need to explore the role of prior sleep for encoding, and to tease apart the contributions to infant memory of different types, features, and stages of sleep. We conclude that considering internal states, such as sleep, is necessary for developing a deeper understanding of early human memory.

Infants exhibit rapid changes in behavioral state (cf. Hayne, 2004): Within minutes, an infant can transition from interacting happily with an adult to crying irritably and back again. Although the reasons for these behavioral fluctuations vary, changes in infants' behavior are typically associated with changes in infants' internal context, or state. For example, whether an infant is tired or well-rested, hungry or satiated, calm or stressed can influence how he or she processes information about, and interacts with, the world. While this might sound like a truism that many parents confirm readily, studies on infant memory rarely consider how infants' state influences their performance. In this article, we review the emerging literature on infant sleep and memory to show how the fate of early memories can depend on infants' internal state at different stages of memory processing. We also call for studies that enrich our understanding of the role of sleep for infant memory and, more broadly, that increase the range of internal states considered in research on early memory.

Memory and Sleep

Stages and Systems of Memory

Chronologically, a memory is thought to develop in several distinct stages (cf. Walker & Stickgold, 2006). At the most basic level, three stages can be distinguished: encoding, consolidation/storage, and retrieval. Encoding occurs when encountering an experience or particular stimuli, causing a representation of this experience to form in the brain. The newly formed representation then undergoes a period of consolidation. Historically, consolidation has referred to a memory becoming increasingly resistant to interference over time. However, researchers are acknowledging increasingly that consolidation goes beyond mere preservation, for example, to include how new memory traces become embedded into existing knowledge networks and undergo qualitative changes so entire new structures of knowledge might evolve (Stickgold & Walker, 2013). Following consolidation, a memory might be available for retrieval so the episode or key features can be recalled. All three stages of memory processing exist across development, although speed and proficiency in each stage develop dramatically in infancy (see Hayne, 2004).

In terms of memory systems, the broadest and most widely acknowledged distinction refers to declarative versus nondeclarative memory (Squire, 1992). Declarative memories are consciously available memories for facts and events. Forming declarative memories depends heavily on brain structures in the medial temporal lobe (Squire & Zola-Morgan, 1991). In contrast, nondeclarative memories are thought to be nonconscious in nature and include, for example, memories for motor skills and habits. From a developmental perspective, controversy around the existence and ontogeny of different memory systems in infancy has been longstanding (cf. Gómez & Edgin, 2015; Hayne, 2004; Richmond & Nelson, 2007; Rovee-Collier, & Cuevas, 2009). Since infants cannot declare their memories, one way to determine the memory type measured in an infant task is to test whether adult amnesic patients with damage to their medial temporal lobes, particularly to the hippocampus, pass age-appropriate task variations. Amnesic patients with damage to the hippocampal formation fail deferred imitation tasks and visual recognition memory tasks, or at least show severe impairments (Adlam, Vargha-Khadem, Mishkin, & Haan, 2005; McDonough, Mandler, McKee, & Squire, 1995; McKee & Squire, 1993). Therefore, both deferred imitation and visual recognition tasks are considered measures of nonverbal declarative memory and are present within the first 6-12 months after birth in humans. However, for a variety of other infant memory tasks, it is less clear into which memory system they primarily tap.

Stages and Features of Sleep

In adults, sleep is broadly divided into rapid eye movement (REM) and non-REM (NREM) sleep, which alternate in 90-minute cycles throughout the night. NREM sleep has been further divided into substages 1 to 4, with higher numbers referring to increasingly deeper states of sleep. Stages 3 and 4 of NREM sleep are often referred to as slow-wave sleep (SWS).

In newborns, two different sleep states are commonly distinguished: quiet sleep and active sleep. From about 2 months, active sleep is referred to as REM sleep and quiet sleep is referred to as NREM sleep (Ednick et al., 2009). From about 8 to 11 weeks, sleep spindles are observable (cf. Grigg-Damberger et al., 2007); sleep spindles are “a group of rhythmic waves which progressively increase and then gradually decrease in amplitude” (Silber et al., 2007, p. 127). From about 4 to 4½ months, SWS starts to emerge (Ficca, Fagioli, & Salzarulo, 2000). Both SWS and sleep spindles play a critical role in sleep-dependent memory processing in adults (for a review, see Diekelmann & Born, 2010).

The Role of Sleep for Early Memory

It is well established that sleep after encoding facilitates the consolidation of both declarative and nondeclarative memories in human adults (Rasch & Born, 2013). A small but growing body of experimental research has revealed that post-learning sleep also facilitates the consolidation of recently encoded memories in infants across different paradigms (Friedrich, Wilhelm, Born, & Friederici, 2015; Horváth, Hannon, Ujma, Gombos, & Plunkett, 2018; Horváth, Myers, Foster, & Plunkett, 2015; Konrad, Herbert, Schneider, & Seehagen, 2016a; Seehagen, Konrad, Herbert, & Schneider, 2015). For example, in a visual recognition memory paradigm, 3-month-olds were repeatedly shown a cartoon-style face on a screen until their attention declined below a predefined criterion. At test 1 to 2 hours later, researchers assessed the infants’ visual attention to the habituated face and to a novel face. Only infants who took a nap between habituation and the test showed recognition memory, as evidenced by a visual preference for the novel face. Infants who stayed awake did not exhibit visual recognition. The study found no significant correlations between visual recognition memory and sleep spindles, length of sleep, and sleep stages in infants who slept (Horváth et al., 2018).

In a word learning study, 9- to 16-month-olds were exposed to picture-word pairs in which the shown objects could be encoded either as specific word meaning or as part of a category (i.e., general word meanings). During encoding, infants did not acquire the general word meanings, but they did acquire the specific word meanings, as indicated by event-related potentials (ERPs). Only infants who napped during the 1- to 2-hour delay remembered the specific word meanings, as assessed using ERPs (Friedrich et al., 2015). Infants who stayed awake did not retain the word meanings. In infants who slept, neither slow-wave activity nor any measures of spindle activity was significantly related to retention.

In an intermodal preferential-looking task, 16-month-olds' behavior also varied as a function of their sleeping behavior. Infants who slept in the 2-hour interval between encoding and the test increased preferential looking to a previously seen target stimulus, compared to a distractor, after hearing its label. The performance of infants who stayed awake remained unchanged (Horváth et al., 2015).

Finally, 6- and 12-month-olds exhibited retention in a deferred imitation task after a 4- or 24-hour delay if they took an extended nap ($\geq$ 30 minutes) within 4 hours after encoding, but not if they stayed awake (Seehagen et al., 2015). Retention was inferred if infants performed a significantly higher number of previously shown target actions at test than infants in an additional baseline control group who had not received demonstrations of the target actions. [AU: Please revise previous sentence to avoid repetition of "demonstrated/demonstrations."] Tested with the same task, 12-month-olds retained gist information about the deferred imitation stimuli over a 4-hour delay if they took a nap during the retention interval but not if they stayed awake (Konrad et al., 2016a).

In addition to strengthening memories, sleep also supports generalization, the ability to apply recently acquired memories to novel circumstances. Generalization reflects flexibility of memory retrieval, that is, the degree to which cues present at encoding must match those present at recall for retrieval to occur. Flexibility of memory retrieval is limited in young infants (see Hayne, 2004). For example, 2-month-olds who were trained to kick their legs to produce movement in an overhead mobile retained this memory for 24 hours if they were tested with the same mobile. However, if more than one item on the mobile was replaced with a new item at test, the infants' memory retrieval failed. This shows young infants' capability for detailed discrimination between the stored representation of the original mobile and the test mobile (Hayne, Greco, Griesler, & Rovee-Collier, 1986). Hence, early memories are characterized by a high degree of specificity. To our knowledge, there is no evidence that generalization in infants improves when the stored representation [of an experience weakens (Hayne, MacDonald, & Barr, 1997, but see Werchan & Gómez, 2014, for different findings on sleep-related language processing in 2½-year-olds).

In terms of sleep-dependent generalization, in a deferred imitation study, napping after learning enabled 12-month-olds to transfer previously acquired knowledge about actions demonstrated on a particular hand puppet to a novel hand puppet that was functionally identical but perceptually different. Only infants who napped during the 4-hour retention delay imitated the target actions with the novel puppet at test (Konrad, Seehagen, Schneider, & Herbert, 2016). Infants who stayed awake did not recall the target actions. In the context of language learning, napping after learning facilitates semantic generalization. In the aforementioned study (Friedrich et al., 2015), only 9- to 16-month-olds who napped between encoding and retrieval could apply newly learned words for objects to new, perceptually similar members of the same object category (Friedrich et al., 2015). For infants who slept, sleep spindle activity, but not slow-wave activity, was related significantly to this semantic generalization effect. Using a similar methodological approach, in another study (Friedrich, Wilhelm, Mölle, Born, & Friederici, 2017), 6- to 8-month-olds' generalization to novel category exemplars depended on their sleep status during the retention interval of about 1 hour. There was no evidence of generalization in infants who stayed awake. However, infants who napped briefly showed evidence of perceptual-associative memory (matching visual with auditory information). There was evidence for generalization, indicating genuine semantic long-term memory, in infants who slept longer. Sleep spindle activity was related to this shift from an immature to a more mature memory. Similarly, napping after encoding an object-label association improved 16-month-olds' ability to generalize the new label to an object of a different color (Horváth, Liu, & Plunkett, 2016).

Although the underlying memory processes are less clear, sleep also seems to support infants' sensitivity to certain features of a language they hear. Taking an extended nap ($\geq$30 minutes) within 4 hours of encoding shaped 15-month-olds' preference for word strings that had the same or different nonadjacent elements they had been familiarized with in a procedure involving head-turn preferences (Gómez, Bootzin, & Nadel, 2006; Hupbach, Gómez, Bootzin, & Nadel, 2009).

This growing body of research shows that, even in early life, sleep soon after encoding plays an important role in strengthening new memories and facilitating the reorganization and integration of newly formed memories, as reflected by generalization. However, the lack of significant relations between sleep spindles and slow-wave-sleep and retention leaves open the possibility that sleep supports infant memory through different mechanisms than it does in older people. Given the few datasets available that speak to these issues this is an important issue for ongoing research. Another possibility is that infants and older people may use different brain structures or networks to support declarative memory.. Initial evidence suggests that sleep spindles are implicated in generalization processes. A role of SWS has not yet been confirmed, but again, few studies with infants obtain these measures.

How Does Sleep Support Memory?

A major account for sleep-dependent memory consolidation in adults is the active system consolidation hypothesis. According to this view, sleep facilitates memory consolidation by helping transfer recently encoded information from a temporary buffer to a long-term store where it becomes embedded and connected to related existing knowledge networks (see Diekelmann & Born, 2010, for a review). Reactivation of new memories during SWS is a causal factor for sleep-dependent consolidation of declarative memory (Rasch, Büchel, Gais, & Born, 2007). Furthermore, sleep spindles are related to memory performance in adults and thought to be involved in the dialogue between the hippocampus (temporary store) and the neocortex (long-term store) during consolidation of declarative memory (Gais, Mölle, Helms, & Born, 2002; Schabus et al., 2004). Although less well explored, active system consolidation might also explain sleep-dependent consolidation in other nondeclarative memory systems (Diekelmann & Born, 2010).

Active system consolidation can help explain findings on retention and generalization in infants. Presumably by facilitating the transfer of memories from a temporary to a permanent store, sleep helps consolidation, as reflected by improved retention. The temporary store’s capacity might be limited in infants, necessitating more frequent periods of sleep (cf. Kurdziel, Duclos, & Spencer, 2013; Seehagen et al., 2015). By embedding a new memory into existing related knowledge networks, sleep helps make memories retrievable through a wider range of cues related to the original experience (cf. Konrad et al., 2016). Although this distinction is plausible, it is difficult to tease apart the effects of postlearning sleep on memory retrieval versus memory consolidation. For example, while generalization is indicated by an improved ability to use a wider range of cues at *retrieval*, the reason is thought to lie in processes that have taken place during consolidation when embedding new knowledge into existing networks.

Sleep-Dependent Memory in Infants: Looking Ahead

Current knowledge suggests that the timing of a particular learning experience within an infant’s naturally occurring sleep-wake cycle determines how much he or she will recall from it. However, a number of issues still require clarification.

First, we need systematic research on the role of *prior* sleep for memory encoding. Sleep deprivation impairs the encoding of new information in adults (Yoo, Hu, Gujar, Jolesz, & Walker, 2007). For ethical and practical reasons, infants cannot be deprived of sleep for research. However, scheduling a learning event shortly after infants wake from a nap versus shortly before they wake provides opportunities to explore potential fluctuations in encoding capacity during infants’ regular sleep-wake rhythm. In a study using this approach, albeit with small groups, 6- and 12-month-olds’ encoding of a deferred imitation task did not vary as a function of having taken an extended nap ($\geq$ 30min) or not having napped within the last 4 hours (Seehagen, Konrad et al., 2015) Correlational data suggest that quality of sleep prior to encoding may be an important consideration. In another study, this one of 6-month-olds (Konrad, Herbert, Schneider & Seehagen, 2016b), encoding in an imitation task correlated significantly with quality of sleep during the night before participation. Parents’ reports of infants’ habitual day and night sleep patterns in the week before the learning event also suggests relations to infants’ immediate imitation and generalization (Lukowski & Milojevich, 2013). Further research with a wider range of paradigms is needed to clarify the role of daytime and nighttime sleep directly prior to encoding, and of daytime and nighttime sleep that occurs habitually.

A second and related issue for research into sleep-dependent *consolidation* during infancy is the need to consider, and ideally control for, initial encoding levels before sleep. Encoding, subsequent sleep, and consolidation are intertwined tightly. In a study of 14- to 16-month-olds (Friedrich, Mölle, Friederici, & Born, 2018), hearing unknown labels for exemplars of unknown categories produced more sleep spindle activity during a subsequent nap than hearing known labels for exemplars of known categories. In turn, sleep spindle activity was related to memory performance assessed 24 hours later. By scheduling participation in a study around naturally occurring sleeping patterns, encoding in a sleep condition occurs after the infant has had an extended period of wakefulness. Encoding in a no-sleep condition typically occurs when the infant has recently woken from sleep. Therefore, systematic differences in alertness during encoding might induce variability in the data. If the paradigm permits, a within-subject design may help control for potential differences in encoding performance. Alternatively, researchers could use only data from subsamples of infants in each condition who showed comparable encoding performance, although substantial increases in sample size may be required. In imitation paradigms, where motor practice before the delay is typically prevented, this approach is not suitable. In these cases, additional encoding performance in age-matched infants could be assessed as a function of length of their prior wakefulness (Seehagen, Konrad et al., 2015).

A third direction for research is to distinguish the effects and relations between different types and units of sleep and infant memory. One approach is to begin including longer retention periods (at least 24 hours) between encoding and the test to help tease apart the contribution of sleep occurring soon after encoding and sleep that follows much later (e.g., nighttime sleep). The few infant studies that have used this design (Hupbach et al., 2009; Konrad et al., 2018; Seehagen, Konrad et al., 2015) suggest that later-occurring sleep does not make up for missing sleep soon after encoding. In addition, allowing all infants a recovery sleep can help rule out tiredness at test in the no-sleep condition as a potential explanation for observed differences between conditions..

While the importance of sleep for early memory in general has been established, more fine-grained analysis of both sleep and memory processes are needed. Using measures like polysomnography will help identify which sleep features and stages facilitate infant memory processing and how this might change with age. Polysomnography is a multi-channel assessment of physiological functions during sleep, such as brain activity, eye movements, muscle tone, and heart rate. As the range of experimental tasks used in infant memory studies increases, so too will the generalizability of the conclusions. Given that both declarative and nondeclarative memory are thought to consist of several subsystems, some, but not all, types of memory may turn out to be sleep dependent in infants, depending on the underlying neural structures.

Beyond Sleep: Internal State and Infant Memory

As a final thought, we acknowledge that sleep is just one internal state, or context, variable that may affect infants' memory processing. In adults, stress levels, mood, and degree of satiation are also important influences on memory encoding and further processing (e.g., Bower, 1981; Critchley & Harrison, 2013; Schwabe & Wolf, 2013). The extent to which such states might influence infant memory is largely unexplored, although in one study, acute stress fostered infants' use of a habitual, rigid memory system at the cost of a cognitive, flexible memory system (Seehagen, Schneider, Rudolph, Ernst, & Zmyj, 2015). Studying the impact of stress and other internal states on infant memory has unique ethical and methodological challenges (e.g., around experimental manipulation and assessment of stress levels or mood), and will require creative and careful research designs. Nevertheless, in our view, considering the impact of internal states is necessary for developing a fuller understanding of early human memory.

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